Influence of Japanese Beetle Popillia japonica Larvae and Fungal Endophytes on Competition between Turfgrasses and Dandelion

Douglas S. Richmond,* Parwinder S. Grewal, and John Cardina

ABSTRACT

In a series of greenhouse experiments, we examined the influence of below-ground herbivory by larvae of the Japanese beetle, Popillia japonica Newman, on performance and competitive interactions between dandelion, Taraxacum officinale Weber, and two turfgrass species, Lolium perenne L. ( perennial ryegrass) and Festuca arundinacea Schreb. (tall fescue) infected or uninfected by Neotyphodium endophytes. In doing so, we aimed to determine how below-ground insect feeding and endophyte infection might influence the ability of dandelion to act as a turfgrass weed. In monocultures of perennial ryegrass or tall fescue, herbivory significantly reduced the number of tillers per plant and above- and below-ground biomass. Endophyte infection significantly reduced perennial ryegrass tillers but significantly increased the number of tall fescue tillers and above- and below-ground biomass. Herbivory had no significant influence on dandelion growth parameters in monocultures. In mixtures of dandelion and either grass species, herbivory significantly reduced the number of grass tillers and above- and below-ground biomass, whereas endophyte infection significantly reduced the number of perennial ryegrass tillers but had little influence on tall fescue. Herbivory significantly increased the number of dandelion leaves and above- and below-ground biomass in mixtures with perennial ryegrass or tall fescue. Endophyte infection had no significant influence on Japanese beetle larval survival or biomass in monocultures or mixtures. Findings indicate that below-ground herbivory by Japanese beetle larvae alters competitive interactions between grasses and dandelion in a way that favors dandelion. Data support the view that endophyte-related effects on interactions between plants may not always be predictable and that below-ground herbivory may not affect endophyte-infected and uninfected plants differentially.

Phytophagous insects can have a substantial influence on the composition of plant communities (McBrien et al., 1983; Müller-Schärer and Brown, 1995). Differential herbivory can provide a competitive advantage to some plant species by reducing the growth of species that are more favored by herbivores. In managed perennial systems such as turfgrass lawns, herbivory can encourage weed encroachment by reducing the growth or vigor of desirable plant species (Watschke, 1995). Many studies have demonstrated the influence of above-ground insects on the composition of plant communities, but grasses are particularly well suited to endure above-ground herbivory. Because of a number of adaptations, including placement of the meristematic zone close to the soil surface and storage of nutrient reserves in underground tissues (Beard, 1973; Murray et al., 1996), grasses can quickly replace foliage so long as basic resources are available (Alward and Joern, 1993). Below-ground herbivory, however, imposes a different suite of pressures on plants that may have stronger effects than above-ground herbivory (Morón-Ríos et al., 1997). Root-feeding insects can influence plant growth, biomass production, and nutrient status, and may alter the nutrient profile of the rhizosphere (Jamarillo and Detling, 1988; Murray et al., 1996). There are relatively few studies on the effects of root-feeding insects on the growth and development of grassland species, and even fewer studies detailing the influence of below-ground herbivory on competitive interactions between grasses and co-occurring plant species.

Perennial ryegrass and tall fescue are infected by the symbiotic fungal endophytes Neotyphodium lolii Glenn, Bacon, Price and Hanlon, and N. coenophialum Glenn et al., respectively. Fungi in the genus Neotyphodium form mutualistic symbioses with a large number of cool-season perennial grasses. The fungi benefit from access to plant nutrient and photosynthetic resources while infected plants benefit from enhanced tolerance or resistance to environmental stress (Elmi and West, 1995; Ravel et al., 1995). Endophyte-infected plants also benefit from acquisition of fungal alkaloids that provide defense against herbivory (Breen, 1994; Porter, 1994). These defensive alkaloids are unevenly distributed within infected plants (Justus et al., 1997) with much lower concentrations occurring in root tissues compared with aerial plant tissues (West and Gwinn, 1993). A number of studies indicate that endophyte-infected plants experience a considerable competitive advantage over their nonendophytic congeners (Latch et al., 1985; Clay et al., 1993) and research has demonstrated that endophyte-infected plants may come to dominate certain ecosystems with time (Clay and Holah, 1999). However, the importance of herbivore defense in bolstering the competitive abilities of infected plants has only been examined in the case of above-ground folivores (Clay et al., 1993) which are likely exposed to much higher concentrations of endophyte-related defensive compounds.

