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Compensation for herbivory by *Cucumis sativus* through increased photosynthetic capacity and efficiency

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Abstract Herbivory is an important selective pressure in the life history of most plant species, as it usually results in reduced plant fitness. In some situations, however, plants are able to compensate for the resources lost to herbivory and do not suffer any reduction in growth or reproduction after attack. We examined the ability of Lebanese cucumber (*Cucumis sativus*) to compensate for both pre-flowering and during-flowering foliar herbivory through increased photosynthetic efficiency and capacity. Plants that were damaged before flowering were able to compensate, in terms of vegetative biomass and fruit production for up to 80% leaf area loss. Plants that were damaged during the flowering period were less able to compensate and fruit production declined with increasing herbivory. Damaged plants had higher photosynthetic efficiency and capacity, and dissipated less light energy as heat. Herbivore-damaged plants may be induced to use a greater proportion of the absorbed light energy for photosynthesis as a result of altered carbohydrate source-sink relationships.

Keywords Chlorophyll fluorescence · Plant–animal interactions · Source-sink dynamics · Light use efficiency · Photosynthesis

Introduction

For most plants, loss of leaf tissue to herbivores is a constant feature of the environment (Cyr and Pace 1993). Herbivory results in resource reduction through a loss of nutrients and/or photosynthetic area, often leading to a reduction in plant fitness. However, within the last 30 years, increasing evidence has indicated that many plants are able to compensate for lost tissue by replacing it through rapid growth (McNaughton 1983). In this study, we examined the ability of Lebanese Cucumber (*Cucumis sativus*) to compensate for foliar herbivory by the brown garden snail (*Helix aspersa*).

Compensatory ability, defined as the difference in fitness between herbivore damaged and undamaged individuals of the same genotype (Belski 1986), varies widely across plant species. For example, *Piper arieanum* suffered a reduction in growth and reproduction with only 10% leaf loss (Marquis 1984), whereas *Abutilon theophrasti* fully compensated for 75% defoliation under certain conditions (Mabry and Wayne 1997). The degree of compensation depends on the plant species, amount of leaf lost, mode of herbivore damage, environmental conditions and the timing of the herbivory event (Maschinski and Whitham 1989; Simons and Johnston 1999). Plants are more likely to compensate if the damage occurs early in the growing season, before the reproductive phase has started (Maschinski and Whitham 1989; Lehtila and Syrjänen 1995; Scarré et al. 1996; Lennartsson et al. 1998). Proposed mechanisms for compensation include increased photosynthetic rate (Dyer et al. 1991; Houle and Simard 1996; Meyer 1998), increased growth rate (Danckwerts 1993; Oba et al. 2000), increased branching or tillering after the release from apical dominance (Scarré et al. 1996; Sacchi and Connor 1999; Simons and Johnston 1999; Lortie and Aarssen 2000), high pre-herbivory levels of stored carbon (Hochwender et al. 2000) and the ability to reallocate those stored resources (Caldwell et al. 1981; Mabry and Wayne 1997), alteration of the external light environment (Jãremo et al. 1996; Mabry and Wayne 1997), and higher reproductive efficiency through increased percentage of fruit set (Mabry and Wayne 1997).

The capacity for a plant to compensate for herbivory depends on carbohydrate source-sink dynamics. Net sources of carbohydrates include mature photosynthesis-

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ing leaves or stored reserves. All parts of the plant can be considered sinks of fixed carbohydrates, but growing structures such as new leaves, flowers and fruit are particularly strong sinks. Sink strength depends on both external resource availability and internal factors such as the strength of other sinks and the concentration of hormones (Honkanen et al. 1994; Kaitaniemi and Honkanen 1996). Sink strength can regulate the photosynthetic activity of the source leaves (Kaitaniemi and Honkanen 1996) and increases in the number or strength of sinks can stimulate photosynthesis (Bazzaz et al. 1987). Partial removal of source leaves by herbivory results in an initial decrease in carbon assimilation, without a change in carbon demand. The relatively higher demand placed on the remaining leaf area can induce a mature leaf to fix larger amounts of carbon, and translocate photosynthate to growing structures at faster rates than in undamaged plants (Dyer et al. 1991; Lehtila and Syrjänen 1995; Kaitaniemi and Honkanen 1996).

