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Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass

Abstract Environmental stresses affect plant growth and performance in nature. Host plant quality in turn affects herbivore performance and population dynamics. In view of these interactions, two major hypotheses were formulated. The plant stress hypothesis proposes that physiologically stressed plants become more susceptible to herbivores. The plant vigour hypothesis proposes that plants that grow vigorously are favourable to herbivores. Here we test the plant stress/plant vigour hypotheses for a leaf miner, *Agromyza nigripes* (Diptera; Agromyzidae), on the grass *Holcus lanatus*. We assessed larval performance (survival, developmental time, pupal mass) on grasses growing under different levels of nutrients (Hoagland solution) and drought stress, under controlled field and greenhouse conditions. Plant vigour and nutrient content were high on soils with an intermediate nutrient concentration and lower under drought stress and soil nutrient shortage and overdose. Larval performance was also highest on wet soils with intermediate nutrient supply. The results of the mining flies support the plant vigour hypothesis (density, survival and development better on vigorous plants). Herbivore performance is higher on leaves with a higher protein content.

Keywords Environmental stress · Plant vigour · Nutritional quality · Soluble proteins · Agromyzidae

Introduction

Environmental stresses such as water deficit, or nutrient imbalances, affect plant physiology, development and performance. Host plant quality in turn affects herbivore performance and population dynamics. In view of these interactions, two major hypotheses were formulated.

The plant stress hypothesis postulates that stressed plants become more susceptible to herbivores (e.g. White 1974, 1984; Mattson and Haack 1987a). Although the underlying mechanisms were not tested in most studies, proposed explanations imply direct effects through improved nutrient quality and/or reduced chemical defence (e.g. White 1974, 1984, 1993; Rhoades 1983; Waring and Pitman 1985) and indirect effect through reduced efficiency of natural enemies (e.g. Hanski 1990; Kytö et al. 1996). Important to notice is the time scale on which the stress component operates. Under the plant stress hypothesis it is assumed to be a temporary state, following a normal situation (Larsson 1989; White 1993).

More recently, the plant vigour hypothesis was developed which postulates that plants, or plant modules, that grow vigorously are favourable to herbivores (e.g. Craig et al. 1986; Price et al. 1987; Preszler and Price 1988). Plant vigour was defined as "any plant or plant module that grows rapidly and ultimately reaches a large size relative to the mean of the population" (Price 1991). Several plant-herbivore systems supported the plant vigour hypothesis (reviewed in Price 1991). However, currently there are insufficient data available on the kinetics of plant chemical responses to plant vigour and how this influences herbivore performance.

The present study examines the effects of environmental stress (soil nutrient stress and drought stress) on the interactions between the leaf miner, *Agromyza nigripes* Meigen (Diptera; Agromyzidae), and one of its common hosts, Yorkshire-fog, *Holcus lanatus* L. (Poaceae).

H. lanatus is a perennial, 30–100 cm tall, tufted grass. It is very common, growing in all kinds of grasslands, open woods, roadsides and waste ground. Optimal growth occurs in moist conditions; it grows well in very wet conditions and can survive moderate periods of drought (Watt 1978). *H. lanatus* occurs on soils of moderate to low fertility, but fertilisation appears to improve its competitive ability (Remison and Snaydon 1980).

A. nigripes is an oligophagous miner that infests grasses from the tribes Glycerieae, Aveneae and Agrosteaea (Spencer 1990). Its commonest food plants are *Glyceria maxima* and *Holcus* spp.

We tested whether the *H. lanatus-A. nigripes* system supports the plant vigour hypothesis or the plant stress hypothesis; more particularly: (1) is larval performance higher on vigorous than on stressed grasses, and (2) is there a relationship between host vigour and nutritional leaf quality?

Earlier studies indicated that stress-induced effects in plants, and their effects on insect survival and development, might be non-linear (Mattson and Haack 1987b; English-Loeb 1989; Koricheva et al. 1998). Because *H. lanatus* normally occurs on soils of moderate to low fertility (Remison and Snaydon 1980) we suspected that the plants of high nutrient treatments are possibly subjected to a stress situation due to a nutrient overdose. Therefore we formulated two specific hypotheses about the treatments a priori.