Below-ground herbivory has received little attention as a potential factor influencing the competitive ability of endophyte-infected grasses. With few exceptions (see Elmi et al., 2000), studies concerning the influence of fungal endophytes on below-ground herbivory indicate little or no direct influence on herbivore populations (Potter et al., 1992; Davidson and Potter, 1995). This study used larvae of the Japanese beetle to determine if below-ground herbivory plays an important role in determining the outcome of competitive interactions between dandelion and two cool-season perennial grasses, perennial ryegrass and tall fescue, under conditions sim-
ulating a turfgrass ecosystem. We chose dandelion because it is a common weed problem in turfgrass and is often the target of repeated herbicide applications. We hypothesized that below-ground herbivory would provide an ecological advantage to dandelion because its roots are less favored by *P. japonica* larvae (Crutchfield and Potter, 1995). Endophyte-infected and uninfected plants should not be differentially affected in this regard because of the low concentrations of endophyte-mediated defensive compounds present in below-ground plant tissues.

**MATERIALS AND METHODS**

**Plant Material**

Seeds of ‘Goal Keeper’ perennial ryegrass and ‘Alamo’ tall fescue were obtained from Lofts Seed, Inc. (Winston Salem, NC). Both of these cultivars are infected with their respective fungal endophytes *N. loli* and *N. coenophialum*. To maintain seed and endophyte viability, seeds were stored at 5°C. Uninfected plants of each species were obtained by heat treating half of the seeds (Kunkel et al., unpublished data), which slightly reduced seed germination but drastically reduced the level of endophyte infection in the resulting plant population. We confirmed endophyte infection levels using the Phyto-screen immunoblot kit (Agrinositics Ltd. Co., Watkinsville, GA). In perennial ryegrass, heat treatment reduced endophyte infection from ≈90 to ≈5%, while endophyte infection in tall fescue was reduced from ≈60 to ≈5%. Therefore, endophyte-infected and uninfected seed lots were not absolutely pure. Statistical comparisons between means from infected and uninfected categories are more conservative as a result of this contamination. Dandelion seeds were obtained from a wild population located in an abandoned yard in Wayne County, OH. Seeds were collected by hand, cleaned, and stored at 5°C until needed.

For all experiments, seeds were germinated in Petri dishes on moist filter paper and transplanted to 10.2-cm-diam. plastic pots filled with a steam-sterilized soil mixture (1:1:1, sand to soil to peat). The soil component of the mixture was a Wooster silty-loam soil (fine-loamy, mixed, mesic Oxyaque Fragudalphp) collected locally on the grounds of the Ohio Agricultural Research and Development Center, Wooster, OH, USA. Plant density was held constant at eight plants per pot and plants were watered as needed (usually daily) and fertilized biweekly by drenching each pot with 100 mL of water-soluble 20:15:20 (N-P-K) fertilizer (30 mg kg⁻¹ N). Greenhouse temperatures were maintained between 15 and 29°C with no supplemental lighting.

**Monocultures**

Experiments were conducted using monospecific stands of dandelion and endophyte-infected or uninfected tall fescue and perennial ryegrass to determine the influence of below-ground herbivory and/or endophyte infection on performance parameters of each species. Planting of germinated seedlings was initiated the first week of June 2001, and one complete replicate of each grass and dandelion mixture was planted each day for 10 d. Each replicate consisted of eight pots, four containing dandelion and endophyte-infected grass, and four containing dandelion and uninfected grass. Of the four pots containing either endophyte-infected or uninfected grass plants, two pots were designated to receive insect larvae and two were designated to be insect free. Within each replicate, one pot from each endophyte × herbivory combination was randomly assigned for measuring either the response of the grass or the response of dandelion. Pots were arranged on the greenhouse bench in a randomized block design with 10 replicates.

**Experimental Protocol**

Plants were allowed to establish and grow for three months after planting and were cut monthly to a height of 6.0 cm to simulate a turfgrass system. During the last week of September 2001, three field collected 3rd-instar *P. japonica* larvae were added to each designated pot. Larvae that had not burrowed into the soil after 1 h were removed and replaced with another individual. After two more months (last week of November), the number of tillers (grass) or leaves (dandelion) were recorded and above-ground biomass was collected by cutting plants at the soil surface and placing the material into paper bags. Roots belonging to individual plants were carefully separated, washed free of soil and organic matter, and also placed into paper bags. In monocultures, four randomly selected plants from each pot were sampled, whereas either grass or dandelion plants were sampled in the mixtures. All *P. japonica* larvae recovered from the soil were counted and euthanized by placing them into small plastic cups containing 70% ethanol. All insect and plant material was dried at 80°C for 48 h before measuring biomass. Dry weights for all plant and insect materials were used for analysis.