Photosynthetic responses to herbivory can be assessed rapidly through non-invasive and non-destructive measurement of chlorophyll fluorescence. Chlorophyll fluorescence techniques have recently been applied to assess environmental stresses in plants (Ball et al. 1995; Valladares and Pearcy 2002); however, to the best of our knowledge, never to studies of compensation to herbivory. When chlorophyll absorbs photosynthetically active light, the radiant energy can be used in photosynthesis, dissipated harmlessly as heat, or re-emitted at a longer wavelength as fluorescence. Measurements of chlorophyll fluorescence at room temperature can provide accurate quantitative estimates of three parameters that are useful in assessing photosynthetic compensation to herbivory: photosynthetic light use efficiency, photosynthetic capacity and the extent of protective dissipation of excess light energy as heat (Schreiber et al. 1994; Walz 1999). Photosynthetic light use efficiency (called photosynthetic efficiency hereafter) is the amount of carbon gained per unit of light absorbed (also known as potential quantum yield). Photosynthetic efficiency is correlated with the ratio of variable to maximum fluorescence (Fv/Fm, Bolhàr-Nordenkampf and Öquist 1993). Photosynthetic capacity, the maximum photosynthetic rate of a leaf, can be estimated by measuring the photosynthetic electron transport rate (ETR) under saturating light (Walz 1999; calculated using the method of Genty et al. 1989). Heat dissipation of light energy (via the xanthophyll cycle) occurs when a leaf absorbs more energy than can be used for photochemistry, and serves as a protective process that enables the leaf to balance the absorption of light energy with the capacity to use it (Osmond et al. 1999). The extent of heat dissipation of excess light energy can be estimated by measurement of the non-photochemical quenching of fluorescence (NPQ).

We examined the effects of foliar herbivory by the garden snail, *Helix aspersa*, on photosynthesis, growth and fruit production of *Cucumis sativus* plants. We hypothesized that herbivory would cause a relative increase in sink strength, resulting in a greater carbon demand on the remaining source leaves. In response, source leaves would increase their photosynthetic capacity and/or efficiency, and decrease the proportion of light energy dissipated as heat. Further, we predicted that this physiological response would result in compensation as measured by vegetative and reproductive biomass, though the strength or even direction of the above responses might differ with the timing and intensity of herbivory, and with the amount of fruit produced by a plant.

Materials and methods

Study species

Cucumis sativus (Lebanese cucumber) is a climbing annual herb that is widely cultivated for its edible fruit. It is usually monoecious (has male and female unisexual flowers); however, gynoecious (female), androecious (male) and hermaphroditic plants are also known (Yin and Quinn 1995). *Cucumis sativus* encounters generalist herbivores such as spider mites, roaches, beetles and lepidopteran larvae, as well as specialist herbivores such as diabroticite beetles (Agrawal et al. 1999). Cucumber leaves contain bitter defensive compounds called cucurbitacins, effective against most generalist herbivores. Increases in cucurbitacin content can be induced through herbivory (Agrawal et al. 1999).

Helix aspersa (brown garden snail) is native to Western Europe and the Mediterranean (Bleakney et al. 1989). It has successfully colonised temperate regions of Australia, and is well adapted to warm climates. The generalist feeding strategy of *H. aspersa* makes it a good experimental herbivore. It is classified as a pest of wheat and citrus in Australia, and is a threat to many green vegetable plants (Godan 1983). Terrestrial gastropods can severely damage cucumber leaves, and some species can consume more than half their body weight in 24 h (Godan 1983).

Effects of herbivory prior to flowering

The effects of herbivory prior to flowering on plant photosynthesis and growth were examined in a glasshouse experiment between September and December 2000. The average minimum and maximum glasshouse temperatures for this period were 13.5° and 35°C. Plants were grown in sand in 25 cm diameter pots, watered twice per day and fertilised with an NPK liquid fertiliser (Aquasol, Hortico Nurseries) twice per week. All female flowers were hand pollinated, using pollen from spare plants, to ensure maximum fruit set. Plants were randomly assigned to three treatments: 0%, 40% and 80% herbivory of each leaf, with 12 plants in each treatment spread evenly over three blocks in the glasshouse.

The herbivory treatment was applied when all plants had four leaves and had not yet started flowering. One to five snails were kept on each leaf with a nylon mesh bag, excluding leaves smaller than 4 cm in length. Leaf area was estimated before herbivory using a 4 cm^2 grid, and snails were removed when this area was reduced by the appropriate amount (1–7 days). Leaves on plants in the 0% herbivory treatment were placed in empty mesh bags to control for any bag effect. These bags were removed from the 0% herbivory plants at a similar rate to the bags containing snails. Non-destructive growth measurements of plant height (to nearest centimetre), leaf number and leaf length (of each leaf larger than 4 cm in length, to the nearest 0.5 cm) were taken both before herbivory and 2 weeks after herbivory. Estimated leaf area per plant was calculated from the relationship between leaf length and leaf area (determined from 26 leaves of non-experimental plants; R^2=0.90). After the herbivory treatment, plants were grown for 6 weeks, until they had completed flower and cucumber production, and were then harvested. At harvest, leaves, stems and roots were

separated from each plant and dried for at least 48 h at 60°C, and then weighed. Fruit was collected, counted and weighed fresh.

