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Resource availability and the trichome defenses of tomato plants

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Abstract We conducted two experiments to determine how resource availability influenced allocation by tomato (*Lycopersicon esculentum*) to trichomes, and how different patterns of trichome allocation by plants grown in different resource environments might then influence the behavior of tobacco hornworm (*Manduca sexta*) caterpillars. In the first experiment we used high and low levels of light and water, and then, using scanning electron microscopy, determined trichome densities on the leaves and stems. We sampled leaves and stems at several places throughout the plant to determine whether there were within-plant differences in allocation to trichomes. The results of the first experiment showed that resource availability influenced allocation to trichome growth. Patterns in high and low-light supported both the growth-differentiation balance hypothesis (GDBH) and the carbon-nutrient balance hypothesis (CNBH). However, the GDBH was not supported by differences among water treatments. Contrary, to predictions of the GDBH, plants with intermediate growth did not have the highest trichome densities, and plants with similar growth differed in trichome density. Possible biological and artifactual explanations are discussed. The first experiment also showed that there was within-plant variation in allocation to trichomes, and that plant resource availability may influence within-plant variation in allocation to trichomes. In the second experiment, we grew plants in high and low-light, and then monitored the behavior of tobacco hornworms on the stems of these plants in the laboratory. This experiment demonstrated that the light environment that tomato plants were grown in influenced the resting behavior of caterpillars. Furthermore, it demonstrated that both glandular and non-glandular trichomes impeded caterpillars from searching for food. Overall, this study indicated that plant resource availability can influence allocation to trichome defenses, and that these differences may affect insect herbivores.

Key words Trichome · Growth-differentiation balance · Carbon-nutrient balance · *Lycopersicon esculentum* · *Manduca sexta*

Introduction

Plant trichomes can significantly influence the resistance of plants to invertebrate herbivores (Johnson 1975; Levin 1973). Tomato plants (*Lycopersicon* sp.: Solanaceae) are well endowed with an array of glandular and non-glandular trichomes on their stems and leaves (Luckwill 1943), which may negatively affect invertebrate herbivores (Duffey and Isman 1981; Farrar and Kennedy 1987; Good and Snyder 1988; Kennedy and Sorenson 1985; Lin et al. 1987; Weston et al. 1989). Because of the resistance conferred by trichomes, many studies have examined the distribution and density of trichomes in different species and cultivars with the purpose of breeding trichome-based resistance (Carter and Snyder 1986; Channarayappa et al. 1992; Good and Snyder 1988; Lin et al. 1987; Weston et al. 1989). However, few studies have examined how resource availability influences the phenotypic expression of trichome density in plants (Kennedy et al. 1981; Wellso and Hoxie 1982; Cano-Santana and Oyama 1992).

Plants are often subjected to a range of resource availability (Tilman 1988). Differences in resource availability generate plant-to-plant variation in the defensive chemistry of many plants (Bryant et al. 1987; Larsson et al. 1986; Shure and Wilson 1993; Waterman et al. 1984). Some studies have examined how environmental factors, such as moisture (Cano-Santana and Oyama 1992; Wellso and Hoxie 1982), photoperiod (Gianfagna et al. 1992; Good and Snyder 1988; Kennedy et al. 1981; Lin

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et al. 1987; Weston et al. 1989), temperature (Gianfagna et al. 1992), and light (Kennedy et al. 1981) affected trichome density. However, most of these studies examined only one leaf per experimental plant or did not report differences in trichome density between leaf ages (Cano-Santana and Oyama 1992; Gianfagna et al. 1992; Good and Snyder 1988; Kennedy et al. 1981; Weston et al. 1989). Only one of these studies considering environmental factors, examined trichome density in more than one plant part (e.g., stems and leaves) and more than one leaf age (Lin et al. 1987). Because trichome densities in plants may vary between leaf ages (Johnson 1975) and between plant parts (Lin et al. 1987; Oghiakhe et al. 1992), it is important to consider how resources influence trichome density in leaves and stems of different ages. In this paper, we examine how two levels of light and two levels of water availability influenced the type and density of trichomes on different aged leaves and stems of tomato (*Lycopersicon esculentum*).

Several authors have suggested that the growth-differentiation balance hypothesis (Herms and Mattson 1992; Loomis 1932, 1953; Lorio 1986) and the related carbon-nutrient balance hypothesis (Bryant et al. 1983) might predict patterns of trichome allocation in plants growing in different resource conditions (Ayres 1993; Herms and Mattson 1992; Myers and Bazely 1991). While the carbon-nutrient balance hypothesis (CNBH) and the growth-differentiation balance hyptothesis (GDBH) make generally similar predictions, there are important differences. The CNBH makes predictions based on the availability of mineral nutrients relative to the availability of carbon (light). However, the CNBH does not give a clear framework for predicting patterns of carbon partitioning in plants experiencing a gradient in non-mineral resources such as water (Herms and Mattson 1992). Therefore, we will use the CNBH to assess plant allocation to defenses only in low-light versus high-light treatments. The CNBH predicts that high-light plants should have more carbon production relative to nutrient availability than low-light plants, and thus high-light plants should have higher levels of carbon-based defenses such as trichomes.

The GDBH provides a framework to predict how a plant will balance allocation between differentiation related processes and growth related processes in different environments, including non-mineral resources such as water and different thermal regimes (Herms and Mattson 1992). Growth related processes include the production of leaves, stems, and roots or any other structure that requires a lot of cell division. Differentiation related processes include the production of characters that require enhancements of the structure or function of already existing cells. Tomato trichomes are simple extensions of a single epidermal cell or several celled extensions of the epidermis (Rodriguez et al. 1984) and thus they are a trait related to differentiation. Trichomes may play a role in plant defense (Gentile et al. 1968; Levin 1973) and in reducing plant stress through moderating light absorption (Ehleringer and Mooney 1978; Johnson 1975) and evapotranspiration of plants (Johnson 1975; Woodman and Fernandes 1991).