1. Linear: this first model predicts a linear relationship between the nutrient concentration and the measured performance, i.e. they do better when the nutrient concentration increases.
2. Quadratic: this second model predicts that performance will be reduced (stressed) at low and high nutrient levels, and performance is highest at the intermediate concentration.

Materials and methods

Experiments were carried out in a greenhouse. The host plant was sown from commercially available *H. lanatus* seeds in plastic flowerpots (17 cm diameter, 15 cm height), on a soil mixture (1:1) of white sand and vermiculite. These pots received 300 ml of a 50% concentration of a standard Hoagland solution (Hoagland; Hoagland and Arnon 1950) at weekly intervals. They were further daily watered to saturation. After 3 months, when the grasses were large enough to start the experiments we applied four nutrient concentrations (weekly 300 ml); viz. high (100%) Hoagland, medium (50%) Hoagland, low (25%) Hoagland and no (0%) Hoagland (nutrient stress). In the fifth treatment, the grasses received 300 ml of 50% Hoagland, but no additional water during the rest of the week (drought stress).

After 3 weeks, when the soils had adjusted to the new nutrient concentrations, 15 flowerpots (three pots of each treatment) were placed in a randomised block design in a flight cage (150 cm wide; 260 cm long; 105 cm high). Twenty female flies were hand collected with an aspirator, in a natural *H. lanatus* field at Wuustwezel, Belgium, and were released in the cage to allow oviposition. Exposure time was restricted to 2 days. This allowed us to estimate larval developmental time fairly accurately, and kept female and larval densities low to avoid intraspecific competition. Afterwards, the flowerpots were transferred from the flight cage to separate rearing cages (100 cm diameter; 62 cm high) to analyse larval survival and development, and final pupation. During the experiment, the grasses were exposed to the different nutrient treatments for a relatively short time (about 2 weeks), after a long period of development (3 months) of normal conditions, as assumed by the plant stress hypothesis (Larsson 1989; White 1993).

The same experimental setup was used in a field experiment. Here the 15 pots were placed (randomised block design) in the same natural *H. lanatus* field where the flies for the greenhouse experiment were collected. The experimental plot was sheltered (height ±2 m) with a transparent plastic sheet to prevent rain entering the treatments. The grasses were exposed to ovipositing females for 1 week. Then the pots were transported to the greenhouse in separate rearing cages to analyse larval survival and final pupation.

Larval performance was estimated by larval mortality and pupal mass (Cahn electrobalance model 4100) in the field and the greenhouse. In the greenhouse experiment we also measured larval developmental time (days between oviposition and pupation). As a measure of plant vigour, we measured leaf size (portable leaf area meter, type Lamde LI-3000) in the different treatments ($n=30$/treatment). To assess plant nutritional quality, the grass leaves were chemically analysed. The leaves ($n=10$/treatment) were first lyophilised. Total soluble protein and sugar content were analysed by the Bradford method (Bradford 1976) and anthrone method (Snell et al. 1981), respectively. Water content of the tissues ($n=30$/treatment) was obtained by measuring fresh and oven-dry mass on a microbalance. Grass characteristics were measured on leaves from unparasitised pots to exclude possible influences of the herbivore on the development of the host plant.

The influence of soil nutrient stress was compared between the four (300 ml) Hoagland treatments (none, low, medium and high). The influence of drought stress was compared between the medium treatment (300 ml of 50% Hoagland+additional water to saturation) and the low water treatment (300 ml of 50% Hoagland, no additional water).

Differences among treatments were analysed with one-way (leaf size and water content, larval developmental time), two-way (pupal mass) and multiple (leaf protein/sugar content) ANOVA (Sokal and Rohlf 1995; Neter et al. 1996) (ANOVA/MANOVA module of STATISTICA 5.1; Statsoft 1998). Common procedures for model testing and verification showed that the raw, untransformed data met the requirements for usage in normal ANOVA models (Neter et al. 1996).