All chlorophyll fluorescence measurements were taken using a Photosynthesis Yield Analyser Mini-Pam – Portable Chlorophyll Fluorometer (Walz, Effeltrich, Germany). One week after the herbivory treatment, chlorophyll fluorescence measurements were taken on two leaves per plant: a partially consumed leaf (and a leaf of similar age on the 0% herbivory plants), and an uneaten leaf that had been produced after the herbivory had finished. These leaves are referred to as 'treated leaf' and 'leaf produced after treatment' respectively. Three consecutive measurements were taken on different areas of the leaf to obtain an average for each leaf. Fluorescence measurements were taken when the plants were acclimated to darkness (after 8.30 p.m.) and when plants were acclimated to light, both in the morning (between 9.00 and 10.30 a.m.) and in the afternoon (between 3.00 and 5.00 p.m.). All measurements were taken using a saturation light intensity of approximately 4,500 µmol m^{-2} s^{-1}, and daytime measurements were taken using an actinic light intensity of approximately 800 µmol m^{-2} s^{-1}. Different blocks were usually measured on different but consecutive days. Measurements were taken on each plant immediately before the herbivory treatment had been applied, approximately 1 week after the herbivory had finished, and again approximately 3 weeks after herbivory. The fluorescence measurements were used to calculate F_v/F_m (photosynthetic efficiency), ETR (photosynthetic capacity) and NPQ (heat dissipation; see Walz 1999 for calculation procedures).

Effects of herbivory applied after flowering commenced

The effects of herbivory, during the flowering period, on plant photosynthesis and growth were examined in a glasshouse experiment between December 2000 and February 2001. The average minimum and maximum glasshouse temperatures for this period were 17° and 38°C respectively. Plants were randomly assigned to four treatments in the glasshouse (12 plants per treatment, spread over three blocks): 0%, 40% and 80% herbivory (of each leaf at the six-leaf stage), and continuous 80% herbivory of each leaf as produced. The 0% and continuous herbivory treatments each contained an additional 12 plants, the flowers of which were not hand pollinated, but received pollination from insects visiting the glasshouse (open pollination). The two pollination treatments were included to establish contrasting levels of fruit production, in order to examine the interaction between reproductive allocation and compensation to herbivory.

Herbivory by *H. aspersa* was applied to each plant after it had produced its first three flowers, at the six-leaf stage. For the 40% and 80% herbivory treatments, one to five snails were kept on each of the first six leaves as described for the pre-flowering herbivory experiment. For the continuous herbivory treatment, snails consumed 80% of each new fully-expanded leaf, and continued until just before harvest. Prior to chlorophyll fluorescence measurements and harvest, one leaf on each continuous herbivory plant was left undamaged in order to take measurements on an uneaten leaf. Plants in the 0% herbivory treatment received mesh bags without snails, as described for the pre-flowering herbivory experiment.

Growth and reproductive measurements were conducted as described for the pre-flowering herbivory experiment. Plant height was measured and leaf area estimated immediately before, and 1 week after the herbivory treatment. Plants were harvested 5 weeks after the treatments had started, when most plants had stopped flowering. Leaves, stems, roots and fruit were separated and weighed as described for the pre-flowering herbivory experiment.

Chlorophyll fluorescence was measured on a treated leaf and a leaf produced after treatment, on each plant before herbivory and approximately 1 week after the 40% and 80% herbivory treatments had finished. Fluorescence measurements, as described for the pre-flowering herbivory experiment, were taken when the plants were acclimated to darkness (after 9.15 p.m.) and when the plants were acclimated to light conditions (between 3.00 p.m. and 5.00 p.m.).

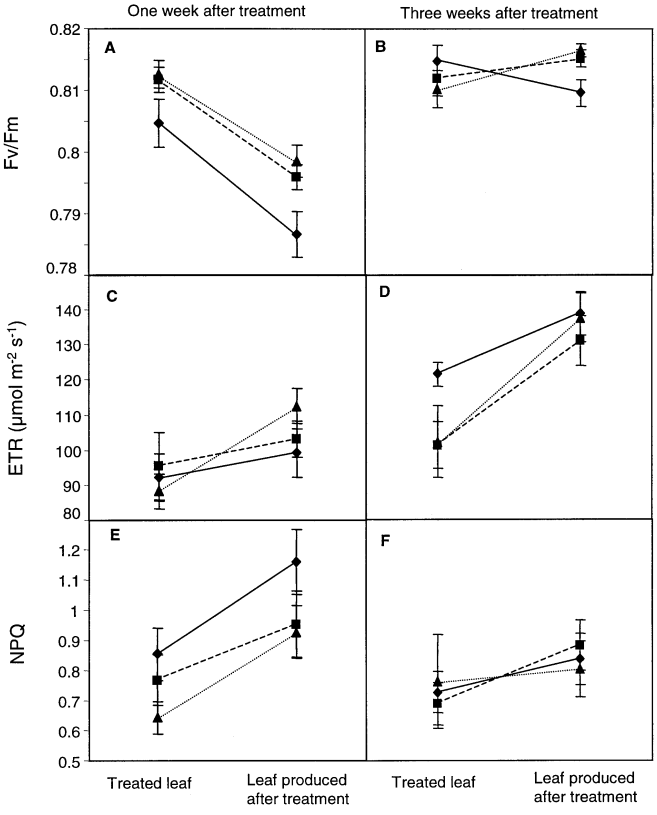

Fig. 1 Effect of pre-flowering herbivory on chlorophyll fluorescence variables: F_v/F_m (**a**, **b**), ETR (**c**, **d**), and NPQ (**e**, **f**). Mean (±SE) for all treatments on treated leaves and leaves produced after treatment, both 1 week (*left hand graphs*) and 3 weeks (*right hand graphs*) after the herbivory treatments had finished. Zero herbivory treatment, *diamonds* and *solid line*; 40% herbivory, *squares* and *dashed line*; 80% herbivory, *triangles* and *dotted line*. Each data point represents 12 plants