The GDBH makes the following predictions:

1. Plants experiencing low levels of resources should be limited in both growth and photosynthetic capability, and therefore exhibit both low biomass gain and low levels of differentiation.
2. Plants experiencing intermediate resource availability will have high levels of differentiation, but an intermediate level of biomass accumulation, relative to plants experiencing higher or lower levels of resources. The GDBH predicts this pattern at intermediate levels of resource availability because growth (through cell division) is inhibited by relatively small shortages of resources, whereas net photosynthesis, and thus cellular differentiation, is less sensitive to the same level of resource limitation (Chapin 1980; Dietz 1989; Körner 1991; Luxmoore 1991). Therefore, trichome growth, a product of cellular differentiation, should be more prevalent in plants photosynthesizing at high levels but also experiencing growth inhibition due to moderate resource shortages.
3. Finally, plants experiencing high resource availability will not be as limited in photosynthesis or growth and, therefore, will allocate a greater portion of the available photosynthate to growth at the expense of allocation to differentiation related traits (Herms and Mattson 1992).

Glandular trichomes may affect the behavior of insects by altering their searching behavior (Goffreda et al. 1988), restricting their movement (Belcher and Thurston 1982; Dimock and Tingey 1987; Tingey and Gibson 1978; Tingey and Laubengayer 1981), and entrapping them (Gentile et al. 1968). However, it is not known whether trichome defenses on plants grown in different resource conditions will differentially influence the behavior of caterpillars. In this paper we present the results of an experiment comparing the behavior of tobacco hornworms (*Manduca sexta*) on tomato stems grown in high-light to that of caterpillars on stems grown previously in low-light. How stem trichomes influence behavior is particularly important for caterpillars foraging on tomato plants, because they have to travel from one leaf to another via the stem. To determine the effect of various trichome types on the behavior of the caterpillars, we manipulate the stems, removing glandular exudate or all trichome types compared to control stems.

Materials and methods

Plant response

Cherry tomato seeds (tomato line: LA1238 from University of California-Davis) were sown in flats containing a 1:1 mix of peat and vermiculite. After germination, seedlings were transferred to 15-cm-diameter pots, and randomly assigned to position on a greenhouse bench. Plants were re-randomized to position 2 weeks after the experimental treatments were first assigned. Plants were given two drops of Schultz-Instant liquid plant food once per week.

To obtain low and high water treatments, the moisture content of the soil was checked daily. Whenever the low-water plants had dry soil, as determined by a soil moisture gauge, they were given an additional 100 ml, and the high water treatment 300 ml. We never allowed the low water plants to reach wilting point. Shade cloth rated at 73% was used for the low-light treatment. High-light plants were grown with ambient light. Two sets of plants were randomly assigned to each of the four treatment combinations: low-light-low water, low-light-high water, high-light-low water, and high-light-high water.

One set of five plants per treatment was used to obtain leaf and stem sections for trichome analysis. Four weeks after starting the treatment conditions, two new, intermediate, and mature leaves were sampled from each plant. New leaves were defined as unexpanded leaves, intermediate leaves as the second and third fully expanded leaves from the apex of the plant, and mature leaves as the second and third non-senescent leaves from the base of the plant. Using a No. 1 cork borer (3.2 mm diameter), four leaf discs were collected from the terminal leaflet of each leaf sampled. Care was taken to avoid veins when possible; however, this was often difficult to accomplish with new leaves. The four discs were immediately placed in vials containing a fixative (3% glutaraldehyde in Sorensen's phosphate buffer 0.1 M, pH 7.0) (McLean and Cook 1952). Two stem sections were taken from the internode of the two intermediate leaves sampled (intermediate-aged stem) and from the internode of the two mature leaves sampled (mature-aged stem). A razor blade was used to cut 3–6 mm stem sections. The stem was then cut into two longitudinal sections and placed in the fixative. After refrigeration, the fixative was removed from each vial and replaced with 1% OsO_4 for 30 min. as a post-fixative for lipid stabilization (Hyat 1981). The sections were given three washings with deionized water. Then the sections were dehydrated with a graded ethanol series, followed by three changes of 100% ethanol. The dehydrated samples were refrigerated in capped vials until ready for ethanol removal. To remove the ethanol from the sections, we used critical point drying (Samdri-790). After drying, the sections were affixed to stubs and labeled by treatment. The stubs were then sputter coated with gold and stored in a desiccating chamber until ready for scanning electron microscopy.

One micrograph (50×) of each leaf disc was made with an Etec Autoscan scanning electron microscope operating at 20 kV. With four disc micrographs, 6.28 mm^2 were sampled per leaf. For each stem, 9.84 mm^2 were sampled per stem age. Trichome densities are reported as number of trichomes per square millimeter. The mean trichome density of a "leaf replicate" four leaf discs from each of two common-aged leaves (= 8 discs), whereas the mean trichome density of a "stem replicate" was derived from two micrographs at 40× (to encompass all of the stem section) from each of two common-aged stem sections. Some samples were destroyed due to faulty vial caps allowing samples to dry. However, there was no treatment combination (water×light×age) that had less than three replicates.

