Suitability of stressed and vigorous plants to various insect herbivores

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We conducted a controlled experiment to test the plant vigor and the plant stress hypotheses. The two hypotheses associate plant physiological conditions to insect feeding mode and performance. We exposed tomato, *Lycopersicon esculentum*, to different types of growing conditions: optimal (vigorous plants), resource based stress (water and/or nutrient deficit), and physical stress (punched hole in terminal leaflets). Plant performance, foliar nutritional value for insects and chemical defenses were analyzed after 14 d. These plants were offered to insects belonging to distinct feeding guilds: the silverleaf whitefly, *Bemisia argentifolii*, a phloem feeder; the leafminer, *Liriomyza trifolii*; and the corn earworm, *Heliothis zea*, a leaf chewing caterpillar.

The experimental conditions generated a gradient of plant growth in the following order: optimal (vigorous) > control = hole punched > no fertilizer > no water > no water and no fertilizer. The last two treatments resulted in plants with poor nutritional value (based on %water, C/N, %N) and higher levels of defensive compounds (i.e., peroxidase and total phenolics) compared with control and the vigorous plants. Hole-punching neither affected plant growth nor any of the phytochemicals measured. In a choice experiment adult whitefly ovipositioning was not affected by either vigor or punching but was reduced on the other plants ($P < 0.01$). Leafminer feeding and oviposition and corn earworm larval growth rates were higher on the vigorous plants and lower on the punched, no fertilizer, no water, and no water and no fertilizer host plants ($P < 0.01$).

Regardless of insect species or bioassay method, the results in the tomato system support the plant vigor hypothesis that predicts positive association between insect performance and plant growth. The results contradict the plant stress hypothesis that rank stressed plants as better hosts for insects. The mechanisms involved are a combination of poor nutritional value and chemical defenses. We demonstrate a negative association between plant growth and chemical defense. However, induced response triggered by hole-punching was not cost effective to the plants.

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Because of their relatively low nutritional value, high concentrations of indigestible materials and a variety of repellant and toxic compounds plants are considered as suboptimal food sources for herbivores (Schoonhoven et al. 1998). In addition, numerous ecological factors may alter plant quality for insect herbivores. Recently, Price (1997) reviewed several hypotheses that used different approaches to explain the complexity of (phy-tophagous) animal-plant interactions. Two main hypotheses addressed the impact of growing condition-based physiological changes in the host plant on insect herbivores. First, the plant stress hypothesis predicts that stressed plants will serve as better hosts for insect herbivores (White 1984, Mattson and Haack 1987). Plants under stress are more suitable for insect herbivores due to increased nutritional value (mainly free

amino acids) and due to reduction in synthesis of defensive chemicals (White 1984). However, experimental studies demonstrate that the effect of host plant stress is in many cases unpredictable and depend on the plant and insect species and the levels of stress (Larsson 1989, Waring and Cobb 1992). Sources of plant stress include temperature, light, mineral, water, physical damage, herbivory, diseases and pollution, and may determine insect response (Heinrichs 1988). The effects of plant stress become even more complicated when more than one factor is involved (Larsson et al. 1986, Dudt and Shure 1994). Larsson (1989) suggested a non-linear relationship between the level of stress and herbivore performance which would be greatly dependent on the insect feeding mode (guild), such as leaf chewers, sap feeders, leafminers, and gall-formers. According to this modification to the plant stress hypothesis, phloem feeders will prefer (to a certain extent) stressed plants, where leaf leafminers and leaf chewers will be negatively affected by stressed host plants (Larsson 1989).

Contrariwise, the plant vigor hypothesis (Price 1991) predicts that herbivorous insects will prefer and perform better on rapidly growing (vigorous) plants or plant modules. It especially refers to those insects with a tight link between adult oviposition site and larval feeding position, and insects whose larval development is closely associated with host plant growth process. Gall formers and leafminers that have the most intimate relationships with their host plant are the best possible candidates to support this hypothesis. The mechanism(s) behind the plant vigor hypothesis is not clear and it is based on empirical studies of insect populations (Price 1991, 1997 and references therein).