Data analysis

Prior to analysis, all variables were examined for homogeneity of variance and normality, and were transformed to meet assumptions when necessary. Both the chlorophyll fluorescence and growth data were analysed using analysis of variance with block included as a random factor. For the analyses of chlorophyll fluorescence, the fixed factors included herbivory treatment, leaf (treated or produced after treatment) and time of day (morning or afternoon, pre-flowering herbivory experiment only). The interaction between treatment and leaf was always included in the analyses, but other interactions were only included when significant. Measurement times (before and after treatment) were analysed separately. Differences between individual treatments and leaves were analysed using Scheffé post hoc tests.

Results

Effects of pre-flowering herbivory

Before treatment, there were no significant differences in any of the growth variables or fluorescence variables between plants in the three treatments (results not shown).

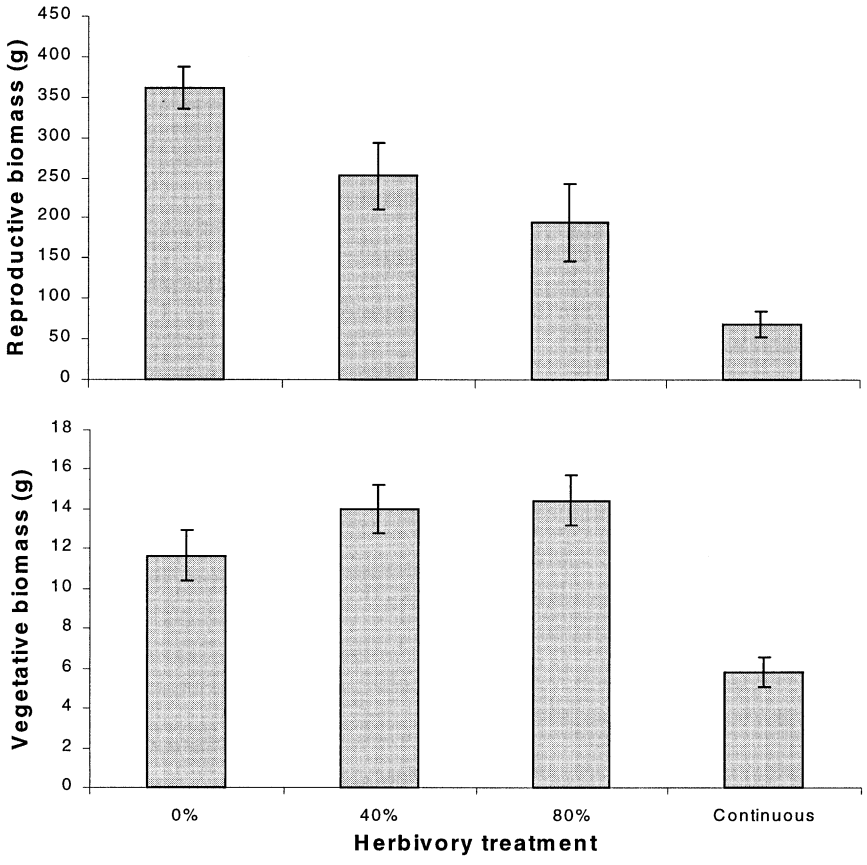

Fig. 2 Effect of during-flowering herbivory on reproductive biomass (*upper graph*) and vegetative biomass (*lower graph*), for four herbivory treatments (mean ± SE). Each data point represents 11 plants (80%, continuous herbivory) or 12 plants (0%, 40% herbivory)

Table 1 Analyses of variance for effect of pre-flowering herbivory on chlorophyll fluorescence variables,1 and 3 weeks after treatment. The factors "Leaf" (treated leaf versus leaf produced after treatment) and "Time" (morning or afternoon measurements) were included where relevant

