Aphid fitness on 13 grass species: a test of plant defence theory

Lauchlan H. Fraser and J. Philip Grime

Abstract: The growth rate hypothesis, which states that fast-growing plants support more herbivores than slow-growing plants, was tested with 12 native and 1 naturalized British grasses using the grain aphid (*Sitobion avenae*). Five aphids were enclosed with grasses for two weeks in a growth chamber. After 2 weeks, fast-growing plants had 38 aphids, whilst slow-growing plants had 6, which supports the growth-rate hypothesis. When aphid numbers were analysed on plants according to "CSR" theory (Grime 1977, 1979), ruderals (R) had 54, competitors (C) had 18, and stress tolerators (S) had 6. This supports the predictions of CSR theory. Furthermore, aphid numbers increased significantly with grass growth rates and a mollusc palatability index, although this largely resulted from a single outlier, *Poa annua*. Aphid number was not affected by hairs on grasses. Finally, the effect of aphid feeding on grasses was tested. Generally, the greatest change in total and aboveground biomass of the grasses was found in the ruderals, whilst stress tolerators had the least amount of change.

Key words: *Sitobion avenae*, herbivory, palatability, plant–animal interactions, plant defence.

Résumé : Les auteurs ont vérifié l'hypothèse du taux de croissance qui énonce que les plantes à croissance rapide supporteraient mieux l'herbivorie que les plantes à croissance lente; il ont vérifié cette hypothèse sur 12 espèces herbacées indigènes de l'Angleterre et 1 espèce naturalisée, en utilisant le puceron des grains (*Sitobion avenae*). On a enfermé ces graminées pendant deux semaines, en chambre de croissance, en présence de cinq pucerons. Après deux semaines, les plantes à croissance rapide portaient 38 pucerons, alors que les espèces à croissance lente n'en avaient que 6, ce qui supporte l'hypothèse du taux de croissance. Lorsqu'on analyse les nombres de puceron sur les plantes selon la théorie 'CSR' (Grime 1997, 1979), les espèces rudérales en portent 54, les espèces compétitives en ont 18 et les espèces tolérantes aux stress n'en ont que 6. Ceci supporte les prédictions de la théorie 'CSR'. De plus, les nombres de pucerons augmentent significativement avec les taux de croissances des graminées ainsi qu'un indice de palatabilité pour les mollusques, bien que ceci résulte en grande partie d'un cas isolé, le *Poa annua*. Le nombre de pucerons n'est pas affecté par les pilosités des graminées. Enfin, les auteurs ont mesuré l'effet de l'aimentation des pucerons sur les graminées. En général, le plus grand changement de la biomasse totale et de la biomase épigée des graminées se retrouve chez les plantes rudérales, alors que les espèces tolérantes aux stress montrent les changements les plus faibles.

Mots clés : *Sitobion avenae*, herbivorie, palatabilité, interactions plante–animal, défence chez les végétaux.

[Traduit par la Rédaction]

Introduction

Herbivores attack and damage plants in a wide variety of ways, including boring, chewing, sucking, mining, and scraping. Plants have many different attributes that make them less attractive to herbivores (Erhlich and Raven 1964; Futuyama and Slatkin 1983) such as thorns (Janzen 1975), tissue toughness (Choong et al. 1992), and secondary metabolites (Feeny 1976; Rhoades and Cates 1976; Coley et al. 1985). A number of theories have been proposed to explain the defensive characters of plants, for example, coevolution (Erhlich and Raven 1964), plant apparency (Feeny 1976; Rhoades and Cates 1976), and the growth-rate hypothesis (Coley et al. 1985; Gulmon and Mooney 1986). Despite

some exceptions (e.g., Feeny 1991), the growth-rate hypotheses has received the most supportive evidence.

The growth-rate hypothesis proposes that fast-growing species will support more generalist herbivores than slow-growing species (Coley et al. 1985; Gulmon and Mooney 1986; Grime et al. 1996). Specifically, plants with intrinsically fast growth rates must allocate more carbon to growth and less carbon to chemical defences, thereby making a small investment in broadly effective plant defences compared with plants with intrinsically slow growth rates. This relationship may arise as a trade-off in allocation of captured resources between active foraging (fast growers) and physical defence (slow growers). A number of studies have shown a correlation with chemical composition and growth rate in a wide variety of plants (e.g., Poorter et al. 1990; Niemann et al. 1992; Poorter and Bergkotte 1992; van Arendonk and Poorter 1994) The growth-rate hypothesis has been tested on several different invertebrate herbivores (Maclean and Jensen 1985; Grime et al. 1996), but it has not been tested on sap suckers. Plants have a number of potential mechanisms to defend against aphids. Studies have shown that total phenols (Leszczynski et al. 1989, 1995) and hydroxamic

acid (Leszczynski et al. 1989; Leszczynski and Dixon 1990; Thackray et al. 1990) might be important in the resistance of plants to *Sitobion avenae* (grain aphids). Trichomes and leaf toughness have also been shown to deter aphid feeding (Levin 1973; Dixon 1985).