Studies examining the two hypotheses have yielded mixed results (e.g., Larsson 1989, Waring and Cobb 1992, De Bruyn 1995, Preszler and Price 1995, Meyer and Root 1996). In this study, tomato plants were exposed to different types of growing conditions: optimal (vigorous), resource based stress (water and/or nutrient deficit), and physical stress (damaged leaves). The effects of the treatments were characterized for plant growth, chemical defense, and nutritional value. Then, the plant stress and vigor hypotheses were tested by examining the performance of three generalist insects belonging to distinct feeding guilds on these plants. One of the insects used was the silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae). Whiteflies are phloem feeders where adults tend to feed and oviposit on the same leaves (Gerling 1990). Another insect used was the leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae). Adult leafminers feed and oviposit on the leaves while the larvae mine the leaves, feeding on the spongy mesophyll (Parrella 1987). The third insect used was the corn earworm, *Heliothis zea* (Lepidoptera: Noctuidae) where the larvae are leaf chewers. The

combination of different insects, different stress agents, and the extensive measurements of plant traits should provide better understanding of the mechanisms involved.

Materials and methods

Plant rearing

Four-week-old (2–3 true leaves) 'Agriset' tomatoes, *Lycopersicon esculentum*, were transplanted into 5.7-cm pots (except 'vigorous plants' see below) with Metro Mix 350® growing medium (Grace Sierra, CA). Plants were watered to saturation and then randomly assigned to six treatments as follows:

1. Control: Each plant received 50 ml water every 3 d. Plants were fertilized twice (days 1 and 9) with 9-45-15 N:P:K, each time with 30 ml of 400 ppm added to the regular watering regime.
2. Optimal conditions (Vigor): Plants were transplanted to 8.9-cm pots and received 60 ml water every 3 d (total 360 ml), and fertilized twice with 9-45-15 N:P:K, each time with 40 ml of 400 ppm N.
3. Hole-punching (punched): Plants were treated as the controls. Five circular 0.5-cm^2 holes were made in the middle of the terminal leaflet. Holes were made with a hole punch, once every 3 d, starting with the first (old) leaf. This procedure removed $4.7 \pm 0.79\%$ of the final leaf area as calculated using a portable leaf area meter (CI – 203, CID Inc., Vancouver, WA).
4. No fertilizer (-N): Plants were watered as for the controls, but no fertilizer was added.
5. No water (-W): Plants were fertilized as for the controls but no additional water was added (i.e., total water 90 ml).
6. No fertilizer and no water (-N-W): no fertilizer was added, plants received 90 ml water which was equivalent to the water added with fertilizer in the control, punched, -W, and -N treatments.

Throughout the experiment the plants were kept in a controlled-atmosphere room with constant conditions of 24°C, 70% RH, L:D 12:12. After 14 d of conditioning period, the plants were used for the various tests (below).

Plant performance and phytochemistry

Fourteen randomly selected plants from each of the six treatments were used for monitoring plant growth and chemistry. As indicators of plant growth (vigor) stem length, number of leaves, and total above ground wet and dry biomass were measured. All leaves were lyophilized, re-weighed and powdered in the tubes.

Acetone (1 ml of 70/30 acetone/water) was added and the samples were vortexed for 1 min. Samples were incubated in the dark on ice for 5 min, and subsequently were centrifuged at 17000 g for 10 min at 4°C. The resulting supernatant was used for measurement of total phenolics. Total phenolics were measured using a modified version of the Folin-Ciocalteu method (Waterman and Mole 1994). Foliar levels of several defensive pathogenesis related (PR) proteins (chitinase, peroxidase, and β-1,3-glucanase) were measured as described previously (Mayer et al. 1996).

The freeze-dried powder was also used for C and N concentration measurements performed with a nitrogen analyzer (Model 1500, Carlo Erba Strumentazione, Milan, Italy). C, N, and water are considered as major nutrients essential for insect development (Slansky and Scriber 1985).