The a priori formulated hypotheses on the influence of nutrient stress on performance were tested with planned comparisons of the means (Day and Quinn 1989). Therefore, we applied two single *df* orthogonal contrasts (linear and quadratic contrasts). Calculations of the orthogonal contrast coefficients for unequal intervals and unequal sample size were according to Kirk (1982).

Larval survival probability was assessed using a logistic regression model (proc LOGISTIC; SAS 1989). A backward stepwise variable selection was applied to obtain the minimal adequate model (Crawley 1993). The variable "experiment" was entered as a two-level factor (field versus greenhouse).

Results

Plant vigour (Fig. 1) was clearly different among the different nutrient treatments. The linear contrast was highly significant ($F_{1,117}=25.993$; $P<0.001$) while the quadratic contrast was just not significant ($F_{1,117}=3.237$, $P=0.074$). When nutrient supply increased in the treatments, the leaves grew larger. In the high nutrient treatment, mean leaf size was only slightly higher than in the medium treatment, suggesting a plateau had been reached around this point. Grasses growing on dry soils also had smaller leaves than grasses on wet soils ($F_{1,58}=25.756$, $P<0.001$).

In the greenhouse, 78 mines yielded 74 pupae (94.87%) while in the field experiment 22 pupae were found in 36 mines (61.11%) suggesting a different mortality between the two experiments. Because the no-Hoagland treatment only produced one mine in the field experiment and none in the greenhouse, this treatment was not included in the logistic analysis. For the three remaining Hoagland treatments, there was no significant
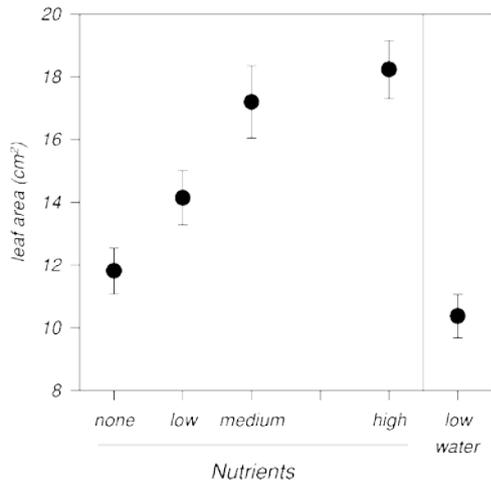
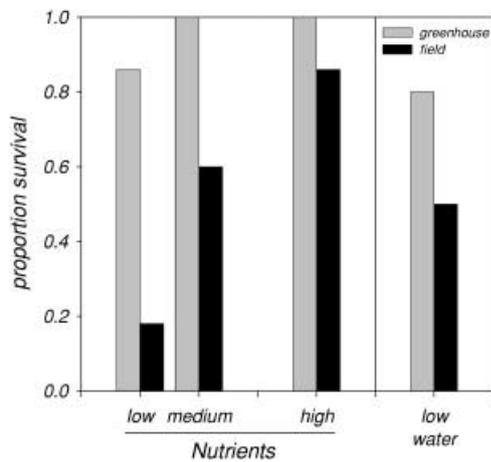**Fig. 1** Plant vigour (leaf area) under different soil nutrient/water treatments (mean±SE)

Fig. 2 Larval survival under different soil nutrient/water treatments

Fig. 3 Larval developmental time. *Upper graph*: cumulative number pupated. *Lower graph*: mean (±SE) pupation date. Oviposition on 30, 31 July. *Aug* August

Fig. 4 Mean (±SE) pupal mass under different soil nutrient/water treatments

difference in the general mortality pattern between the two experiments (stress×experiment interaction $\chi^2=1.59$; $df=1$; $P=0.207$). As indicated by the overall percentage of surviving larvae, there was significantly higher mortality in the field experiment (experiment $\chi^2=24.90$; $df=1$; $P<0.001$). In both situations, larval survival was higher when the nutrient concentration in the soil treatments increased (Fig. 2, ($\chi^2=13.63$; $df=1$; $P<0.001$). In the greenhouse, all larvae in the 50% and 100% Hoagland treatments survived.