Grime's "CSR" plant strategy theory (Grime 1977, 1979) can also be used to explain patterns in the distribution of defence mechanisms between plants. Plant strategy theory is a mechanistic model designed to categorize plants according to the environment in which they grow. Grime recognised stress and disturbance as major evolutionary axes of specialization in plants, and defined stress as "any phenomenon which restricts plant biomass production," and disturbance as "any phenomenon that partially or totally destroys plant dry matter" (Grime 1979). Herbivory obviously falls into the category of a disturbance. A suite of traits has been shown to relate to the three main functional types of plants which emerge from Grime's triangular model: competitor (C), stress tolerator (S), and ruderal (R) (Grime 1979). In essence, ruderals are annuals with high relative growth rates, competitors are perennials with high relative growth rates, and stress tolerators are perennials with low relative growth rates (Grime and Hunt 1975; Grime 1979). This classification allows for a modification of the growth rate hypothesis by separating fast-growing plants into annuals (R) and perennials (C). The CSR theory makes different predictions on plant defense from the growth rate hypothesis by predicting that fast-growing ephemerals (ruderals) should support more herbivores than fast-growing perennials (competitors). The reasoning is that ruderals are short lived and expend most available resources on reproduction and are, therefore, highly vulnerable to herbivores, if found.

The main objective of the experiment was to test the growth-rate hypothesis and the CSR theory by an assessment of the fitness of *Sitobion avenae* on a wide range of native British grass species. The second objective was to determine the effect of aphid feeding on grass seedling growth.

Sitobion avenae are short-lived parthenogenetic and sexually reproducing aphids with extremely rapid reproductive rates (Dixon 1987; Acreman and Dixon 1989). Generally, aphids can respond very quickly to their environment and to their host plant. For example, either very low or very high temperatures (Acreman and Dixon 1989; Sengonca et al. 1994), as well as low foliar nutrient concentration (Dixon 1985, Honek 1991), inhibit reproductive rates. Furthermore, aphids can be very selective of their host plant and can spend a significant amount of time searching for a suitable site to insert their proboscis (Dixon 1985; Havlickova 1993). Factors that may impede an aphid's search for a suitable host plant include chemical deterrents, hairiness, and leaf toughness (Dixon 1985). If an aphid finds a suitable host plant that is growing in a favourable environment for the aphid, it is reasonable to assume the aphid will reproduce early and often within the limitations of the species.

Methods

Experimental design
We used 13 grass species (Table 1). Twelve are common and native to the British Isles, whilst the thirteenth, *Lagurus ovatus*, is native to the Mediterranean Region and has become naturalized in southern England (Hubbard 1984). The grass species encompassed a broad range of primary functional types (Table 1), which is important for the screening or comparative experimental approach (Grime 1993). Some species were glabrous, while others were hairy. A number of the grass species selected for this experiment had been tested in previous palatability trials (Grime et al. 1968, 1970, 1996) using *Cepaea nemoralis*, *Arianta arbustorum*, and *Helix aspersa* (land snails) and *Acheta domestica* (a cricket). *Sitobion avenae* preferentially feed on maturing seeds in nature (Heldon et al. 1994); however, they also feed on grass blades (Acreman and Dixon 1989; Robinson 1992; Caillaud et al. 1995), and seedlings have been used in many studies to assess feeding behaviour and population dynamics of *S. avenae* (e.g., Leszczynski and Dixon 1990, Robinson 1992, Givovich and Niemeyer 1995).

Available space on a plant can limit aphid density (Dixon 1985) and, therefore, could confound our comparative test of *S. avenae* fitness if grass species were of different sizes at the beginning of the experiment. Therefore, we used seedlings of about the same size. As a result, aphids were added to each grass species at slightly different times, but the difference in commencement of the aphid fitness test among grass species was ≤10 days (Table 1).

Sitobion avenae was collected from Tapton Botanical Gardens in Sheffield, England, and a population was reared from a single clone in a mixture of grasses (*Festuca rubra*, *Agropyron repens*, *Alopecurus pratensis*). Although *S. avenae* varies greatly among clones (e.g., Simon et al. 1991; Guo et al. 1996; De Barro et al. 1995; Caillaud et al. 1995), we used a single clone, because we assumed that the variation in defence among the grass species would be greater than the variation within *S. avenae* to tolerate the different possible plant defence mechanisms. Further, our object was to compare grasses, not aphid clones.

Aphid fitness was assessed in independent feeding trials with *S. avenae* using standardized methods in a growth chamber. Ten individual grasses from each species were grown to a standard biomass, approximately 0.5 g aboveground fresh mass per seedling, at which time five aphids were enclosed with each plant. Three individual grasses of each species were grown without aphids. The enclosure was a tube 200 mm high from the lip of the pot made from clear flexible plastic sheeting, with mesh (155 × 245 µm) covering the top.