Insect performance

Fourteen randomly selected plants from each of the six treatments were set in a random order in a Plexiglas cage ($120 \times 60 \times 70$ cm). Approximately 200 adult whiteflies that had been maintained in a greenhouse on collards and tomatoes were released into the cage. After 12 h the plants were shaken and randomly repositioned in the cage for an additional 12 h. The number of whitefly eggs from all terminal trifoliates was counted on three 1-cm^2 discs/trifoliate. Similarly, ~ 200 newly hatched adult leafminers from a laboratory colony maintained on cowpea were released into another cage. Plants ($N = 14$ for each treatment) were shaken and repositioned after 12 h. The experiment was terminated after an additional 12 h where the number of punctures (indicating feeding and oviposition) was counted on all terminal trifoliates. Leaf area of those trifoliates was recorded, thus the results are expressed as punctures/cm^2. A non-choice feeding experiment was conducted with second instar corn earworm, *H. zea*, larvae reared on artificial diet (USDA, ARS, CMAVE, Gainesville, FL). Individual larvae ($N = 14$ for each treatment) were placed in a Petri dish with wet moist filter paper, and fed with detached leaves (leaves nos 2 and 3 from top). The larval relative growth rate (RGR) for 24 h was calculated on a dry weight basis. Larval dry weight at the beginning of the experiment was estimated from 10 sacrificed individuals. It should be emphasized that in all bioassays, insect feeding was involved.

Statistical analyses

Data on enzyme activities and total phenolics were $\log_{10} (x + 1)$ transformed before analysis. Arcsine transformation was used to normalize percentage-based data (water, N, C). The effects of each treatment on plant characteristics and insect performance were analyzed with one-way ANOVA, followed by Student-Newman-Keuls (SNK) mean separation test (Sokal and Rohlf 1981). The effect of each variable on insect performance was tested using exponential regressions that generally provided a higher r^2 than linear regression. A more powerful multiple regression was used to test the combined effects of several variables on insect performance. However, because of multiple regression limitations, only phenolics, plant water content, dry biomass, and % N that represent fundamental plant characteristics were included. All statistical analyses were conducted with the 'Statistica' 5.1G software package for Windows (StatSoft, Inc. Tulsa, OK 1997).

Results

Effect of growing conditions on plant performance (Fig. 1)

The various treatments significantly affected plant growth as measured by dry weight ($F_{5,78} = 86.03$, $P <$
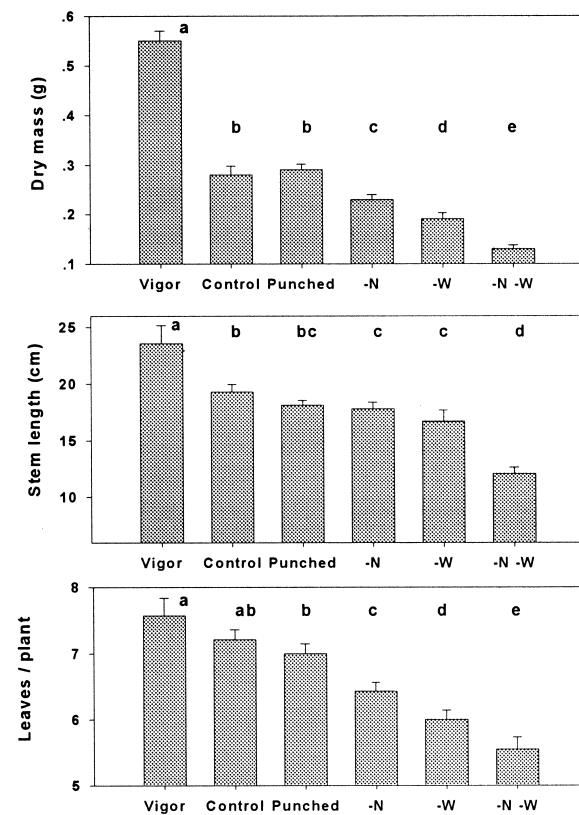

