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.

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 (Leszcynski et al. 1989; Leszcynski 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; Acremen 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 (Acremen 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, *Lagarus 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 (Acremen 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., Leszcynski 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.

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placed in tanks containing leaf samples from a broad range 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). The MPI was calculated using data obtained by recording the amounts of leaf material consumed over a 72-h period (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 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).

Data analysis

ANOVA was 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 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 Helictotrichon 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. 2a). Aphid numbers also varied significantly among CSR types (see Table 1) (df = 2; F = 7.131; P = 0.012) (Fig. 2b). 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 (Lagarus ovatus, and Catapodium rigidum) were included in the analysis.

Aphid number increased significantly with both growth rate (r² = 0.66; P = 0.008) (Fig. 3a) and the mollusc palatability (r² = 0.83; P = 0.002) (Fig. 3b). 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 ($R_{\text{max}}$), 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.
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 than 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 account for 91.0% of the variation between them. Once again, however, *Poa annua* was an outlier, accounting for most of the variation.

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

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

*Significant (p < 0.05) difference between aphid treatments. The table also presents the percentage change with and without aphids.

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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*, *Helicotrichon 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.

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