Experimental procedure
Seeds from each grass species germinated in August 1995, and seedlings from each species were transplanted singly into 0.25-L pots. Each pot was filled with washed and autoclaved builder's sand. The plants were placed in a growth room at 22°C with 14 h days : 10 h nights under a combination of 400-W metal halide and 100-W tungsten bulbs (Hendry and Grime 1993). Plants were watered daily and fertilized weekly with 20 mL full Rorison's solution (1.12 mg nitrogen and 0.62 mg phosphorus). Each of the species reached the feeding trial starting weight of about 0.5 g aboveground fresh mass at marginally different times but approximately 3 months following germination. To ensure that a species was at the required starting mass, several plants were harvested and weighed before the addition of aphids. When necessary, this procedure was repeated. Once a grass species was ready for the aphid introduction, 10 plants of equal size were selected, five aphids were added to each plant, and the plant was sealed for 2 weeks. Each enclosed plant, irrespective of species, was placed in a random design within the growth chamber.

Recording aphid population growth
After 2 weeks, we counted the number of live aphids within each enclosure. Neither adults and juveniles, apterous and alate, nor the size of the aphids were differentiated. The above- and below-ground biomass of each plant was oven-dried at 80°C and weighed.

Table 1. The grass species used in the experiment.

	CSR^a	$R_{max}{}^b$ (week^{-1})	MPI^c	Hair	Age (days)
Agrostis stolonifera L.	C–R	1.48	—	No	72
Anisantha sterilis (L.) Nevski	R/C–R	—	—	Yes	77
Arrhenatherum elatius (L.) Beauv.	C	1.30	0.00	Yes	75
Brachypodium pinnatum (L.) Beauv.	S–C	1.03	0.00	Yes	80
Bromopsis erecta (Huds.) Fourr.	C–S–R/S–C	—	—	Yes	70
Catapodium rigidum (L.) C.E. Hubb.	S–R	—	—	No	75
Festuca ovina L.	S	1.00	0.00	No	75
Helictotrichon pratense (L.) Pilger	S/S–C	0.75	0.00	No	80
Holcus lanatus L.	C–S–R	2.01	6.67	Yes	70
Lagurus ovatus L.	R	—	—	Yes	75
Lolium perenne L.	C–R/C–S–R	1.30	2.67	No	72
Poa annua L.	R	2.70	34.67	No	72
Poa trivialis L.	C–S–R/C–R	1.40	12.00	No	75

Note: The table includes the primary functional types (CSR), the maximum relative growth rate (R_{max}), the mollusc palatability index (MPI), the presence or absence of hairs (Hair), and the age of the grasses (Age) since germination when aphids were introduced for each species. Nomenclature follows Hubbard (1984).

[a]Taken from Grime et al. (1988). C, competitor (fast-growing perennial); S, stress tolerator (slow-growing perennial); R, ruderal (fast-growing annual).

[b]Taken from Grime and Hunt (1975).

[c]Taken from Grime et al. (1996).

Data analysis

ANOVAs were used to determine whether aphid number varied (*i*) among grass species (*ii*) between fast- and slow-growing grasses, (*iii*) among competitors, stress-tolerators, and ruderals, and (*iv*) between plant hairiness. Tukey's honestly significant difference test was used to determine difference between the means. The delineation between competitors, stress tolerators, and ruderals was determined using Grime et al. (1988). Most species share qualities of each group, but in each case the ordination of each species is closest to one of the three primary functional classifications. For example, *Bromopsis erecta* is classified as a C–S–R/S–C, but it is most closely aligned to the stress-tolerant end of the continuum (Table 1). Fast- and slow-growing plants were separated according to both relative growth rate (<1.3/week is a slow-growing grass), and CSR classification (ruderals and competitors are fast growing, stress tolerators are slow growing).

Regression was used to compare the aphid fitness index with the known maximum relative growth rate values (R_{max}) (Grime and Hunt 1975), and mollusc palatability index (MPI) values (Grime et al. 1996).

Grime and Hunt (1975) assigned maximum relative growth rate values to a number of species by measuring the growth rate of individuals grown in growth chambers under optimal conditions (Table 1). The MPI was derived from a cafeteria-style feeding experiment (Grime et al. 1996). *Helix aspersa* (garden snails) were placed in tanks containing leaf samples from a broad range of species, and an index was calculated using data obtained by recording the amounts of leaf material consumed over a 72-h period (Table 1).

The dry masses of the grasses with and without aphids were measured and compared by species using student *t* tests. Furthermore, the effect of aphid feeding was calculated as the dry mass (total, shoots, and roots) of grasses without aphids minus the dry mass with aphids. Percentage change was calculated, which was then used to determine any differences between the three CSR plant strategies by using ANOVAs.

Results

Aphid numbers varied greatly among grass species (df = 12; *F* = 20.017; *P* < 0.0001; Fig. 1). For example, the annuals *Lagurus ovatus* and *Poa annua* had more than 4 times as many aphids as any of the fast-growing perennials (e.g., *Agrostis stolonifera*, *Arrhenatherum elatius*, *Holcus lanatus*, *Lolium perenne*, and *Poa trivialis*) and as much as 50 times more aphids than some of the slow-growing perennials (e.g., *Brachypodium pinnatum*, *Bromopsis erecta*, *Helictotrichon pratense*, and *Festuca ovina*). The initial five aphids added to *Helicotrichon pratense* and *Brachypodium pinnatum* not only did not multiply, but the majority did not survive.