Fig. 1. The effect of the experimental conditions on tomato plant growth. Means + SE are presented. See text for ANOVA results; within histograms, columns with different lowercase letters are significantly different from each other (SNK mean separation, $P < 0.05$).
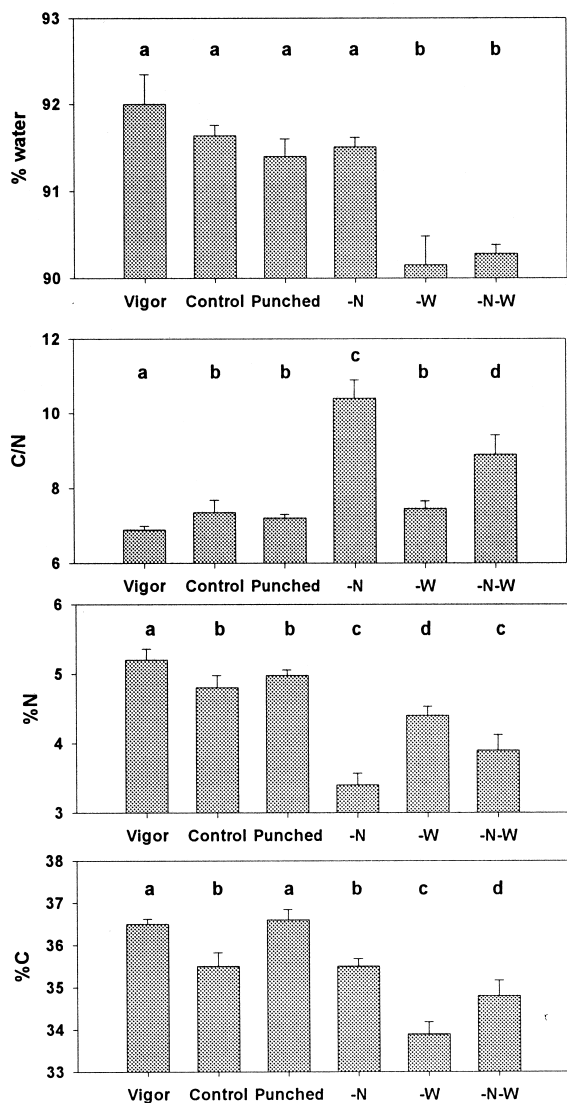
Fig. 2. The effect of the experimental conditions on tomato plant water content and C and N concentration. Means + SE are presented. See text for ANOVA results; within histograms, columns with different lowercase letters are significantly different from each other (SNK mean separation, $P < 0.05$).

0.01), shoot length ($F_{5,78} = 21.8$, $P < 0.01$), and number of leaves ($F_{5,78} = 20.09$, $P < 0.01$). Vigorous plants grew better and -N, -W, and -N-W plants were smaller, respectively. For example, vigorous plant dry biomass was nearly two-fold heavier than the control and more than four-fold heavier than the -N-W plants. Punching did not affect plant growth.

Effect of growing conditions on plant water content and C and N concentration (Fig. 2)
Water content of -W and -N-W plants was significantly lower than all other treatments ($F_{5,78} = 18.64$, $P < 0.01$). Vigorous plants tended to have higher water content than the controls, though these differences were not significant. Compared with the controls, nitrogen levels in the -N, -W, and -N-W plants were reduced by 29.2%, 8.3%, and 18.7%, respectively. Vigorous plants had 8.3% more N than did the controls N ($F_{5,78} = 8.03$, $P < 0.01$). Percentage of C was lower in the water stressed plants ($F_{5,78} = 8.18$, $P < 0.01$). Consequently, C/N levels were lower in vigorous plants and higher in the non-fertilized (-N and -N-W) plants compared with the controls ($F_{5,78} = 18.30$, $P < 0.01$). Punched plants did not differ from the controls in any of the parameters that were measured.

Effect of growing conditions on plant defensive compounds (Fig. 3)
The most obvious trend observed was that all of the defensive compounds measured had lower levels in the vigorous plants (peroxidase was not significant). Chitinase levels were slightly higher in the -W treated plants ($F_{5,78} = 4.44$, $P < 0.01$). Glucanase levels were reduced in the punched plants but were not effected by other stresses ($F_{5,78} = 4.61$, $P < 0.01$). Peroxidase levels were higher in the -N plants and increased 5.7-fold in the -W and four-fold in -N-W plants compared with controls ($F_{5,78} = 13.4$, $P < 0.01$). Total phenolics were similar to peroxidase, where phenolic levels in the -W and -N-W plants increased 39% and 46%, respectively ($F_{5,78} = 4.24$, $P < 0.01$). HPLC analysis revealed that the main phenolics induced in the water stressed plants were rutin and chlorogenic acid (Doostdar, Inbar and Mayer unpubl.).