**Statistical Analysis**

All statistical analyses were conducted using Statistica '99 (Statsoft Inc., Tulsa, OK). Plant biomass data were log-transformed, whereas shoot and leaf count data were square-root transformed to meet the assumptions of the analysis. Percentage larval survival was arcsin transformed before analysis. Plant parameters (number of leaves or tillers, and above- and below-ground biomass) and insect parameter (% survival and biomass) were analyzed by multivariate analysis of variance (MANOVA). Plant parameters from grass monocultures and mixtures were analyzed using a factorial model \([Y = \text{endophyte} \times \text{herbivory} + (\text{endophyte} \times \text{herbivory})]\) whereas plant parameters from dandelion monocultures were analyzed using a main effects model \([Y = \text{herbivory}]\). Insect parameters from grass monocultures or mixtures were also analyzed using a main effects model \([Y = \text{endophyte}]\). However, insect parameters from dandelion monocultures were not subjected to statistical analysis. Replicate was included as a blocking
Table 1. *F* values from ANOVAs showing influence of endophyte infection and herbivory by Japanese beetle (*Popillia japonica*) on perennial ryegrass, tall fescue, and dandelion performance parameters, and influence of endophyte infection in perennial ryegrass and tall fescue on Japanese beetle density and biomass in greenhouse monocultures of each plant species.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Number of tillers</th>
<th>Above-ground biomass (g)</th>
<th>Root biomass (g)</th>
<th><em>P. japonica</em> density</th>
<th><em>P. japonica</em> mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Perennial ryegrass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Endophyte (E)</td>
<td>8.9***</td>
<td>1.8</td>
<td>3.8*</td>
<td>0.1</td>
<td>0.6</td>
</tr>
<tr>
<td>Herbivory (H)</td>
<td>15.8†</td>
<td>4.1†</td>
<td>25.9†</td>
<td>–‡</td>
<td>–‡</td>
</tr>
<tr>
<td>E × H</td>
<td>0.0</td>
<td>0.5</td>
<td>0.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Tall Fescue</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>E</td>
<td>87.9†</td>
<td>14.9†</td>
<td>5.6**</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>H</td>
<td>30.8†</td>
<td>14.7†</td>
<td>33.5†</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>E × H</td>
<td>0.0</td>
<td>0.0</td>
<td>0.8</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><strong>Dandelion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>0.3</td>
<td>1.5</td>
<td>1.6</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

*P ≤ 0.1.
**P ≤ 0.05.
***P ≤ 0.01.
†* P ≤ 0.001.
‡ Effect not applicable.

variable in all analysis. All main effects were evaluated at α = 0.05, whereas interactions were evaluated at α = 0.1 to minimize the probability of type II error. Our objective was to determine how below-ground herbivory and endophyte infection influence plant performance and competitive interactions between plant species, and was not to compare the influence of these factors on inter- vs. intraspecific competition. Therefore, statistical comparisons between monocultures (intraspecific studies) and mixtures (interspecific studies) were not performed.

RESULTS

Monocultures

Herbivory by Japanese beetle larvae and endophyte infection both had a significant influence on response parameters of perennial ryegrass and tall fescue in monoculture (*F* ≥ 16.8; df = 3, 25; *P* < 0.0001 for herbivory, and *F* ≥ 5.0; df = 3, 25; *P* ≤ 0.007 for endophyte infection) and there was no significant interaction between herbivory and endophyte infection (*F* ≤ 0.26; df = 3, 25; *P* ≥ 0.86). Herbivory significantly reduced the number of perennial ryegrass tillers and above- and below-ground biomass of perennial ryegrass plants (Table 1, Fig. 1). Endophyte infection significantly reduced the number of perennial ryegrass tillers, but had no significant influence on above- or below-ground biomass or Japanese beetle larval survival (X̄ = 44.7 ± 16.75%) or biomass (X̄ = 28.0 ± 2.0 mg). The number of larvae recovered from pots containing only perennial ryegrass ranged from 0 to 2.