Using the negatives of the micrographs, we counted the six trichome types found on *Lycopersicon* sp. (Fig. 1). For this study, type IV glands will be referred to as small-glandular trichomes, type V will be referred to as point trichomes, and type VI will be referred to as large-glandular trichomes. Counting of trichomes was conducted on coded negatives and thus without knowledge of the water and light treatments. When a trichome was not recognizable as one of the six types shown in Fig. 1, the trichome was marked as "unknown". Unknown trichomes were included in the total trichome density.

For leaves and stems, trichome density data were analyzed with ANOVA, with light, water, and age as the independent variables. Multiple comparisons were made with Tukey tests. For leaves, trichome data were square root transformed to meet the assumptions of analysis of variance.

To assess the GDBH, it is necessary to examine the effects of resource availability on biomass accumulation relative to differentiation patterns. In this study we used biomass accumulation as an indication of plant allocation to growth related traits and total trichome density as an indication of differentiation related traits. Thus, the second set of plants (22 per treatment combination) was grown to assay the effect of light and water on plant mass. These plants were harvested four weeks after starting the treatment conditions. Roots and shoots were dried at 60°C to constant weight and weighed. We used ANOVA to analyze the plant mass data, with light and water as the independent variables. Plant mass data were square-root transformed to meet the assumptions of ANOVA.

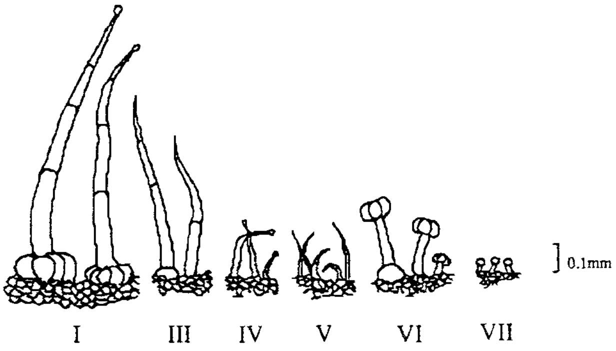

Fig. 1 The six types of trichomes observed on the leaves and stems of *Lycopersicon esculentum*. The figure is based on Luckwill (1943)

Herbivore response

First and third instar *M. sexta* caterpillars were used as the experimental herbivores. These caterpillars are specialists on Solanaceae with a preference for tomato (Yamamoto and Fraenkel 1960). Eggs were obtained from Carolina Biological Supply Company (Burlington, N.C.). Newly hatched caterpillars were placed on artificial diet (BioServ: F9783, Frenchtown, N.J.) in cups and put into a growth chamber at 26:16°C with a 16L:8D photoperiod. Caterpillars were removed from the diet 2 h. prior to testing.

Cherry tomato seeds (tomato line: LA1238 from University of California-Davis) were sown in 8-cm-diameter pots containing a 1:1 mix of peat and vermiculite. After the first few leaves expanded, 60 plants were transferred to 15-cm-diameter pots. To obtain high- and low-light growing conditions for experimental plants in the greenhouse, 30 plants were grown with ambient light and 30 plants were grown under shade cloth rated at 73% blockage. Plants were watered as needed and fertilized with two drops of Schultz-Instant liquid plant food weekly. At 10 weeks, the stems from high-light plants, which were about 4 times larger than low-light plants, were used for the behavioral tests. The stems from low-light plants were used 2 weeks later so that the internode lengths were similar to those of high-light plants.

Before the experimental trials began, the stems of the plants were pruned of leaves and the remaining stems placed in aquapics. Three levels of trichomes were used: (1) no trichomes removed (control), (2) glandular exudate of trichomes removed, and (3) all trichomes removed. To serve as a control, no trichomes were removed from one set of stems. To remove only the glandular exudate of the trichomes, the stems were lightly touched with a small paint brush that had been dipped in ethanol and then they were rinsed off with distilled water (Kennedy and Sorenson 1985). To remove all trichomes, the stems were rubbed with a gauze pad that had been soaked in ethanol and rinsed off with distilled water (modified from Kennedy and Sorenson 1985). The stems were examined with a dissecting microscope to ensure that the manipulations were effectively executed. The stem sections were allowed to dry completely with the aid of a fan. A 12-cm intermediate section of the stem was placed under a dissecting scope adjacent to a ruler, which facilitated measurement of caterpillar movement during the trials.

For a trial, a caterpillar was placed on the left end of a stem with the head facing the other end. Upon placement, the trial last-

Table 1 Means (±SE) for the density (no./mm^2) of leaf and stem trichomes are given for the different types of trichomes in each light and water combination. A *t*-test was used to compare the mean density of type V (point) and type VI (large-glandular) trichomes in each light water treatment combination. The *t*-tests were only used to compare type V and type VI. For total trichome density within a plant part (leaves or stems), means with different letters were significantly different (Tukey tests)

		Type I	Type III	Type IV	Type VII	Type V	Type VI	Total
Leaves								
Low light	Low H_2O	0.5 (0.1)	1.2 (0.3)	0.43 (0.17)	3.9 (0.7)	43.5 (9.7)**	12.2 (2.1)	65.4 (12.9) b
	High H_2O	0.3 (0.1)	1.0 (0.3)	0.17 (0.08)	2.8 (0.5)	26.9 (6.2)*	10.4 (1.9)	45.2 (8.7) c
High light	Low H_2O	0.6 (0.1)	0.4 (0.1)	0.04 (0.02)	2.4 (0.4)	60.4 (10.3)**	16.0 (2.1)	83.7 (11.4) ab
	High H_2O	0.8 (0.2)	0.6 (0.2)	0.07 (0.05)	2.4 (0.3)	90.9 (13.6)**	25.7 (3.0)	125.4 (16.8) a
Stems								
Low light	Low H_2O	0.3 (0.1)	1.0 (0.4)	3.7 (1.1)	2.3 (0.3)	23.8 (5.8) ns	30.3 (3.5)	69.2 (7.2) ab
	High H_2O	0.3 (0.1)	1.6 (0.6)	1.5 (0.5)	2.7 (0.5)	22.9 (3.2) ns	27.0 (2.2)	63.3 (5.5) b
High light	Low H_2O	0.6 (0.1)	0.9 (0.4)	3.3 (1.0)	2.7 (0.5)	30.4 (8.2) ns	46.3 (3.1)	92.7 (7.2) a
	High H_2O	0.7 (0.2)	1.2 (0.9)	3.0 (0.9)	2.5 (0.6)	29.8 (9.2) ns	35.4 (4.3)	83.9 (9.8) ab