Effect of host plant growing conditions on insect performance (Fig. 4)
Adult leafminers preferred vigorous plants as feeding and ovipositioning hosts ($F_{5,78} = 15.35$, $P < 0.01$). Both punching and -N treatments reduced leafminer preference (feeding and ovipositioning) by more than 30% than the punctures found on the controls. Vigorous plants received 3.4 and 6.5 more leafminer punctures/cm^2 than the -W and -N-W plants, respectively.

Corn earworm larval response was nearly identical to the trend found with leafminers. In the non-choice feeding experiment, larval relative growth rate of second larval instar corn earworms on vigorous plants was nearly twice that of the control plants ($F_{5,78} = 12.37$, $P < 0.01$). Punching and -N treatments equally reduced larval development. The most severe effect was found on the -W and especially -N-W plants where larvae lost weight and obtained negative RGR values. The number of eggs laid by whiteflies was not affected by the vigor or punching treatments. However, a 40% reduction in whitefly oviposition was found on the -N plants ($F_{5,78} = 4.91$, $P < 0.01$). Again, the greatest reduction was detected on the -W and -N-W plants that had less than half the eggs/cm^2 as the controls.
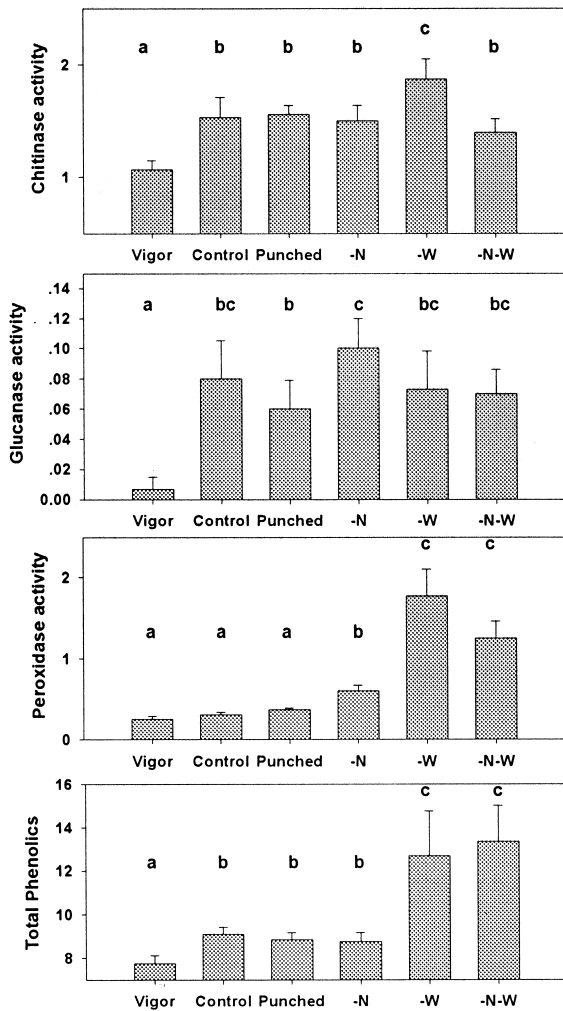
Fig. 3. The effect of the experimental conditions on tomato plant chemical defense. Foliar chemistry units are: chitinase $-\Delta A_{550} min^{-1} g^{-1}$ tissue, glucanase – μmol Glc $min^{-1} g^{-1}$ tissue, peroxidase $-\Delta A_{550} min^{-1} g^{-1}$ tissue, total phenolics – g Tannic acid equiv/g dry tissue. Means + SE are presented. See text for ANOVA results; within histograms, columns with different lowercase letters are significantly different from each other (SNK mean separation, $P < 0.05$).