Fast-growing grasses had significantly more aphids than slow-growing grasses (df = 1; *F* = 19.085; *P* < 0.0001) (Fig. 2*a*). Aphid numbers also varied significantly among CSR types (see Table 1) (df = 2; *F* = 7.131; *P* = 0.012) (Fig. 2*b*). Fast-growing annuals (R) had significantly greater numbers of aphids than either fast-growing perennials (C) or slow-growing perennials (S), and fast-growing perennials had significantly greater numbers of aphids than slow-growing perennials. Hairiness did not appear to have a general effect as a deterrent to aphid fitness (df = 1; *F* = 0.008; *P* = 0.930). *Poa annua* does not act as an outlier in these analyses, unlike the proceeding analyses, because the other fast-growing annuals with high aphid numbers (*Lagurus ovatus*, and *Catapodium rigidum*) were included in the analysis.

Aphid number increased significantly with both growth rate (r^2 = 0.66; *P* = 0.008) (Fig. 3*a*) and the mollusc palatability (r^2 = 0.83; *P* = 0.002) (Fig. 3*b*). The annual *Poa annua*, however, was an outlier in both cases and strongly influenced the results. When *P. annua* was removed from the analyses neither of the relationships were significant.

The aboveground biomasses of *Anisantha sterilis*, *Catapodium rigidum*, *Lagurus ovatus*, *Lolium perenne*, *Poa annua*, and *Poa trivialis* were significantly greater in the absence of aphids (Table 2). In the presence of aphids the aboveground biomass was reduced by up to 34.4%. Only *Poa annua* had significantly less belowground mass in the presence of aphids, with a reduction of 32%. Most species had a greater biomass when aphids were absent, but some, such as *Agrostis stolonifera*, *Bromopsis erecta*, *Brachypodium pinnatum*, *Festuca ovina*, and *Holcus lanatus* had one, or both, above- and below-ground biomasses greater in the presence

Fig. 1. Mean number (± 95% confidence intervals) of aphids found on 13 grass species after 2 weeks. Bars with different letters are significantly different.
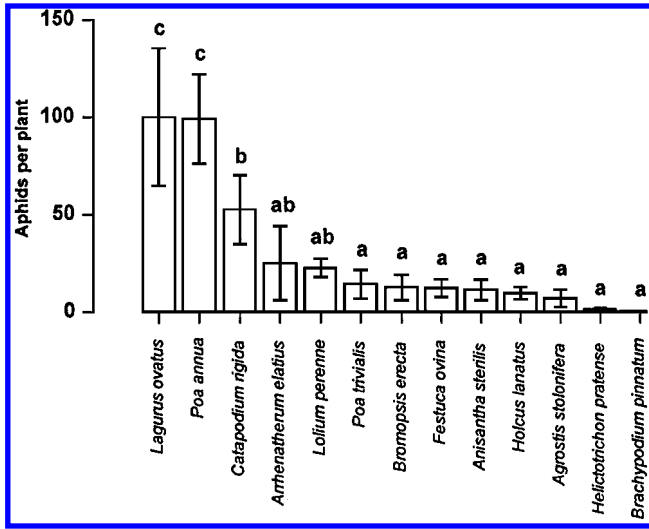