* P<0.002, ** P<0.0002, ns P<0.05

ed 15 min or until the 12-cm stem section was traversed. During the trial, the time and location of changes in behavior were noted. From these, movement rate (cm/min) and the percentage of time that the caterpillars exhibited each of four behaviors was determined. The four distinct behaviors were: (1) cleaning mouthparts, (2) mowing, (3) probing, and (4) resting. Cleaning mouthparts involved raising the head and repeatedly opening and closing mouthparts and also rubbing of the mouth parts with the thoracic legs. This behavior involved no change in location on the stem. Mowing consisted of removing and eating trichomes with the effect of clearing the caterpillar's path. This behavior often resulted in a change of location on the stem. Probing involved movement of the head from side to side. This behavior often resulted in a change of location on the stem. Resting consisted of no movement, and with no other behavior observed.

There were five replicates (= caterpillars) for each stem treatment-plant light level-instar combination. Kruskal-Wallis one-way ANOVA was used to analyze how stem treatments influenced the four behaviors and the movement rate. When the Kruskal-Wallis test was significant, a non-parametric multiple comparison test was employed (Zar 1984). To determine whether the light condition that the plant was grown in influenced the behaviors and movement rate of the caterpillars and to determine whether the two instars behaved differently or had different movement rates, Mann-Whitney *U*-tests were employed.

Table 2 Effect of light, water and leaf age on the density (no./mm^2) of large-glandular, point, and total trichomes on leaves. Results of ANOVA are shown

Source	*df*	MS	*F*
Point trichomes			
Light	1	121.75	34.56****
Water	1	1.87	0.53
Leaf age	2	235.41	66.83****
Light×water	1	36.76	10.44***
Light×leaf age	2	12.84	3.64*
Water×leaf age	2	1.50	0.66
Light×water×leaf age	2	2.76	0.46
Error	72	3.52	
Large-glandular trichomes			
Light	1	20.12	22.64****
Water	1	0.62	0.70
Leaf age	2	22.94	25.81****
Light×water	1	8.56	9.64***
Light×leaf age	2	5.15	5.80***
Water×leaf age	2	1.80	2.03
Light×water×leaf age	2	1.52	1.72
Error	72	0.89	
Total trichomes			
Light	1	116.89	36.33****
Water	1	0.96	0.30
Leaf age	2	266.41	82.80****
Light×water	1	43.27	13.45***
Light×leaf age	2	18.78	5.84***
Water×leaf age	2	2.68	0.83
Light×water×leaf age	2	4.06	1.26
Error	72	3.22	

* P<0.05, *** P<0.005, **** P<0.0001

Results

Plant response

Point (type V) and large-glandular (type VI) trichomes made up a large majority of the total trichome density in both leaves and stems (Table 1). On the leaves, point trichomes had a higher density than large-glandular trichomes, whereas in the stems, point and large-glandular trichomes were similar in density (Table 1). The low densities of the other trichome types on the leaves makes it unlikely that they would affect insect behavior as much as the point and large-glandular trichomes. For this reason, our leaf analysis focuses on the densities of point and large-glandular leaf trichomes.

Although considerably lower than densities of point or large-glandular trichomes on the stems, small-glandular trichomes (IV) attained a density on the stems that was comparable to the small-glandular densities on the leaves of resistant hybrid tomato plants (>5.6/mm^2, Carter and Snyder 1986) Therefore, for the stem, we concentrated on point, large-glandular, and small-glandular trichomes. Small-glandular trichomes have heretofore been undocumented on *L. esculentum* (Luckwill 1943; Snyder and Carter 1985). There are at least two explanations for

Table 3 Effect of light, water and stem age on the density (no./mm^2) of point, large-glandular, small-glandular, and total trichomes on stems. Results of ANOVA are shown

Source	*df*	MS	*F*
Point trichomes			
Light	1	343.06	1.74
Water	1	4.03	0.02
Stem age	2	3127.94	15.85****
Light×water	1	0.26	0.001
Light×stem age	1	926.36	4.70*
Water×stem age	1	406.31	2.06
Light×water×stem age	1	29.25	0.15
Error	23	197.30	
Large-glandular trichomes			
Light	1	1098.82	18.18****
Water	1	365.30	6.05
Stem age	1	670.18	11.09***
Light×water	1	114.64	1.90
Light×stem age	1	109.59	1.81
Water×stem age	1	2.88	0.05
Light×water×stem age	1	0.0005	<0.00001
Error	23	60.43	
Small-glandular trichomes			
Light	1	2.00	80.48
Water	1	10.31	2.47
Stem age	1	59.55	14.26****
Light×water	1	6.87	1.65
Light×stem age	1	9.81	2.35
Water×stem age	1	2.56	0.61
Light×water×stem age	1	0.05	0.01
Error	23	4.18	
Total trichomes			
Light	1	3591.91	8.79**
Water	1	380.73	0.93
Stem age	1	610.43	1.49
Light×water	1	21.20	0.05
Light×stem age	1	429.19	1.05
Water×stem age	1	300.57	0.73
Light×water×stem age	1	107.96	0.26
Error	23	408.58	