The larval survival analysis for high and low water treatments gave approximately the same results as the nutrient treatments (Fig. 2). There was no stress×experiment interaction ($\chi^2=1.93$; $df=1$; $P=0.167$). Mortality in the field and the greenhouse experiments were comparable ($\chi^2=3.22$; $df=1$; $P=0.073$). Finally, larvae from the high water treatment had a higher survival probability than those from the low water treatment ($\chi^2=5.70$; $df=1$; $P=0.017$).
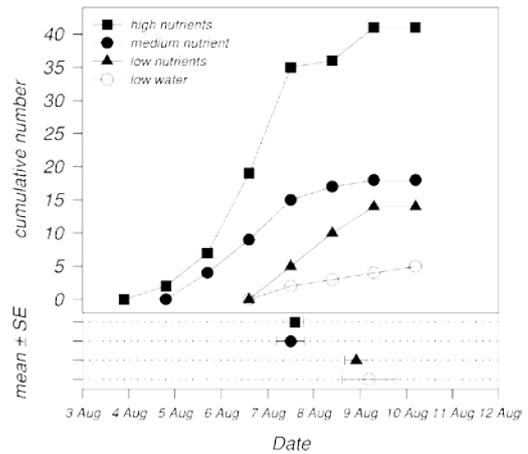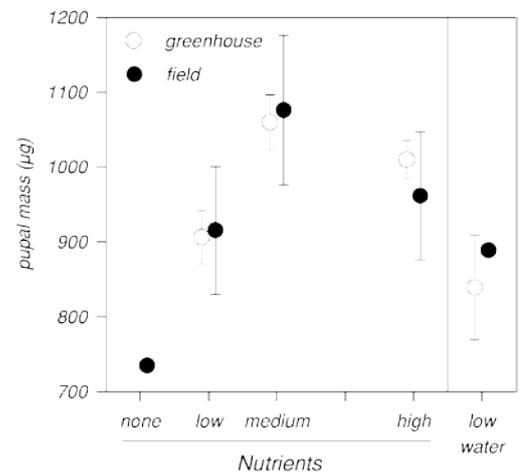
Pupae emerged first in the high Hoagland (5 August), and 1 day later in the medium treatments (Fig. 3, upper graph). Pupae from the low Hoagland and low water treatment emerged 2 days later. Both the linear ($F_{1,70}=9.020$, $P=0.004$) and the quadratic contrast ($F_{1,70}=10.308$, $P=0.002$) showed a significant difference. This means that, in general, larvae of the higher Hoagland treatments developed much faster than those in the lower nutrient treatments, while on average developmental time was shortest in the medium Hoagland treatment. The pupae from the drought-stress treatment also emerged significantly later than those from the non-stressed grasses ($F_{1,21}=8.105$, $P=0.010$).

For the nutrient treatments, there was no difference in pupal mass (Fig. 4) between field and greenhouse grown pupae ($F_{1,82}=0.017$, $P=0.896$), nor was there a significant interaction with nutrient level ($F_{2,82}=0.195$, $P=0.823$). Therefore, we combined the field and greenhouse experiment data to carry out the planned compari-
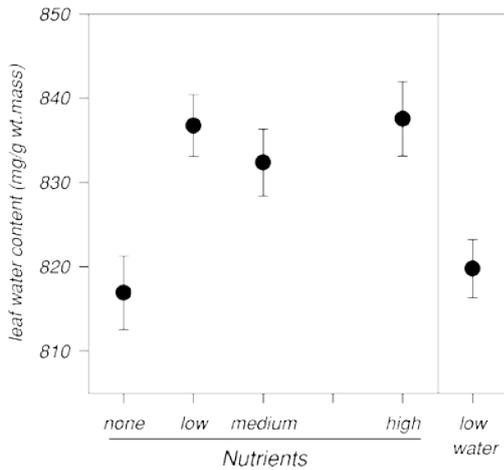
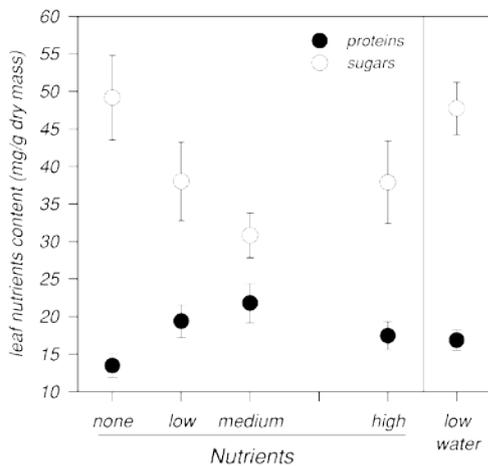**Fig. 5** Mean (±SE) water content of the grass leaves under different soil nutrient/water treatments