	F_v/F_m				ETR				NPQ (log)			
	df	MS	*F*-ratio	*P*	*df*	MS	*F*-ratio	P	*df*	MS	*F*-ratio	*P*
One week after treatment												
Block	2	3×10^{-5}	0.26	0.77	2	111,53.9	31.1	**<0.001**	2	0.81	29.61	**<0.001**
Herbivory	2	0.0007	6.6	**0.003**	2	62.59	0.17	0.84	2	0.14	4.98	**0.008**
Leaf	1	0.005	45.8	**<0.001**	1	5,874	16.38	**<0.001**	1	0.66	23.99	**<0.001**
Time	–	–	–	–	1	164	0.14	0.74	1	0.5	18.34	**<0.001**
Herb×Leaf	2	2×10^{-5}	0.23	0.8	2	2,012	5.61	**0.005**	2	0.003	0.1	0.9
Block×Time	–	–	–	–	2	1,181	3.29	**0.04**	–	–	–	–
Error	64	0.0001			133	358			135	0.027		
Three weeks after treatment												
Block	2	0.0002	2.46	0.09	2	282	0.51	0.6	2	1.03	37.29	**<0.001**
Herbivory	2	0.00002	0.31	0.74	2	2,307	4.16	**0.02**	2	0.0008	0.03	0.97
Leaf	1	0.00005	0.82	0.37	1	34,708	62.57	**<0.001**	1	0.14	4.9	**0.03**
Time	–	–	–	–	1	2,418	4.36	**0.04**	1	0.78	0.86	0.45
Herb×Leaf	2	0.0002	3.61	**0.03**	2	2,401	4.33	**0.02**	2	0.04	1.57	0.21
Block×Time	–	–	–	–	–	–	–	–	2	0.9	32.65	**<0.001**
Error	63	0.00006			135	555			133	0.03		

Three weeks after the pre-flowering herbivory had finished, there were no differences between plants of the three treatments in either height or estimated leaf area (P=0.93 and 0.43 respectively). At harvest, there were no significant differences between plants in the different treatments in either total biomass (P=0.39), or in the allocation of biomass to roots, stems, leaves or fruit (results not shown). This indicates that plants in both the 40% and 80% herbivory treatments were able to compensate for pre-flowering herbivory, in terms of biomass and fruit production, within 6 weeks of the herbivory event.

One week after herbivory, F_v/F_m was significantly higher for the plants in the 80% and 40% herbivory treatments than the plants in the 0% herbivory treatment, indicating that damaged plants had a higher photosynthetic efficiency in both leaves measured (Fig. 1 a, Table 1). Three weeks after herbivory, this higher photosynthetic efficiency in herbivore-damaged plants was still apparent in the leaves produced after treatment. However, the treated leaves of plants in the 40% and 80% herbivory treatments had a slightly lower photosynthetic efficiency than plants in the 0% herbivory treatment (Fig. 1b, Table 1).

Herbivory had differential effects on the ETR of the treated leaves and leaves produced after treatment. After 1 week, ETR was significantly lower in the treated leaves of the plants in the 80% herbivory treatment than those of plants in the 0% herbivory treatment. However, the ETR of the leaves produced after treatment was higher (although not significantly so) for plants in both the 40% and 80% herbivory treatments (Fig. 1c, Table 1). The differences in ETR were still apparent 3 weeks after the herbivory finished. ETR was significantly lower in the treated leaves of both herbivory treatments than the 0% herbivory treatment, but the ETR of the leaves produced after treatment was the same across all treatments (Fig. 1d, Table 1). The changes in F_v/F_m and ETR in herbivore damaged plants indicate that plants affected by herbivory decrease the use of their damaged leaves, while maintaining or increasing photosynthesis in their new leaves.

The increases in photosynthetic efficiency and capacity in herbivore damaged plants were accompanied by decreases in NPQ. NPQ was significantly lower for plants in the 80% herbivory treatment than for plants in the 0% herbivory treatment. This difference occurred in both treated leaves, and leaves produced after treatment, 1 week after herbivory, but was not detected 3 weeks after herbivory (Fig. 1e, f, Table 1). This suggests that damaged plants reduced the amount of light energy being dissipated as heat, which probably resulted in more light used for photosynthesis.