Herbivory significantly reduced the number of tall fescue tillers and above- and below-ground biomass in monocultures (Fig. 2). Endophyte infection significantly increased all three tall fescue response parameters, but had no significant influence on Japanese beetle larval survival (X̄ = 47.2 ± 17.4%) or biomass (X̄ = 26.0 ± 2.0 mg). The number of larvae recovered from pots containing only tall fescue ranged from 0 to 2.

Herbivory had no significant influence on the number of leaves (X̄ = 7.7 ± 0.5), or above- (X̄ = 0.60 ± 0.14 g) or below-ground (X̄ = 1.60 ± 0.33 g) biomass of dandelion plants growing in monoculture (Fig. 3). Japanese beetle larvae survived poorly in dandelion monocultures (29.2 ± 21.9% survival) and surviving larvae had very low dry weights (10.0 ± 1.0 mg). The number of larvae recovered from the pots containing only dandelion ranged from 0 to 1.

Mixtures

Herbivory by Japanese beetle larvae and endophyte infection both had a significant influence on response parameters of perennial ryegrass growing in mixtures with dandelion (*F* = 14.9; df = 3, 25; *P* < 0.0001, and *F* = 8.6; df = 3, 25; *P* = 0.0004, respectively), but there was no significant interaction between herbivory and endophyte infection (*F* = 0.38; df = 3, 25; *P* = 0.77). Herbivory significantly reduced the number of perennial ryegrass tillers and above- and below-ground biomass whereas endophyte infection significantly reduced the number of perennial ryegrass tillers and above-ground biomass (Table 2). Conversely, herbivory significantly increased the number of dandelion leaves and above- and below-ground biomass in mixtures with perennial ryegrass whereas endophyte infection in competing perennial ryegrass plants had no significant influence on dandelion response parameters (Table 3). Endophyte infection status of perennial ryegrass plants had no significant influence on Japanese beetle larval survival (X̄ = 52.5 ± 21.8%) or biomass (X̄ = 27.0 ± 4.0 mg) in mixtures of perennial ryegrass and dandelion. The number of larvae recovered from the pots ranged from 0 to 2.

Herbivory by Japanese beetle larvae had a significant influence on response parameters of tall fescue growing in mixtures with dandelion (*F* = 13.4; df = 3, 25; *P* < 0.0001), endophyte infection had no significant influence (*F* = 1.48; df = 3, 25; *P* = 0.24), and there was no significant interaction between herbivory and endophyte infection (*F* = 0.64; df = 3, 25; *P* = 0.59). Herbivory significantly reduced the number of tall fescue tillers and above- and below-ground biomass in such mixtures. Furthermore, herbivory significantly increased the number of dandelion leaves and above- and below-ground biomass in mixtures of tall fescue and dandelion. Endophyte infection in competing tall fescue plants sig-
Perennial Ryegrass

- Number of Tillers
- Above-Ground Biomass (g)
- Below-Ground Biomass (g)

Monoculture vs. Mixture

Tall Fescue

- Number of Tillers
- Above-Ground Biomass (g)
- Below-Ground Biomass (g)

Monoculture vs. Mixture

Fig. 1. Influence of below-ground herbivory by larvae of the Japanese beetle (JB, JB+) and endophyte infection (E-, E+) on (a) number of tillers, and (b) above- and (c) below-ground biomass of 'Alamo' tall fescue plants in monocultures or mixtures with dandelion in the greenhouse. Data were collected during November 2001. Bars = mean ± SE.

Fig. 2. Influence of below-ground herbivory by larvae of the Japanese beetle (JB, JB+), and endophyte infection (E-, E+) on (a) number of tillers, and (b) above- and (c) below-ground biomass of 'Goal Keeper' perennial ryegrass plants in monocultures or mixtures with dandelion in the greenhouse. Data were collected during November 2001. Bars = mean ± SE.

- Significantly decreased the number of dandelion leaves and above-ground biomass, but had no significant influence on dandelion below-ground biomass. Endophyte infection had no significant influence on Japanese beetle larval survival (X = 45.0 ± 18.4%) or biomass (X = 27 ± 2.0 mg) in mixtures of tall fescue and dandelion. The number of larvae recovered from the pots ranged from 0 to 2.