Across treatments, the relationships between each of plant traits (Figs 1, 2, 3) and insect performance (Fig. 4) are given in Table 1. Exponential regression revealed highly positive relationships between the performance of leafminers, corn earworms and whiteflies and host-plant water content, number of leaves per plant, shoot length and dry weight. Significant negative relationships were found between insect performance and the levels of peroxidase and total phenolics but not with chitinase and glucanase. Surprisingly, C/N had no significant relationships with insect performance. Stepwise multiple regression found highly significant relationships between total phenolics, % water, dry biomass, and C/N,

and leafminer ($r^2 = 0.88$, $F_{2,3} = 20.67$, $P = 0.017$), corn earworm ($r^2 = 0.82$, $F_{2,3} = 25.07$, $P = 0.007$), and whitefly ($r^2 = 0.93$, $F_{2,3} = 24.06$, $P = 0.04$) performances.

Discussion

Although we exposed the plants to various stress agents and adopted independent methods (choice and non-choice experiments) to evaluate plant suitability to several insect herbivores belonging to distinct feeding guilds, we found no support for the plant stress hypothesis in the tomato system. Resource based stressed hosts had poor nutritional value, high levels of chemical defense, and consequently lower insect performance. The data support the plant vigor hypothesis especially
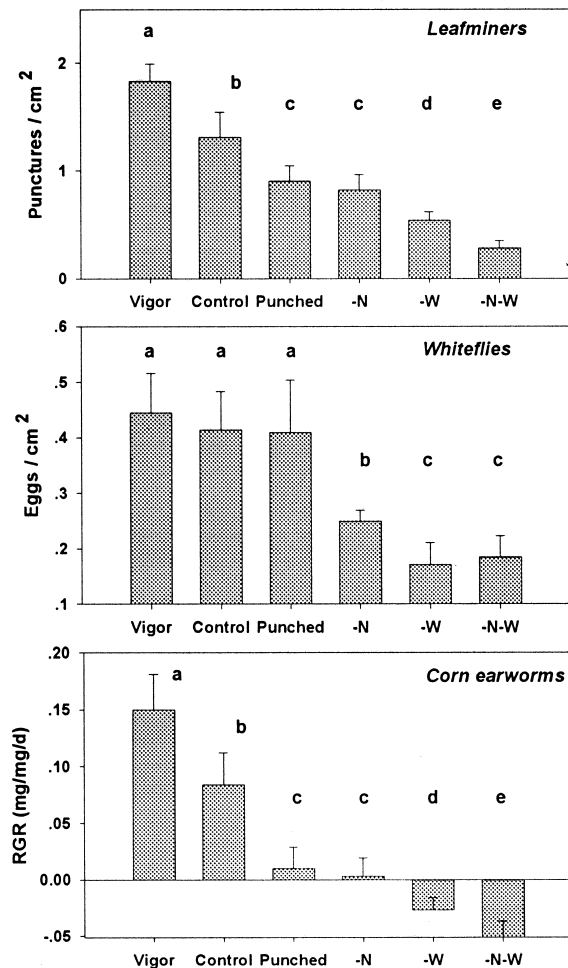

Fig. 4. The effect of the experimental conditions on leafminer and whitefly host plant preference and corn earworm RGR. Means + SE are presented. See text for ANOVA results; within histograms, columns with different lowercase letters are significantly different from each other (SNK mean separation, $P < 0.05$).

Table 1. Exponential regression (df = 1, 4) between insect performance and each variable of plant characteristic that was measured. For foliar chemistry units see Figs 2 and 3.