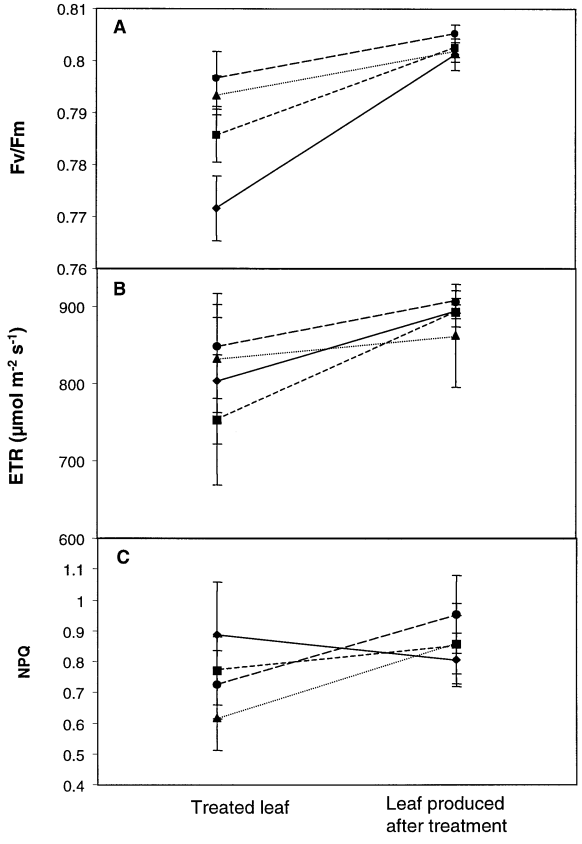

Fig. 3 Effect of during-flowering herbivory on chlorophyll fluorescence variables, measured 1 week after herbivory: F_v/F_m (**a**), ETR (**b**), and NPQ (**c**). Mean (± SE) for all treatments on treated leaves and leaves produced after treatment. Zero herbivory 40% and 80% herbivory as in Fig. 1; continuous herbivory, *circles and dashed line*. Each data point represents 11 plants (80%, continuous herbivory) or 12 plants (0%, 40% herbivory)

Effects of herbivory during flowering

Before the herbivory treatments were applied, there were no significant differences between plants in different treatments in any of the growth or fluorescence variables except F_v/F_m. F_v/F_m was significantly higher in the plants in the 40% herbivory treatment than the plants in the 80% treatment before the herbivory experiment started

Table 2 Analyses of variance for effect of during-flowering herbivory on chlorophyll fluorescence variables one week after treatment. The factors "Leaf" (treated leaf versus leaf produced after treatment) and "Time" (morning or afternoon measurements) were included where relevant

	F_v/F_m				ETR				NPQ (log)			
	Df	MS	*F*-ratio	*P*	*df*	MS	*F*-ratio	*P*	*df*	MS	*F*-ratio	*P*
Block	2	0.004	46.47	**<0.001**	2	2,932	11.68	**<0.001**	2	4.55	76.98	**<0.001**
Herbivory	3	0.0008	3.22	0.1	3	1,933	7.7	**<0.001**	3	0.08	1.3	0.28
Leaf	1	0.006	12.03	0.07	1	20,975	83.52	**<0.001**	1	0.32	5.45	**0.02**
Herb×Leaf	3	0.0006	7.48	**0.0002**	3	1,060	4.22	**0.008**	3	0.13	2.24	0.09
Herb×Blk	6	0.0003	3.51	**0.004**	–	–	–	–	–	–	–	–
Leaf×Blk	2	0.0005	6.63	**0.002**	–	–	–	–	–	–	–	–
Error	74	0.0001			82	251			82	0.06		

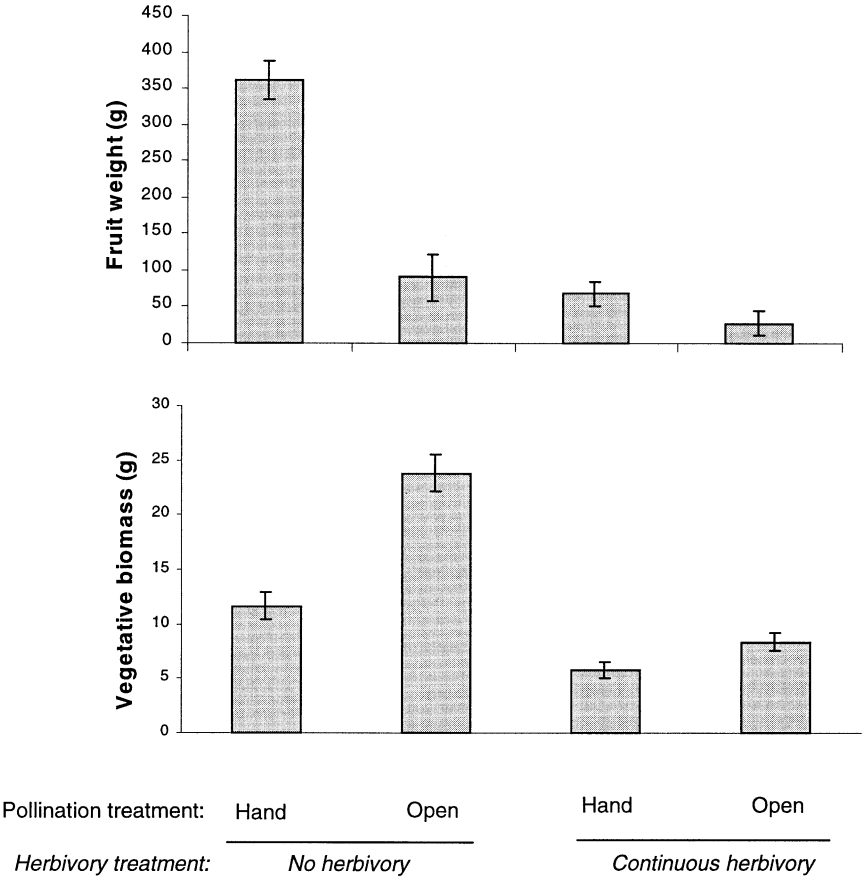

Fig. 4 Effect of pollination (hand vs open) and herbivory (continuous vs none) on reproductive biomass (*upper graph*) and vegetative biomass (*lower graph*) (mean ± SE). Each data point represents 11 plants (continuous herbivory, hand pollination) or 12 plants (other treatments)

(P=0.03). The 'before herbivory' measurements of F_v/F_m were not included as covariates in subsequent ANOVAs, as their inclusion made no difference to the outcome of any analysis.