DISCUSSION

Below-ground herbivory by Japanese beetle larvae had a differential influence on perennial ryegrass, tall fescue, and dandelion, which was reflected in competitive interactions between these species. Japanese beetle larvae consistently reduced tiller numbers and above- and below-ground biomass of the grasses in monoculture but had no such influence on dandelion. Under competitive conditions, dandelion plants benefited from herbivory at the expense of both grasses by producing more leaves and greater above- and below-ground biomass. Previous work by Crutchfield and Potter (1995) concluded that dandelion is a poor host for *P. japonica*, and our results support their findings. However, results of the present study further indicate that plant species that are less preferable to below-ground herbivores may enjoy a competitive advantage as a result of preferential herbivory on neighboring plants. Evidence suggests that feeding activity of Japanese beetles may encourage growth...
defensive compounds adequate to deter feeding. Field studies indicate that endophyte infection does not have a strong influence on the population density of scarab larvae (Murphy et al., 1993; Davidson and Potter, 1995). The present study indicates that below-ground herbivory does not differentially affect the performance or competitive abilities of endophyte-infected and uninfected plants.

Endophyte infection exerted a significant but variable influence on the competitive ability of infected grasses independent of below-ground herbivory. In monocultures, endophyte infection was generally advantageous to tall fescue which produced more tillers, and had greater above- and below-ground biomass when infected. This was not the case for perennial ryegrass, which produced fewer tillers in monoculture when infected by *N. lolii*. Differences in the performance of endophyte-infected and uninfected grasses were often reflected in competitive interactions with dandelion. Dandelion plants produced more biomass in mixtures with endophyte-infected perennial ryegrass but fewer tillers and lower above-ground biomass in mixtures with endophyte-infected tall fescue. The reasons for this differential influence most probably lie in endophyte-mediation of plant physiological processes. The physiological cost associated with endophyte infection is an often-neglected aspect of endophyte–host interactions. Because the endophyte has “insignificant biomass” (Hiatt and Hill, 1997), the percentage of total plant resources used by the fungus is likely small. However, studies have shown reduced growth for endophyte-infected plants (Marks et al., 1991; Richmond et al., 2003) and demonstrated that resource availability can determine whether the endophyte has a positive or negative influence on plant growth (Cheplick et al., 1989). Malinowski and Belesky (1999) showed that endophyte infection enhanced phosphorus uptake in tall fescue and demonstrated that differential uptake efficiency between infected and uninfected tall fescue was not related to differences in root biomass or surface area. Likewise, Richardson et al. (1993) found that endophyte infection enhanced the photosynthetic efficiency of tall fescue by inducing a more favorable turgor pressure under water deficit stress. In our own studies, endophyte infection negatively influenced the ability of perennial ryegrass to compete with large crabgrass (*Digitaria sanguinalis* (L.) Scop.) even though nutrients were not limited (Richardson et al., 2003). The ecological contingency of the endophyte–host relationship has been recognized for some time (Cheplick, 1997; Saikkonen et al., 1998). Mutualistic endophytes of grasses can become parasitic under certain ecological conditions, depending on water or nutrient availability, plant competition, and degree of herbivory (Cheplick et al., 1989; Clay, 1990). Variation in the costs or benefits of endophyte infection may explain why uninfected plants are still found in many populations. However, such unpredictability in the behavior of the endophyte-grass complex is no doubt a concern for turfgrass breeders producing endophyte-enhanced varieties.

Grub survival in the greenhouse was relatively poor,
Although there were still measurable differences in plant performance and competitive interactions between pots receiving larvae and those that did not. Because some feeding likely took place in all pots receiving larvae, even pots with no surviving larvae were included in our analyses. For this reason, the results concerning the influence of larval feeding are somewhat conservative. However, poor larval survival was not surprising under greenhouse conditions for a couple of reasons. First, the rapid wetting and drying of the soil in this environment undoubtedly stressed the larvae. Scarab larvae will move in response to soil conditions (Hsieh, 1982) and tend to experience better survival under moist soil conditions (Potter et al., 1996). However, rapid changes in soil moisture occurring in the greenhouse may present a considerable challenge to these insects. Second, soil compaction is a common problem in greenhouses. Such compaction would only make it more difficult for larvae to move in response to soil conditions. Therefore, the combined impact of rapidly changing soil conditions and soil compaction are likely responsible for the relatively low larval survival we observed.

There was a tendency for dandelion performance to be compromised more by competition with perennial ryegrass than by competition with tall fescue, especially with regard to above- and below-ground biomass. This trend likely reflects known differences in establishment and growth characteristics between the two grass species. Perennial ryegrass establishes more rapidly than tall fescue (Parks and Henderlong, 1967; Beard, 1973) and is often used in seed mixtures where rapid soil stabilization is a priority (Beard, 1973). Therefore, perennial ryegrass would predictably be a stronger competitor against dandelion in relatively short term greenhouse experiments.