Fig. 2. Mean number of aphids (± 95% confidence intervals) on (*a*) fast- and slow-growing plants, and (*b*) the three CSR plant functional groups. Bars with different letters are significantly different.
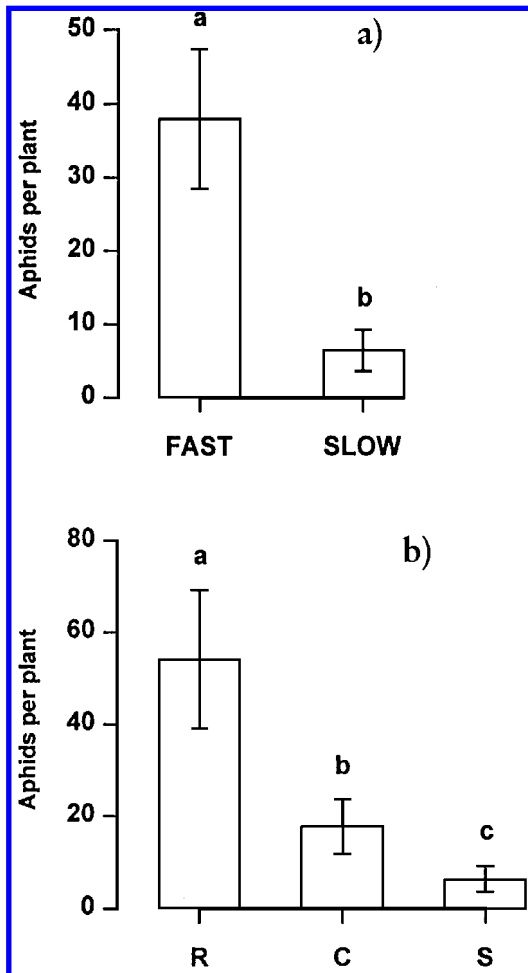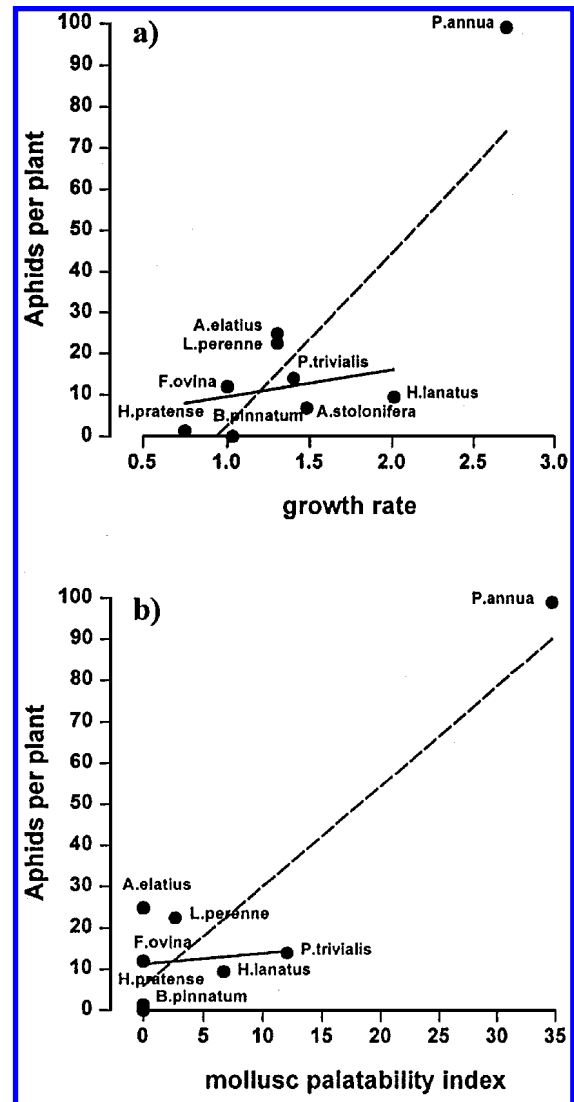

Fig. 3. Aphid numbers as a function of (*a*) the maximum relative growth rate (R_{max}), and (*b*) the mollusc palatability index. Broken lines are for the total data set, while solid lines are linear regressions of the data set after the outlier, *Poa annua*, has been removed.

of aphids. However, none of these differences was significant. When grasses were grouped according to the CSR theory, the percentage changes in total mass (df = 2, F = 6.415, P = 0.002), shoots (df = 2, F = 10.675, P < 0.0001) and roots (df = 2, F = 3.573, P = 0.031) mediated by the aphids were significantly different (Fig. 4). Generally, ruderals experienced the greatest percentage change in mass. The group that had the least amount of change in all categories of biomass was the stress tolerators.

Discussion

The main purpose of our experiment was to test the hypothesis that aphids achieve more rapid population growth on fast-growing grasses compared with slow-growing grasses. The performance of aphids in this case was defined as the comparative fecundity of the aphids on each plant

Table 2. Mean aboveground and belowground mass (g) of the 13 grass species grown without and with aphids.

		Without aphids	With aphids	Difference (%)
Agrostis stolonifera	Above	0.149	0.142	−4.7
	Below	0.096	0.118	22.9
Anisantha sterilis	Above	0.129	0.098*	−24.0
	Below	0.413	0.320	−22.5
Arrhenatherum elatius	Above	0.109	0.088	−19.3
	Below	0.064	0.045	−29.7
Brachypodium pinnatum	Above	0.134	0.159	18.7
	Below	0.121	0.126	4.1
Bromopsis erecta	Above	0.089	0.075	−15.7
	Below	0.099	0.123	24.2
Catapodium rigidum	Above	0.090	0.073*	−18.9
	Below	0.191	0.177	−7.3
Festuca ovina	Above	0.125	0.119	−4.8
	Below	0.143	0.163	14.0
Helictotrichon pratense	Above	0.105	0.105	0.0
	Below	0.186	0.154	−17.2
Holcus lanatus	Above	0.098	0.092	−6.1
	Below	0.516	0.547	6
Lagurus ovatus	Above	0.154	0.101*	−34.4
	Below	0.189	0.169	−10.6
Lolium perenne	Above	0.157	0.108*	−31.2
	Below	0.333	0.307	−7.8
Poa annua	Above	0.121	0.096*	−20.7
	Below	0.246	0.167*	−32.1
Poa trivialis	Above	0.147	0.112*	−23.8
	Below	0.244	0.171	−29.9