One week after the herbivory had finished, both plant height and estimated leaf area were significantly lower for plants in the continuous herbivory treatment than for plants in the other three treatments (P=0.02 and P<0.001 respectively). At harvest, total vegetative biomass was significantly lower for plants in the continuous herbivory treatment than for plants in the other treatments (Fig. 2, P<0.001). Vegetative biomass was slightly (but not significantly) higher for plants in the 40% and 80% herbivory treatments than for plants in the 0% herbivory treatment. The average total fruit weight per plant declined with increasing herbivory levels (Fig. 2, P<0.001), indicating that plants suffering 40% and 80% herbivory were able to compensate in terms of vegetative biomass, but not fruit biomass. The relative allocation of biomass to roots, stems and leaves did not differ between plants in different herbivory treatments (results not shown).

In contrast to the pre-flowering herbivory experiment, plants suffering herbivory later in their life cycle increased photosynthesis in the damaged leaves, rather than in the new leaves. After herbivory, photosynthetic efficiency (F_v/F_m) was significantly higher in the treated leaves of plants in the 40%, 80% and continuous herbivory treatments than of the 0% herbivory plants (Fig. 3a, Table 2). ETR was also significantly higher in the treated leaves of plants in the continuous herbivory treatment than for plants in all other treatments (Fig. 3b, Table 2). There were no differences between treatments in F_v/F_m or ETR in the leaves produced after treatment. Increases in photosynthetic efficiency and capacity in herbivore damaged plants were associated with small reductions in NPQ. NPQ was lower in the treated leaves of the plants in all herbivory treatments, compared to plants in the 0% herbivory treatment (Fig. 3c), however, the reduction was only significant for plants in the 80% herbivory treatment (Table 2).

At the time of harvest, plants that had supplemental hand pollination produced significantly more fruit, and less vegetative biomass than open pollinated plants, regardless of herbivory level (Fig. 4, P=0.001 and P<0.001 respectively). Photosynthetic efficiency (F_v/F_m) was significantly higher for open pollinated plants than for pollen supplemented plants (P=0.009), but the interaction between pollination system and herbivory was not significant (P=0.15, Fig. 5a). There were no significant differences in ETR or NPQ between supplemented and open pollinated plants (Fig. 5b, c, P=0.18 and 0.32 respectively).

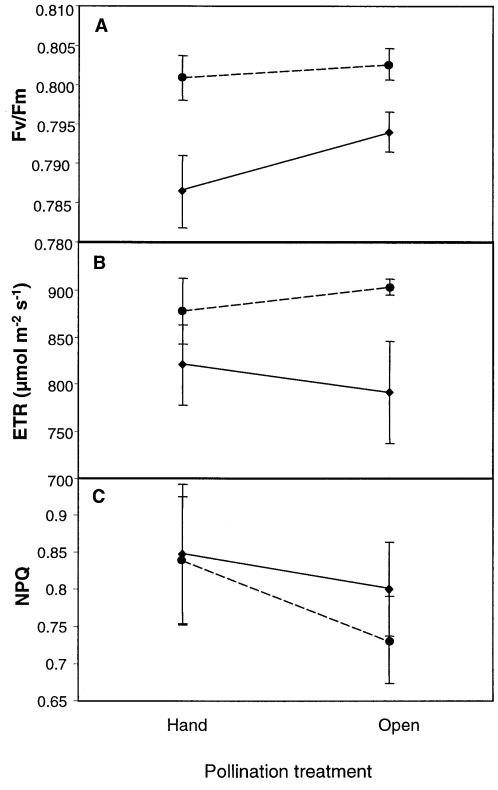

Fig. 5 Effect of pollination on chlorophyll fluorescence variables, 1 week after herbivory in the continuous (*diamonds and solid line*) and zero herbivory (circles and dashed line) treatments. F_v/F_m (**a**), ETR (**b**), and NPQ (**c**). Mean (± SE) for treated leaves. Each data point represents 11 plants (continuous herbivory, hand pollination) or 12 plants (other treatments)

Discussion

Cucumis sativus plants that were subject to a single herbivory event were able to compensate for herbivore damage, in terms of vegetative and/or reproductive biomass. These plants compensated by increasing their photosynthetic efficiency and capacity, and by using a higher proportion of the absorbed light energy for photosynthesis.