Fig. 6 Mean (±SE) soluble protein and sugar content of the grass leaves under different soil nutrient/water treatments

sons. The linear planned comparison tests reveals no significant difference between the treatments ($F_{1,85}=1.145$, $P=0.288$). The quadratic contrast on the contrary is highly significant ($F_{1,85}=7.482$, $P=0.008$). The pupae from the medium nutrient treatment were significantly heavier than those from the other treatments. The two-way ANOVA for the drought-stress experiment also shows no differences in pupal mass in the field and in the greenhouse ($F_{1,28}=0.071$, $P=0.792$) and no experiment×drought interaction ($F_{1,28}=0.018$, $P=0.894$). Again we could combine the field and greenhouse data to estimate the effect of drought stress. The pupae from the drought-stressed grasses were significantly lighter than those from unstressed grasses ($F_{1,30}=4.846$, $P=0.035$) (Fig. 4).

According to the linear contrast ($F_{1,116}=9.495$, $P=0.003$) there is a significant linear relationship between the Hoagland concentration and the water content of the leaves. A closer examination of Fig. 5 indicates that the latter is mainly due to the low water content of

the no-Hoagland treatment. The quadratic contrast gives no significant result ($F_{1,116}=9.587$, $P=0.445$). The water content in the low water treatment was slightly, but significantly, lower than in the high water treatment ($F_{1,58}=4.105$, $P=0.047$).

Leaf soluble protein and sugar (Fig. 6) content was measured simultaneously on the same leaves and could therefore be analysed in a MANOVA design. The multivariate statistic of the quadratic planned comparison is highly significant (Wilks' $\lambda_{2,29}=0.637$, $P=0.001$) while the linear contrast is not (Wilks' $\lambda_{2,29}=0.844$, $P=0.085$). The univariate quadratic ANOVAs of the individual factors also show a clear difference between the nutrient treatments (sugars, $F_{1,30}=5.496$, $P=0.026$, proteins, $F_{1,30}=6.343$, $P=0.017$). The soluble protein content was highest in the medium Hoagland treatment and decreased at both higher and lower Hoagland concentrations. The sugar content showed the opposite relationship. Drought-stressed grasses were significantly different from non-stressed grasses (Wilks' $\lambda_{2,17}=0.545$, $P=0.006$). The latter was mainly due to a higher sugar content ($F_{1,18}=13.823$, $P=0.002$) in the stressed grasses. Although the protein content was lower in the drought-stressed grasses, this difference was not significant ($F_{1,18}=2.758$, $P=0.114$).

Overall, protein content of the leaves in the different treatments was positively correlated with pupal mass (Pearson $r=0.86$, $n=9$, $P=0.003$) and negatively correlated with developmental time ($r=-0.92$, $n=4$, $P=0.08$). There was no relationship with survival ($r=-0.01$, $n=8$, $P=0.97$).

Discussion

The host plant, *H. lanatus,* reacts in different ways to the imposed nutritional stresses (including drought). Leaf size (plant vigour) increased with Hoagland concentration. However, the curve levelled off at 100% Hoagland, suggesting that a plateau phase had been reached. Analogous results were found for ryegrass and barley where leaf growth (leaf size and dry weight) increased with increasing application of fertiliser, but eventually levelled off (leaf size) or even declined (dry weight) at higher fertiliser levels (Wilman and Wright 1983; Tisdale et al. 1984).