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, **** $P<0.0001$

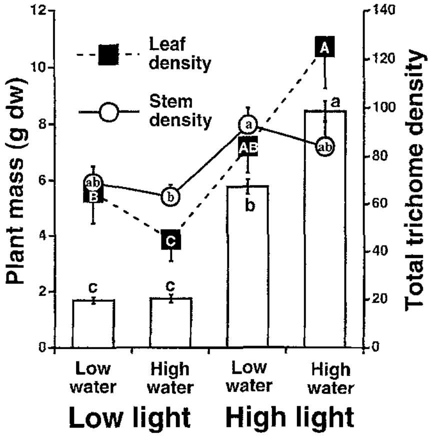

Fig. 2 The effect of light and water on plant mass (g dry weight) and on total stem and leaf trichome density (number/mm^2). *Bars* represent plant mass, and *connected squares* and *circles* represent total trichome density. Means ± SE are shown. Means that have no *letters* in common are significantly different (Turkey tests)

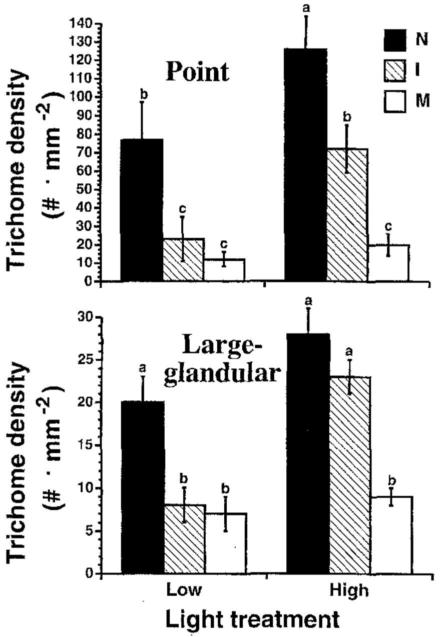

Fig. 3 The effect of light and leaf age on the density (number/mm^2) of large-glandular (type VI) and point (type V) trichomes. Means ± SE are shown (*N* new, *I* intermediate aged, *M* mature). Means with different *letters* were significantly different from each other

the presence of small-glandular trichomes on our tomato plants. Because stems are not often examined, this trichome type may have been overlooked. It is also possible that this cultivar has characteristics unlike more modern cultivars of *L. esculentum.*

Light affected the densities of point, large-glandular, and total trichomes on the leaves (Table 2). However, for each of these there was an interactive effect of light with water (Table 2). At low-light, plants grown with low water generally had higher point and large-glandular trichome densities than those with high water, whereas at high-light, plants grown with low water generally had lower trichome densities than those with high water (Table 1).

Total trichome density on the stems was affected only by light, with high-light plants having generally higher densities of trichomes (Table 3; Fig. 2). Neither light nor water influenced the densities of point and small-glandular trichomes on the stems (Table 3). However, both light and water affected the density of large-glandular trichomes on the stems (Table 3). Low-light plants had lower densities of large-glandular trichomes on the stems than high-light plants (low-light: 28.6 per mm^2 ± 2.0 SE; high-light: 41.6 per mm^2 ± 2.9 SE). Low water plants had higher densities of large-glandular trichomes on the stems than high water plants (low water: 38.3 per mm^2 ± 3.1 SE; high water: 30.6 per mm^2 ± 2.4 SE).

There was an interactive effect between light and leaf age for the densities of both point and large-glandular trichomes (Table 2). At low-light, the densities of point trichomes were similar for the intermediate-aged and mature leaves and less than that of new leaves, whereas at high-light, density of point trichomes became progressively less from new to intermediate-aged to mature leaves (Fig. 3). For large-glandular trichomes on low-light plants, densities on intermediate-aged and mature leaves showed a similar reduction in large-glandular trichome density relative to the new leaves (Fig. 3). For large-glandular trichomes on high-light plants, new and intermediate-aged leaves did not differ from each other; however, both were higher than that of the mature leaves (Fig. 3). Mature stems had higher densities of small-glandular trichomes than intermediate-aged stems (mature: 2.6 per mm^2 ± 0.3 SE; intermediate: 2.1 per mm^2 ± 0.3 SE; Table 3). Mature stems also had a higher density of large-glandular trichomes than intermediate-aged stems (mature: 39.4 per mm^2 ± 3.0 SE; intermediate: 29.8 per mm^2 ± 2.4 SE; Table 3). The opposite was true for point trichome density: mature stems had lower point trichome densities than intermediate-aged stems (mature: 16.5 per mm^2 ± 2.4 SE, intermediate: 35.7 per mm^2 ± 4.7 SE; Table 3). Consequently, basal (mature) areas of the stem had a higher ratio of large-glandular trichomes to point trichomes than the mid section of the stem (mature section: 2.4; intermediate-aged section: 0.8).

Plants grown in high-light conditions were larger than plants grown in low-light conditions (Table 4; Fig. 2). Only plants grown in high-light showed a positive response to increased water availability, which explains the significant interactive effect (Table 4; Fig. 2).