Plants that were subject to pre-flowering herbivory were able to compensate within 3 weeks for up to 80% loss in leaf area due to a once-off herbivory event. Plants that were subject to herbivory during the flowering period were able to maintain their vegetative growth, but not their fruit production. It may be more difficult for plants to compensate for later herbivory because there is less time to recover before reproduction, or because there are physiological changes within the plant over its life cycle which may limit its ability to compensate (Maschinski and Whitham 1989; Lehtila and Syrjänen 1995; Scarré et al. 1996; Lennartsson et al. 1998). The plants of the two experiments also differed in the way in which they compensated. Plants suffering from pre-flowering herbivory increased the photosynthetic efficiency and capacity in the uneaten leaves that were produced after herbivory. In contrast, plants suffering from herbivory during flowering up-regulated photosynthetic capacity and efficiency in the older leaves that had been partially eaten.

The level of pollination received by the plants (open pollination vs pollen supplementation) changed both plant growth and photosynthesis, but did not alter the way in which plants compensate for herbivory. Hand pollen supplementation resulted in higher fruit weight, but a lower vegetative biomass, for plants subject to both continuous herbivory, and no herbivory. Hand pollen supplementation also resulted in a lower photosynthetic efficiency, although the difference between herbivore damaged and undamaged plants was unchanged.

This study illustrates that compensation to herbivory may occur through alteration of the source-sink relationships within a plant, as leaf loss due to herbivory results in a higher demand for carbon from the remaining leaves. Additionally, herbivory shifts the balance between above and below ground resource uptake, resulting in greater nutrients and water available per unit area of remaining source leaf. These relative increases in carbon demand and water and nutrient availability induced plants to use their absorbed light more efficiently, as indicated by the decrease in NPQ, or energy lost as heat, in the leaves of herbivore-damaged plants. A decrease in heat dissipation may lead to increased photosynthetic rate, as was demonstrated by the increases in both photosynthetic efficiency and capacity in the herbivore-damaged plants of both experiments. While the differences in photosynthetic efficiency were small, these differences can compound in time to make a substantial contribution to differences in photosynthetic activity, and hence carbon gain.

Compensation to herbivory, by the mechanism described above, is only possible if *C. sativus* plants were photosynthesising at a rate below their potential in herbivore-free conditions. We propose two possible reasons why this may occur: as an adaptation to an environment where levels of herbivory are predictably high, or as an adaptation to maximise light capture in a light-limiting environment.

Plants that grow in environments where high levels of herbivory are normal may evolve compensatory mechanisms as a way to maximise fitness in these environments. Whilst a non-compensating plant may have higher fitness than a compensating plant when no herbivory is present, when herbivory is constantly high, the non-compensating plant would suffer reduced fitness, whereas the compensating plant would maintain its fitness. This idea is supported by numerous studies that have found compensating and overcompensating species in environments, such as grasslands, which are renowned for predictably high herbivory (Paige and Whitham 1987; Alward and Joern 1993; Wallace and Macko 1993; Hicks and Reader 1995). Some authors have suggested that herbivory may act as a cue for the start of reproduction in some plants, and that these plants reserve the majority of their resources until the herbivory event has passed (Nilsson et al. 1996; Simons and Johnston 1999).

Compensation for herbivory may be a physiological consequence of adaptations to competition for light, rather than an adaptation to herbivory itself (Jãremo et al. 1996; Simons and Johnston 1999). For plants grown in a light limited environment, the heat dissipation of light energy would be minimal, and it is unlikely that the plants would be able to compensate for herbivory. The potential importance of the light environment to the pattern of compensation is well illustrated by Mabry and Wayne (1997), who found that *Abutilon theophrasti* was able to compensate for 75% defoliation when grown in the absence of stem competition, but unable to compensate when grown under light competition. Also, Marquis (1984) demonstrated plant fitness reductions after only a small amount of leaf herbivory to *Piper arieanum*, a deep understorey shrub that is known for its adaptation to low-light environments (Chazdon and Kaufman 1993). Plants that are unable to compensate for herbivory are rare in temperate grasslands (a high light environment); in contrast, plants that are able to compensate are abundant in these areas (Hulme 1996). *Cucumis sativus* is a cultivated plant, so its natural environment is difficult to determine. However, many non-cultivated members of the Cucurbitaceae are understorey plants in tropical or sub-tropical areas (Harden 2000). It is possible that plasticity in use of heat dissipation in cucumber plants evolved in a light-limited environment as a mechanism to maximise light capture, rather than as a mechanism for compensation to herbivory. The high light conditions of the glasshouse experiments may have resulted in a greater degree of compensation than would be observed in a natural environment.

This paper has described two experiments that examined the effects of herbivory on the compensatory growth of *C. sativus* plants. Compensatory responses differed with the amount, timing and mode of herbivory. Regardless of specifics, herbivory resulted in increased photosynthetic capacity and efficiency, stimulating compensatory growth. We propose that increased photosynthesis is due to altered source-sink relationships, which induced the damaged plants to use absorbed light more efficiently. Compensation to herbivory, in this case, may have evolved as consequence of adaptation to a low light environment.

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