Resource availability and the trichome defenses of tomato plants

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Received: 11 January 1995 / Accepted: 17 November 1995

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; Weston et al. 1989), and temperature (Kennedy et al. 1981; Wellso and Hoxie 1982; Good and Snyder 1988; Kennedy et al. 1981; Lim et al. 1987; Weston et al. 1989; Waterman et al. 1984).
lated processes and growth related processes in different resource conditions (Ayres 1993; Herms and Mattson 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; Ogbiakhe 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 hypothesis (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 evaportranspiration 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.