Table 4 The effect of light and water on plant mass (g dry weight). The results of ANOVA are shown

Source	*df*	MS	*F*
Light	1	24.62	585.11*****
Water	1	0.61	14.48***
Light×water	1	0.52	12.31***
Error	79	0.04	

*** $P<0.001$, ***** $P<0.00001$

Herbivore response

Caterpillars placed on stems from high-light plants rested a higher percentage of time than those on stems from low-light plants (Table 5). But caterpillar movement rate and the percentage of time caterpillars spent mowing, cleaning mouthparts, and probing were not affected by the light treatment experienced by the plants (Table 5). First and third instars showed no differences in the percentage of time they spent exhibiting the four behaviors (Table 5). However, third instar caterpillars had a higher movement rate than first instar caterpillars (Table 5).

The trichome treatments on the stems affected the percentage of time that the caterpillars spent cleaning mouthparts (Kruskal-Wallis test, $H = 16.84$, $P < 0.0003$), mowing ($H = 6.57$, $P < 0.05$), and probing ($H = 13.12$, $P < 0.002$) (Fig. 4). Caterpillars showed an eightfold increase in the percentage of time spent cleaning mouth parts between the exudate removed and the control stems; when all trichomes were removed the caterpillars spent an intermediate percentage of their time cleaning mouth parts (Fig. 4). The caterpillars spent the greatest percentage of their time mowing trichomes when no trichomes had been removed and the lowest percentage of time mowing when all trichomes were removed (in this case, the caterpillars bit the denuded stem using a mowing-like motion). When only exudate was removed, they spent an intermediate percentage of time mowing (Fig. 3). The caterpillars spent the highest percentage of time probing when they were on stems with all trichomes removed and the lowest percentage of time probing when no trichomes were removed; when only glandular exudate was removed, they spent an intermediate amount of time probing (Fig. 4). The trichome treatments did not affect the percentage of time spent resting ($H = 5.24$, $P > 0.08$). Although not statistically significant, the general pattern exhibited for the percentage of

Table 5 The effect of light and instar on the percentage of time spent exhibiting four behaviors and on movement rate of the caterpillars. Means (±SE) are given along with the results of Mann-Whitney *U*-tests

Behavior	Low light		High light		Mann-Whitney *U*-test
Cleaning mouthparts (%)	4	(1)	2	(1)	$P=0.68$
Mowing (%)	44	(10)	34	(10)	$P=0.18$
Resting (%)	10	(4)	21	(5)	$P=0.001$*
Probing (%)	29	(10)	40	(10)	$P=0.12$
Movement rate (cm/min)	0.61	(0.13)	0.37	(0.06)	$P=0.32$

Behavior	Instar I		Instar II		Mann-Whitney *U*-test
Cleaning mouthparts (%)	4	(1)	3	(1)	$P=0.74$
Mowing (%)	36	(5)	42	(6)	$P=0.39$
Resting (%)	19	(5)	13	(3)	$P=0.40$
Probing (%)	30	(5)	39	(7)	$P=0.64$
Movement rate (cm/min)	0.32	(0.06)	0.67	(0.12)	$P=0.002$*

* $P\leq 0.002$

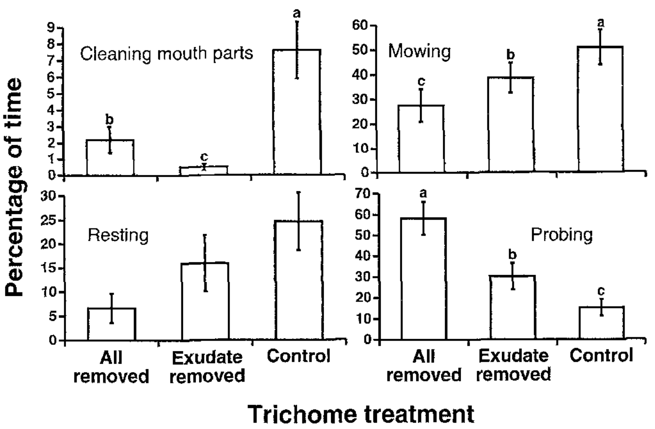

Fig. 4 The percentage of time that different behaviors of the caterpillars were observed in the trichome treatments (*all removed* all trichomes removed, *exudate removed* glandular exudate of trichomes removed, *control* no manipulation of trichomes). *Columns* with different *letters* were significantly different from each other. Means ± SE are shown

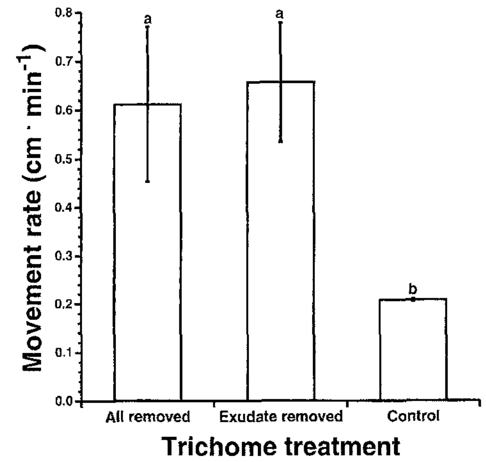

Fig. 5 The average rate of movement of the caterpillars on stem. *Bars* with different *letters* were significantly different from each other. Means ± SE are shown

time resting by the caterpillars over the stem treatments was similar to the pattern for mowing (Fig. 4). The trichome treatments affected the movement rate of the caterpillars (H = 11.74; $P < 0.003$). When all trichomes were present, caterpillars had a threefold decrease in their movement rates relative to caterpillars moving on stems with all trichomes removed or just glandular exudate removed (Fig. 5).