	Chitinase	Glucanase	Peroxidase	Phenolics	Water (%)	Leaves/plant	Shoot length	Dry weight	N (%)	C (%)	C/N
Leafminers											
R^2	0.19	0.22	0.61	0.83	0.82	0.94	0.94	0.73	0.39	0.47	0.19
B	−1.11	−9.88	−0.84	−0.002	0.78	0.83	0.17	0.28	0.6	0.44	−0.21
F	0.95	1.13	6.52	19.9	18.36	75.01	63.1	11.29	2.57	3.54	0.99
P	0.52	0.44	0.03	0.002	0.003	0.0001	0.0002	0.009	0.6	0.09	0.5
Whiteflies											
R^2	0.29	0.29	0.87	0.76	0.81	0.9	0.6	0.59	0.5	0.73	0.25
B	−0.9	−6.7	−0.65	−0.0001	0.51	0.53	0.09	0.18	0.44	0.37	−0.16
F	1.67	1.24	26.9	13.25	17.83	40.23	6.13	5.9	4.14	14.99	1.32
P	0.29	0.4	0.001	0.006	0.003	0.0005	0.03	0.03	0.07	0.005	0.38
Corn earworms											
R^2	0.43	0.44	0.54	0.61	0.71	0.84	0.85	0.86	0.47	0.4	0.25
B	−1.68	−1.59	−0.089	−0.0001	0.008	0.08	0.017	0.07	0.07	0.05	−0.02
F	3.07	3.18	4.78	6.4	9.83	21.77	22.67	24.9	3.29	2.74	1.38
P	0.12	0.14	0.055	0.03	0.01	0.002	0.0019	0.0015	0.1	0.14	0.36

with leafminers and corn earworms (leaf chewers). Whiteflies did not discriminate between vigorous and control plants that were clearly preferred over the resource based stressed plants. Support for our results comes from reports on leafminer and whitefly preferences for fertilized tomatoes (Jauset et al. 1998, Minkenberg and Ottenheim 1990) and the negative impact on the former by tomato induced response (Stout and Duffey 1996, Inbar et al. 1998, 1999). Caterpillar (including corn earworms) performance is known to be affected by tomato induced responses and its constitutive allelochemicals (e.g., Stout and Duffey 1996, English-Loeb et al. 1997).

Defensive chemicals and the fundamental nutrients such as water, C, N, and C/N (Slansky and Scriber 1985) were reduced in the -W and -N-W stressed plants, and tended to be higher in the control and vigorous plants (Fig. 2). Water stressed plants (-W and -N-W) were the worst hosts for all insect herbivores tested (Fig. 4). Neither fertilizer stress nor punching restricted insect performance to that level. Shortage of water could itself restrict insect performance (Slansky and Scriber 1985, Schoonhoven et al. 1998). In addition, only water stress caused a two-fold increase in the concentrations of phenolics and peroxidase activity (Isman and Duffey 1982). Phenolics (especially rutin and chlorogenic acid) are the dominant allelochemicals in tomato (and many other plants) and known to decrease insect growth, development and survivorship (Isman and Duffey 1982, Stamp 1990, Wilkens et al. 1996, English-Loeb et al. 1997). Peroxidases are involved in production and polymerization of phenolics, lignification, and hypersensitive responses, thus affecting food digestibility and protein availability to herbivores (Bowles 1990, Duffey and Stout 1996). Fertilizer stressed plants (-N) probably directly affected the insects via their low nitrogen levels (high C/N) since this treatment did not alter the plant's water content or levels of defensive compounds (except minor increase in peroxidase levels). Punching that did not affect host phytochemistry (for those parameters measured) probably affected the insect through the induced response mechanism (below).

Hole punching differs from other "resource related stresses" in two aspects. First, punching treatment did not affect above-ground plant growth or any of the phytochemicals measured. Indeed, wound (punching) induced responses primarily include proteinase inhibitors Ryan and Green (1974) that were not measured in this study. It also is possible that the lack of increase in phenolics and peroxidase in these plants is due to the pot bound effect (Baldwin 1988), where plants with limited root growing conditions are less likely to induce defensive chemicals. Secondly, punching had differential impact on the insects; punching that did not affect whitefly performance had a remarkable impact on corn earworms and leafminers (Fig. 4; Stout and Duffey
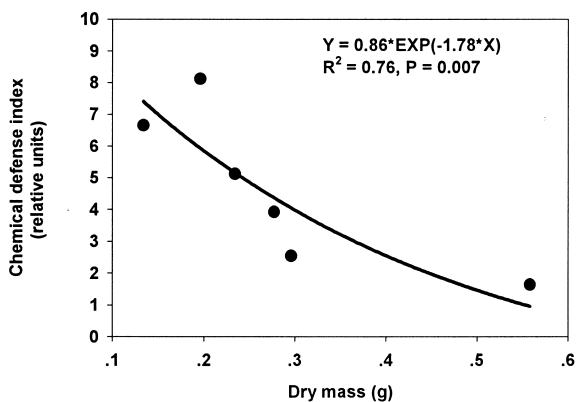
Fig. 5. Exponential relationships between plant growth (above-ground dry biomass) and chemical defense in the six growing conditions. Index of chemicals defense is based on data presented in Fig. 3 for phenolics, peroxidase, glucanase and chitinase. The index is the sum of the proportion of all defensive compounds invested in each treated group. The bottom right point is off the vigorous plants and the top left points are off the -W and -N-W treated plants.