Although the results reported herein come from greenhouse studies that can only approximate field conditions, the data illustrate a linkage between below-ground herbivory and weed performance in turfgrass systems that has not been previously demonstrated. The idea that pest insects may benefit weeds by choosing not to feed on the roots of certain species implies a direct relationship between weed and insect management that should be considered. Our results imply that because insects can influence the relative success of certain weeds, proper insect management may be an important part of weed management. Although there is presently no clear consensus on the relative importance of above- vs. below-ground herbivory in relation to plant competition, most studies on endophyte-mediated plant defense have focused on above-ground herbivory (Hardy et al., 1985; Clay et al., 1993; Richmond and Shetlar, 2000; and many others) and endophyte-infected grasses have been widely marketed for their strong resistance to surface-feeding insects. However, with few exceptions (see Elmi et al., 2000), studies concerning the influence of fungal endophytes on below-ground insect herbivory indicate little or no influence on the herbivores (Potter et al., 1992; Davidson and Potter, 1995), and our study bolsters this assertion. Although endophyte-enhanced turfgrasses may provide a variety of benefits, resistance to scarab larvae is likely not among these. Biological or chemical tools may still be required to manage these insects in endophyte-infected stands of turf.

**ACKNOWLEDGMENTS**

This work was supported by the United States Department of Agriculture NRI grant number 00-35316-9249 and by state and federal funds appropriated to the Ohio Agricultural Research and Development Center.

### Table 2. F values from ANOVA showing influence of endophyte infection and herbivory by Japanese beetle larvae on perennial ryegrass and tall fescue performance parameters and influence of endophyte infection on Japanese beetle (P. japonica) larval density and biomass in mixed stands of tall fescue or perennial ryegrass and dandelion.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Number of tillers</th>
<th>Above-ground biomass (g)</th>
<th>Root biomass (g)</th>
<th>P. japonica density</th>
<th>P. japonica mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perennial ryegrass</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Endophyte (E)</td>
<td>27.3†</td>
<td>7.6**</td>
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<td>0.1</td>
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<td>Herbivory (H)</td>
<td>27.8†</td>
<td>14.6†</td>
<td>13.5***</td>
<td>~†</td>
<td>~</td>
</tr>
<tr>
<td>E × H</td>
<td>0.0</td>
<td>9.9</td>
<td>0.2</td>
<td>~</td>
<td>~</td>
</tr>
<tr>
<td>Tall fescue</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>0.6</td>
<td>0.7</td>
<td>2.9*</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>H</td>
<td>12.9***</td>
<td>13.8†</td>
<td>17.2†</td>
<td>~</td>
<td>~</td>
</tr>
<tr>
<td>E × H</td>
<td>0.7</td>
<td>1.0</td>
<td>0.3</td>
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<td>~</td>
</tr>
</tbody>
</table>

* P ≤ 0.1.
** P ≤ 0.05.
*** P ≤ 0.01.
† P ≤ 0.001.
‡ Effect not applicable.

### Table 3. F values for dandelion response to endophyte infection in perennial ryegrass and tall fescue competitors, and herbivory by Japanese beetle larvae in greenhouse mixtures with each grass.

<table>
<thead>
<tr>
<th>Effect</th>
<th>No. of leaves</th>
<th>Above-ground biomass (g)</th>
<th>Root biomass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competitor = perennial ryegrass</td>
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<td></td>
</tr>
<tr>
<td>Endophyte (E)</td>
<td>18.1†</td>
<td>5.9**</td>
<td>3.6*</td>
</tr>
<tr>
<td>Herbivory (H)</td>
<td>16.3†</td>
<td>12.0**</td>
<td>21.6†</td>
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<td>E × H</td>
<td>0.6</td>
<td>0.8</td>
<td>0.1</td>
</tr>
<tr>
<td>Competitor = tall fescue</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>18.1†</td>
<td>5.9**</td>
<td>0.3</td>
</tr>
<tr>
<td>H</td>
<td>13.5†</td>
<td>6.3**</td>
<td>10.4***</td>
</tr>
<tr>
<td>E × H</td>
<td>0.4</td>
<td>0.8</td>
<td>1.6</td>
</tr>
</tbody>
</table>

* P ≤ 0.1.
** P ≤ 0.05.
*** P ≤ 0.01.
† P ≤ 0.001.
REFERENCES