In this study, we used plant vigour as defined by Price (1991) in his plant vigour hypothesis, i.e. "a plant module that grows rapidly and ultimately reaches a large size relative to the mean of the population". Although net leaf production is not an absolute measure of plant fitness, it is generally accepted as an indicator of plant vigour and reproductive success. It is often found that when plants are subjected to drought and other stresses, growth rate is negatively affected before other physiological parameters such as photosynthesis (e.g. Chapin 1991). It is interesting to note that the chemical composition of the *H. lanatus* leaves changes earlier than growth reduction, which might indicate that in our species

changes in chemical composition are more sensitive for the detection of even subtle stress effects.

Under severe nutrient stress (no nutrients) and drought stress, *A. nigripes* development is weak; practically no pupae emerge, and the larvae that survive grow slowly, resulting in small pupae. When the soil nutrient supply rises, more larvae survive up to pupation. They also grow faster and become heavier. However, when the soil nutrient supply gets too high (100% Hoagland), larval developmental time increases again and final pupal mass is smaller. Non-linear responses to abiotic stresses of plants and their herbivores are probably very common in nature (Mattson and Haack 1987b; English-Loeb 1989; Raispere 1990; Koricheva et al. 1998). However, because only few studies apply multiple stress levels in their experiments, this pattern remains generally undetected. Because larval performance in our study was highest on the intermediate Hoagland concentration, where plant vigour was highest, we can state that the studied *H. lanatus-A. nigripes* system supports the plant vigour hypothesis.

In general, soluble nitrogen plays an important role because plants usually contain less nitrogen than is optimal for herbivorous insects (Mattson 1980; Strong et al. 1984a, 1984b; Bernays and Chapman 1994). This can explain, why during our study, *A. nigripes* larval performance was highest on the grasses with the highest protein content. That the soluble nitrogen level drops under nutrient stress and does not change under drought stress seems to contradict the direct effect of the plant stress hypothesis which assumes that levels should increase under stress conditions, at least under drought stress (e.g. White 1984; Mattson and Haack 1987a). Because nitrogen metabolism is among the processes most sensitive to water deficit it is possible that the soluble proteins are broken further down to the basic amino acids. However, previous studies with mineral fertilisers also showed that the increase in the total N content of the plant decreases at high fertiliser levels (Whitehead 1995). Moreover, when the supply of nitrogen exceeds the requirements for growth, it is stored as nitrate (up to >60% in ryegrass and timothy swards). Our observation might possibly be more widely applicable. In a general review, Waring and Cobb (1992) already reported that herbaceous plant can respond differently to environmental stress than trees and shrubs.

Former studies on the influence of nutrient stress on plant-insect interactions produced contradictory results. A major cause for these inconsistent results can be found in the experimental approaches used in the different studies. Many studies investigated natural environmental variation (e.g. Caouette and Price 1989; Lightfoot and Whitford 1989; Waring and Price 1990). Others manipulated nutrient supply by adding extra fertilisers (e.g. Prestidge 1982a, 1982b; Loader and Damman 1991; Spike and Tollefson 1991; Meyer and Root 1996), by root trenching (e.g. Tisdale and Wagner 1991) or by applying different nutrient mixtures (e.g. Horner and Abrahamson 1992). The relationships are not simple. They first depend on the response of the plant species to the stress implied, and secondly to the ability of the herbivore to take advantage of changes in host plant chemistry. Because the conclusions of most studies were solely based on the experimental setup and failed to test the nutritional composition of the host plant tissues, it is not always clear which range of the plants' response curves to environmental conditions is tested. Therefore, it is important to test a wide range of environmental conditions to include the host plants' optimum, as well as stress situations due to a shortage and overdose of the applied stress factor. Moreover, it is necessary to measure plant performance, nutritional quality of the digested tissues and herbivore performance simultaneously to make a profound interpretation possible.

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