*Significant ($p < 0.05$) difference between aphid treatments. The table also presents the percentage change with and without aphids.
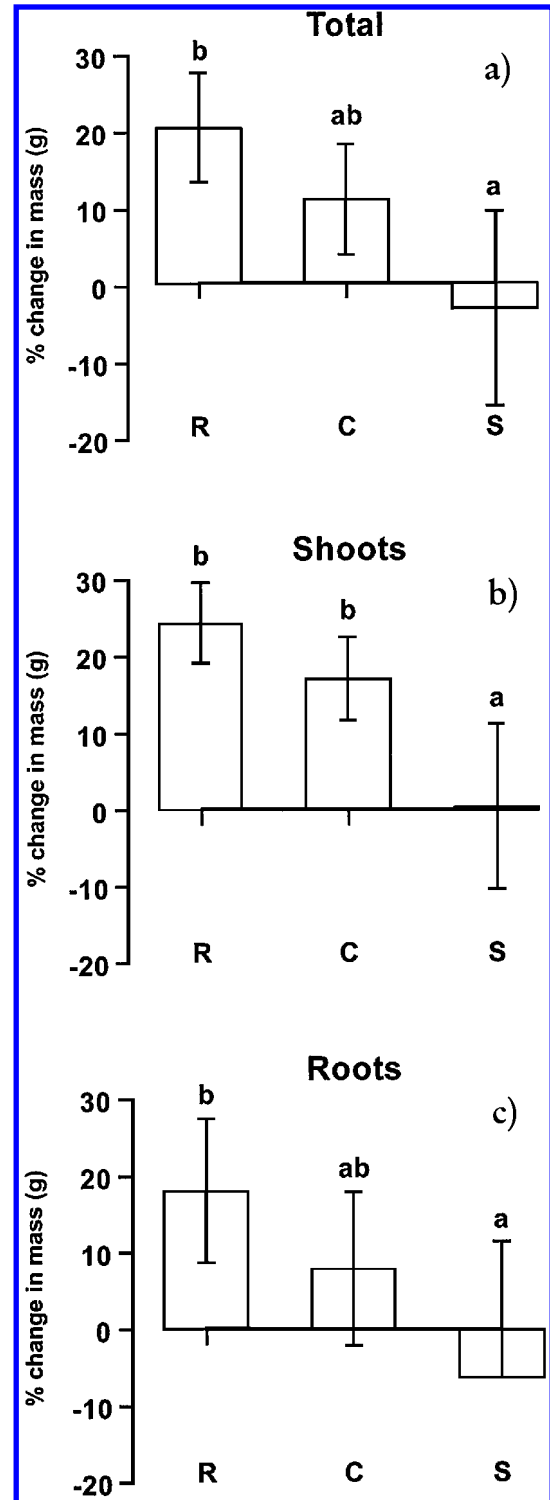
species. The logic behind this experiment involved the assumption that the more suitable a host plant, the more offspring would be produced.

The results presented certainly give some evidence in support of the growth rate hypothesis. Aphid numbers were greater on faster growing plants (as defined by CSR theory; Grime et al. 1988). Furthermore, the most suitable grasses for aphids were fast-growing annuals (ruderals), followed by fast-growing perennials (competitors), and the least suitable grasses being slow-growing perennials (stress tolerators) (Fig. 2b). These results show support for the CSR theory. Although growth rate was highly correlated with aphid numbers, *Poa annua*, an outlier, accounted for most of the variation. Unfortunately, the growth rate, as well as the MPI values, of the three other annual grasses (*Anisantha sterilis*, *Catapodium rigidum*, and *Lagurus ovatus*) were not known. Had they been known, the results may have been more conclusive. The mean numbers of aphids between the CSR functional groups, however, were highly significant. Hairiness did not appear to be a factor exerting a strong influence on the suitability of the grasses to the aphids.

Other studies have also found that fast-growing plants are more palatable then slow-growing plants (Grime et al. 1968, 1970, 1996), but these studies all included leaf-chewing herbivores, while the present study was only concerned with a leaf sucker. However, the MPI (Grime et al. 1996) was highly correlated with aphid numbers and was able to ac-

Fig. 4. Percentage change in mass (g) of the grasses owing to aphid feeding between the three primary plant strategies (CSR plant classification system (C, competitor; S, stress tolerator; R, ruderal; Grime 1977, 1979)). (*a*) Total plant. (*b*) Shoots. (*c*) Roots. Error bars represent 95% confidence limits. Bars with different letters are significantly different.

count for 91.0% of the variation between them. Once again, however, *Poa annua* was an outlier, accounting for most of the variation.

The mean aboveground biomasses of all grass species were reduced, significantly so in the case of fast-growing species, in the presence of aphids (Table 2). Although *Brachypodium pinnatum* had a greater mean aboveground biomass in the presence of aphids, this was a result of doubtful significance because no aphids survived on *Brachypodium pinnatum*. Stress tolerators as a group had the least amount of change in biomass owing to aphid feeding, which is likely largely due to the low numbers of aphids surviving on stress-tolerant grasses. The effect of herbivory by aphids was not as consistent for the mean belowground biomass of the grass species. The only significant effect was experienced by *Poa annua*, with a lower biomass in the presence of aphids.