Discussion

Between-plant variation in trichome density

For the predictions of the GDBH to be supported in this experiment, plants receiving intermediate resources, such as high-light-low water plants, should have exhibited less growth relative to plants with high resource availability, such as high-light-high water plants. In contrast, high-light-low water plants should have exhibited higher allocation to differentiation related traits, such as trichomes, than high-light -high water plants (Herms and Mattson 1992). A greater allocation to trichomes by high-light-low water plants, relative to high-light-high water plants, was not observed on either the leaves or stems. In particular, high-light-low water plants had total trichome densities that were generally similar to those of the high-light-high water plants, and not the highest densities as predicted by the GDBH (Fig. 2; Table 1).

How can we explain this discrepancy? In its purest form, the GDBH argues that at some point along a resource gradient, growth processes will be such a dominant sink for fixed carbon, that the production of differentiation related products will decrease and eventually cease. However, it is very difficult to determine where on the resource gradient our treatments fell. While we label it the "high-water" treatment, perhaps a more appropriate label would be the "higher-water" treatment. Such a label would more properly indicate that the treatment level is labeled relative to another treatment and not as a description of the plant's resource status. It is possible that if we had a third water treatment, "very high water", that growth would have again increased by a large amount and defenses would have then shown a decrease as predicted by the GDB.

Is there any reason to suspect that we did not attain a very high level of water availability in the-high water treatment? Because we never allowed the low-water plants to reach wilting point, our low water level likely represented intermediate water stress. Therefore, we expected relatively high trichome defense for the high-light-low water plants. But the "high-water" level may have been suboptimal too. To avoid high-light-low water plants from reaching wilting point, we administered water whenever the soil of high-light-low water plants became dry, at which time we added 3 times as much water to high-light-high water plants. However, it is certain that high-light-high water plants still experienced significant drying between waterings, because this experiment was conducted in July and August when temperatures were warm and evaporation of moisture from 15-cm pots was rapid. Thus, it is unlikely that the soil of the high-light-high water plants was continuously saturated with water, which was evidenced by no more than a few milliliters of water draining from the pots at watering. Therefore, even the so-called high-water level was suboptimal with regard to water level. Thus, the peak of differentiation related products, as predicted by the GDBH, may not be coincident with our low-water treatment but some other untested water level. This problem indicates to us that future experiments concerning the phenotypic response of plants to resource availability and the GDBH should attempt to use at least three and probably six to ten levels of resources. Then, it might be possible to observe curvilinear subtleties in phenotypic response across a gradient.

The GDBH predicts that plants that are alike in allocation to growth related processes, should also be alike in production of differentiation related traits (Herms and Mattson 1992). The GDBH makes this prediction because plants allocating similar amounts of photosynthate to growth should have similar pools of remaining photosynthate for allocation to differentiation related products, such as trichomes. At low-light in this study, water did not influence plant mass (Fig. 2), so according to the GDBH, these plants should have also been similar in trichomes densities. However, there was a significant difference between low-light-low water plants and low-light-high water plants in total trichome density on the leaves. Therefore, this study suggests that the GDBH does not predict the patterns of leaf trichome allocation by tomato plants in response to different water environments.

However, the GDBH was more effective in explaining the patterns of allocation to trichomes in different light conditions. The GDBH predicts that plants severely limited in resources should exhibit low growth and low differentiation. Low-light plants, whether experiencing the low water or high water treatment, were likely severely depressed in their rates of photosynthesis and growth relative to high-light plants due to a 73% reduction in light availability. Indeed, low-light plants generally exhibited reduced total trichome densities, and also reduced plant mass relative to high-light plants (Fig. 2). At high levels of mineral or water resources, the GDBH does predict that carbon-based defenses, such as trichomes, should decrease. However, high levels of water availability were likely not attained in either high or low-light, and thus we observe a general increase in trichome defenses associated with the larger carbon budget of high-light plants. Higher trichome densities in high-light plants is also consistent with the predictions of the CNBH, which predicts that high-light plants should have a higher carbon/nutrient ratio, and thus, a higher proportion of carbon allocated to secondary defenses. Reduced glandular trichome density in low-light conditions was also observed for *L. hirsutum* (Kennedy et al. 1981).

Some studies suggest a negative correlation between different types of plant defenses (Berenbaum et al. 1986; Björkman and Andersson 1990; Simms and Rausher 1987). In addition to the various types of trichomes seen in tomato plants, there are also a number of secondary metabolites including the soluble phenolics rutin and chlorogenic acid (Elliger et al. 1981). Rutin and chlorogenic acid are present in concentrations of 0.5–6% dry weight in tomato leaves (Wilkens et al. 1995; R.T. Wilkens and N.E. Stamp, unpublished work). They reduce growth and prolong development of insect herbivores (Elliger et al. 1981; Isman and Duffey 1982). Thus, these phenolics are a potentially significant source of plant resistance to herbivores. In previous experiments, low-light plants had significantly lower concentrations of phenolics than high-light plants (Wilkens et al. 1995; R.T. Wilkens and N.E. Stamp, unpublished work), and in this study, low-light plants had lower densities of total trichome growth (Fig. 3). Therefore, there appears to be a positive correlation between these two differentiation related traits, which suggests that there is not a tradeoff between allocation to trichomes and allocation to the phenolics.

Within-plant variation in trichome density

Trichome density decreased as leaves expanded (Fig. 3). This pattern has been reported before (Johnson 1975; Lin et al. 1987; Wellso and Hoxie 1982). But we found that light availability influenced whether this pattern occurred between new and intermediate-aged leaves, or instead between new and mature leaves and between intermediate and mature leaves. This finding demonstrates one way that resource availability may influence the within-plant variation in trichome density.

If we assume that trichomes in tomato serve primarily as a defense against insect herbivores, the general patterns of within-plant variation are consistent with one of the key tenets of the optimal-defense hypothesis of plants, which is that not all parts should be equally defended (McKey 1979; Rhoades 1979). According to the hypothesis, new leaves are more valuable than older leaves and should therefore be more heavily defended (Rhoades 1979). In this experiment, new leaves generally had the highest trichome densities (Fig. 3).