1996). Earlier we showed that tomato induced responses triggered by biotic agents and exogenous elicitors failed to influence whitefly preference and performance (Inbar et al. 1998, 1999). One explanation for these results could be that proteinase inhibitors in tomatoes are stored in intracytoplasmic vacuoles in parenchyma and epidermal cells (Walker-Simmons and Ryan 1977). Thus, whiteflies as phloem feeders may avoid their negative effect. However, only research that will include additional insect species from all feeding guilds will be able to confirm this hypothesis.

The experimental protocol resulted in a gradient of host plant growth performance with the vigorous plants being the largest and water and fertilizer stressed plants being the smallest (Fig. 1). Defense chemicals (phenolics and defensive-proteins) were clearly lower in the vigorous plants, while the levels of phenolics and peroxidases were elevated in the fertilizer and water stressed plants (Fig. 3). This trend can be expressed as an inverse exponential relationship between plant growth (dry biomass) and an index of plant defense (Fig. 5; but see Koricheva 1999 for dilution effect). Our results are in agreement with the optimal defense hypothesis (Rhoades 1979) and the growth differentiation balance hypothesis (Herms and Mattson 1992) that predicts a trade-off between resources allocated for growth and those devoted for defense (Herms and Mattson 1992, Wilkens et al. 1996). In stress plants (e.g., drought), plant growth rate is declining before the photosynthesis process, which causes an increase of assimilate reservoirs. These photosynthates can be allocated to non-nitrogen based defensive compounds such as phenolics (Chapin 1991, Herms and Mattson 1992). We also observed increases in peroxidase (N base-compound) activities in the water stressed plants (Fig. 3; see En-

glish-Loeb et al. 1997). The growth differentiation balance hypothesis predicts a non-linear relationship between growth and defense; severely stressed plants will not invest in defense or growth (Herms and Mattson 1992, Wilkens et al. 1996; see English-Loeb et al. 1997). Such a trend was not found in the present study where defense increased with growth limitation (Fig. 5; see English-Loeb et al. 1997). Although we produced a gradient of growth, we did not create a gradient of stress for each of the stress agents and thus may have failed to detect the nonlinear response. The punching treatment had no association with plant growth indicating the lack of trade-off between induced resistance and growth in tomatoes. Similarly, Brown (1988) found no effect on tomato growth and fitness when proteinase inhibitors were elicited with injected chitin. It was concluded that tomato induced response demands only a small fraction of plant resources (Brown 1988). Nevertheless, since below-ground biomass was not calculated there is still a possibility that the root system was affected by the treatment.

Several studies reported that whiteflies prefer water-stressed cotton plants (Flint et al. 1996, Skinner 1996). We found that whitefly host preferences are severely affected by fertilizer and water-stressed host plants (see also Jauset et al. 1998). The level of stress may explain this contradiction. As predicted by Larsson (1989), the response of phloem feeders to plant stress will depend on the degree of stress. In moderate stress, phloem feeders may perform better, but will be negatively affected by a more severe stress. It is also possible that water stress in cotton has different effects on whiteflies than water stress in tomatoes.

The effect of stress on insect herbivores may be related to three main factors: species (plant and insect), type of stress, and the level of stress. This study did not deal with the level of stress but did create a gradient of plant growth rates. We could not discriminate between insect feeding guilds since only one member of each guild was tested. However, the gradient of resource stressed plants indicated the inferiority of stressed plants to herbivores. The mechanisms are a combination of poor nutritional value and chemical defenses.

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