Holcus lanatus was apparently not a suitable host plant, because it did not support many aphids. This is despite the fact that *H. lanatus* had one of the highest maximum relative growth rate values and is classified as a fast-growing perennial. The other grasses which supported few aphids were slow-growing perennials: *Agrostis stolonifera*, *Helictotrichon pratense*, and *Brachypodium pinnatum*. Perhaps the reason is that the primary functional classification of *H. lanatus* is C–S–R (Grime et al. 1988), meaning that it encompasses relatively equal attributes of competitors, stress tolerators, and ruderals: a "jack of all trades." Another feature of *H. lanatus* is that it is very hairy. Generally, though, hairiness did not seem to be a significant factor in limiting aphid fitness. For example, *Lagurus ovatus* is hairy, and yet, it had the highest number of aphids. However, the other hairy ruderal (*Anisantha sterilis*) had the lowest number of aphids of the ruderals. It may be the degree of hairiness or the type of hairs that play a more important role in determining aphid fitness levels.

The complexity and overall number of interactions between plants and insects has resulted in a multitude of defensive characters. For a plant to focus on any one plant defence strategy against phytophagous insects is not very effective (Hochuli 1996). However, relative growth rate has been shown to relate to many differences in chemical composition and anatomical structure of plants (Poorter et al. 1990; Niemann et al. 1992; Poorter and Bergkotte 1992; van Arendonk and Poorter 1994). These differences may affect palatability and the resulting fitness of phytophagous insects. Our results on the relative fitness of *Sitobion avenae* show some support for the growth rate hypothesis, as well as CSR theory.

Acknowledgements

References

Acreman, S.J., and Dixon A.F.G. 1989. The effects of temperature and host quality on the rate of increase of the grain aphid *Sitobion avenae* on wheat. Ann. Appl. Biol. **115**: 3–10.

Caillaud, C.M., Dedryver, C.A., De Pietro, J.P., Simon, J.C., Fima, F., and Chaubet, B. 1995. Clonal variability in the response of *Sitobion avenae* (Homoptera: Aphididae) to resistant and susceptible wheat. Bull. Entomol. Res. **85**: 189–195.

Choong, M.F., Luca, P.W., Ong, J.S.Y., Pereira, B., Tan, H.T.W., and Turner, I.M. 1992. Leaf fracture toughness and sclerophylly: their correlations and ecological implications. New Phytol. **121**: 597–610.

Coley, P.D., Bryant, J.P., and Chapin, F. S., III 1985. Resource availability and plant antiherbivore defense. Science (Washington, D.C.), **230**: 895–899.

De Barro, P.J., Sherratt, T.N., David, O., and Maclean, M. 1995. An investigation of the differential performance of clones of the aphid *Sitobion avenae* on two host species. Oecologia, **104**: 379–385.

Dixon, A.F.G. 1985. Aphid ecology. Blackie, Glasgow.

Dixon, A.F.G. 1987. Parthenogenetic reproduction and the rate of increase in aphids. *In* World crop pests. Vol. 2A. Aphids, their biology, natural enemies, and control. *Edited by* A.K. Minks and P. Harrewijn.. Elsevier, Amsterdam. pp 289–297.

Ehrlich, P.R., and Raven, P.H. 1964. Butterflies and plants: a study in coevolution. Evolution, **18**: 586–608.

Feeny, P. 1976. Plant apparency and chemical defense. Recent Adv. Phytochem. No. 10. pp. 1–40.

Feeny, P. 1991. Theories of plant chemical defense: a brief historical survey. *In* Insects and plants. *Edited by* T. Jermy and A. Szentesi. S.P. Bakker Academic Publishers, The Hague, the Netherlands. pp 163–175.

Futuyama, D.J., and Slatkin, M. 1983. Coevolution. Sinauer Associates Inc., Sunderland, Mass.

Givovich, A., and Niemeyer, H.M. 1995. Comparison of the effect of hydroxamic acids from wheat on five species of cereal aphids. Entomol. Exp. Appl. **74**: 115–119.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. **111**: 1169–1194.

Grime, J.P. 1979. Plant strategies and vegetation processes. J. Wiley, New York.

Grime, J.P. 1993. Ecology sans frontieres. Oikos, **68**: 385–392.

Grime, J.P., and Hunt, R. 1975. Relative growth rate: its range and adaptive significance in a local flora. J. Ecol. **63**: 393–422.

Grime, J.P., MacPherson-Stewart, S.F., and Dearman, R.S. 1968. An investigation of leaf palatability using the snail *Cepaea nemoralis* L. J. Ecol. **56**: 405–420.

Grime, J.P., Blythe, G.M., and Thornton, J.D. 1970. Food selection by the snail *Cepaea nemoralis* L. *In* Animal populations in relation to their food resources. *Edited by* A. Watson. Blackwell Scientific Publications, Oxford. pp 73–99.

Grime, J.P., Hodgson, J.G., and Hunt, R. 1988. Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.