The patterns of trichome density on the stems were also supportive of the assertion of the optimal-defense hypothesis that more valuable plant parts will be more highly defended (McKey 1979; Rhoades 1979). The main stem of a plant provides the only connection of a plant to water and mineral nutrients. If a stem were partially severed near the base of the plant, that could cut off much of the shoot from soil-borne resources. Therefore, the closer to the base of the plant that stem injury occurs, the more serious the injury (Zangerl and Bazzaz 1992). The optimal-defense hyptothesis, therefore, would predict that basal sections of the stem should be better defended than sections higher on the stem. Although there were no differences between total trichome densities of mature and intermediate-aged stems, we found that basal sections had higher densities of large- and small-glandular trichomes than intermediate-aged sections of the stems. These glandular trichome types do confer resistance against invertebrate herbivores of tomato (Carter and Snyder 1986; Kennedy and Sorenson 1985; Lin et al. 1987).

Trichomes and caterpillar behavior

The three key results of the behavioral experiment were: (1) light availability affected how trichomes influenced caterpillar resting behavior, but this was the only behavior that was affected by light treatment, (2) movement rate was impeded by glandular trichomes, which may strongly affect first instar caterpillars, and (3) both glandular and non-glandular trichomes reduced the amount of time that a caterpillar spent searching for food, with a concomitant increase in other non-feeding activities.

This experiment is the first to show that resource availability affects how trichomes influence caterpillar behavior. Caterpillars rested for a greater percentage of time on stems from high-light plants than caterpillars on low-light plants (Table 5). In the plant response experiment, we found that the stems of high-light plants had higher densities of large-glandular trichomes, which in *L. esculentum* contain the soluble phenolic rutin (Isman and Duffey 1982). As the glandular exudate dries, it gums up the mandibles and legs of insects (Dimock and Tingey 1987). The longer time spent resting at high-light may reflect the higher density of these large-glandular trichomes on high-light plant stems (Table 1). However, it is striking that this was the only behavior for which we observed differences between caterpillars on high-light and low-light plants. The general lack of behavioral responses suggest that differences in trichome density may have been too small to dramatically affect the short-term behavior of the caterpillar. It would be interesting to investigate the longer-term affects of resource mediated trichome differences on caterpillar behavior and development.

Caterpillars moving from one part of the plant to another, via the stem, would be impeded by glandular trichomes (Fig. 5). Thus, glandular trichomes may subject the caterpillar to higher predation risk by increasing time of exposure on the stem, and therefore trichomes may indirectly decrease caterpillar damage to the plant. For first-instar caterpillars, which moved only half as fast as third instars (Table 5), traversing the stem may be particularly difficult due to the presence of glandular trichomes (Belcher and Thurston 1982; Tingey and Gibson 1978). Large glandular trichomes on the stem are approximately 10–20% as wide as the head capsule of a first instar caterpillar. So if a first instar caterpillar burst a gland, which happened often during the herbivore response experiment, it would get a large dose of glandular exudate relative to its body size. First-instar caterpillars generally finish that stadium on a single leaf (McFadden 1968); however, if they fall or are forced to move for some reason, the large-glandular trichomes of the stem may present a strong impediment to finding suitable (newer) leaves on which to feed.

We interpret probing as food searching behavior and the other documented behaviors as mechanisms to remove impediments to movement (mowing), to remove obstructions to the mouthparts (cleaning mouthparts), and to recover from mowing and cleaning mouthparts (resting). Time spent exhibiting cleaning, mowing, and resting behaviors decreased the amount of time that caterpillars probed, which is the behavior that locates food. When trichomes were completely removed, the caterpillars spent the greatest amount of time probing, whereas the amount of time they probed decreased when all trichomes were present ("all removed" and "control"; Fig. 4). This result is similar to the finding that glandular trichomes of *L. pennelii* delayed the time for aphids to first probe (Goffreda et al. 1988), and to the finding that high glandular trichome density on potatoes decreased the amount of time that a parasitoid spent searching for prey (Obrycki and Tauber 1984). Studies using solanaceous plants have emphasized the effects of glandular trichomes on behavior (Belcher and Thurston 1982; Dimock and Tingey 1987; Neal et al. 1989; Obrycki 1986; Tingey and Gibson 1978), but several studies have shown that non-glandular trichomes may influence insect behavior on plants as well (Dillon et al. 1983; Hulley 1988; Ramalho et al. 1984). This experiment suggests that non-glandular trichomes of tomato plants also play a role in impeding insect herbivores on tomato plants. In the "exudate removed" treatment in which the trichomes present had all glandular exudate removed (and thus were, in effect, nonglandular trichomes) the amount of time that the caterpillars spent probing decreased and the amount of time the caterpillar spent mowing increased relative to the denuded stems ("all removed" treatment; Fig. 4). Therefore, the presence of trichomes, even without glandular exudate, can influence the behavior of caterpillars.

Conclusions

Resource availability influenced allocation by tomato plants to trichome growth, and the patterns of trichome allocation in high and low-light conditions supported the GDBH and the CNBH. That trichome allocation observed in different water regimes did not support the GDBH may reflect physiological effects of water not related to growth-differentiation tradeoffs. This study shows how changes in allocation patterns to trichome growth, mediated by plant resource availability, influenced the behavior of an insect herbivore. The high-light plants, with their high trichome densities, were more difficult for caterpillars to negotiate. However, this conclusion is based on the negative effect of high-light stems on a single behavior, resting.

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