Grime, J.P., Cornelissen, J.H.C., Thompson, K., and Hodgson, J.G. 1996. Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos, **96**: 489–494.

Gulmon, L.L., and Mooney, H.A. 1986. Costs of defense and their effects on plant productivity. *In* On the economy of plant form and function. *Edited by* T.J. Givnish. Cambridge University Press, Cambridge, U.K. pp. 681–698.

Guo, J.Q., Moreau, J.P., and Lapierre, H. 1996. Variability among aphid clones of *Rhopalosiphum padi* L., and *Sitobion avenae* Fabr. (Homoptera: Aphididae) in transmission of three PAV isolates of barley yellow dwarf viruses. Can. Entomol. **128**: 209–217.

Havlickova, H. 1993. Level and nature of the resistance to the cereal aphid (*Sitobion avenae*) in 13 winter wheat cultivars. J. Agron. Crop Sci. **171**: 133–137.

Heldon, A.J., Dixon, A.F.G., and Carter, N. 1994. Environmental factors and morphological discrimination between spring and summer migrants of the grain aphid, *Sitobion avenae*. Eur. J. Entomol. **91**: 23–28.

Hendry, G.A.F., and Grime, J.P. 1993. Methods in comparative plant ecology: a laboratory manual. Chapman & Hall, London.

Hochuli, D.R. 1996. The ecology of plant/insect interactions: implications of digestive strategy for feeding by phytophagus insects. Oikos, **75**: 133–141.

Honek, A. 1991. Nitrogen fertilization and abundance of the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae* Hompoptera Aphididae. Aeitschrift fuer Pflanzenkrankheiten und Pflanzenschutz, **98**: 655–660.

Hubbard, C.E. 1984. Grasses. Penguin, London.

Janzen, D.H. 1975. Behaviour of *H. couboril* when its predispersal seed predator is absent. Science (Washington, D.C.), **189**: 145–147.

Leszczynski, B., and Dixon, A.F.G. 1990. Resistance of cereals to aphids interaction between hydroxamic acis and the aphid *Sitobion avenae* Homoptera Aphididae. Ann. Appl. Biol. **117**: 21–30.

Leszczynski, B., Wright, L.C., and Bakowski, T. 1989. Effect of secondary plant substances on winter wheat resistance to grain aphid. Entomol. Exp. Appl. **52**: 135–140.

Leszczynski, B., Thallingii, W.F., Dixon, A.F.G., and Swiderski, R. 1995. Effect of methoxyphenols on grain aphid feeding behaviour. Entomol. Exp. Appl. **76**: 157–162.

Levin, D.A. 1973. The role of trichomes in plant defense. Q. Rev. Biol. **48**: 3–15.

Maclean, S.F., and Jensen, T.S. 1985. Food plant selection by insect herbivores in Alaskan arctic tundra: the role of plant life form. Oikos, **44**: 211

Niemann, G.J., Pureveen, J.B.M., Eijkel, G.B., Poorter, H., and Boon, J.J. 1992. Differences in relative growth rate in 11 grasses correlate with differences in chemical composition was determined by pyrolysis mass spectrometry. Oecologia, **89**: 567–573.

Poorter, H., and Bergkotte, M. 1992. Chemical composition of 24 wild species differing in relative growth rate. Plant Cell Environ. **15**: 221–229.

Poorter, H., Remkes, C., and Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. Plant Physiol. **94**: 621–627.

Rhoades, D.F., and Cates, R.G. 1976. Towards a general theory of plant antiherbivore chemistry. Recent Adv. Phytochem. No. 10. pp. 168–213.

Robinson, J. 1992. Modes of resistance in barley seedlings to six aphid Homoptera Aphididae species. J. Econ. Entomol. **85**: 2510–2515.

Sengonca, C., Hoffmann, A., and Kleinhenz, B. 1994. Investigations of development, survival and fertility of the cereal aphids *Sitobion avenae* and *Rhopalosiphum padi* at different low temperatures. J. Appl. Entomol. **117**: 224–233.

Simon, J.C., Dedryver, C.A., Pierre, J.S., Tanguy, S., and Wegorek, P. 1991. The influence of clone and morph on the parameters of intrinsic rate of increase in the cereal aphids *Sitobion avenae* and *Rhopalosiphum padi*. Entomol. Exp. Appl. **58**: 211–220.

Thackray, D.J., Wrateen, S.D. Edwards, P.J., and Niemeyer, H.M. 1990. Resistance to the aphids *Sitobion avenae* and *Rhopalosiphum padi* in Gramineae in relation to hydroxamic acid levels. Ann. Appl. Biol. **116**: 573–582.

van Arendonk, J.J.C.M., and Poorter, H. 1994. The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. Plant Cell Environ. **17**: 963–970.

This article has been cited by:

1. Minglong Sun, Lijiao Xu, Yingli Peng, Tong Liu, Yuhong Zhang, Zhiqiang Zhou. 2016. Multiscale analysis of the contents of palmatine in the Nature populations of Phellodendron amurense in Northeast China. *Journal of Forestry Research* **27**:2, 265-272. [Crossref]