# Host Plant Resistance of Cool-Season (C3) Turfgrasses to Above- and Belowground Feeding by *Tipula paludosa* (Diptera: Tipulidae)

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**ABSTRACT** Feeding on above- and belowground plant tissues by *Tipula paludosa* Meigen during the period of rapid growth from second to forth instars is highly damaging to cool-season (C3) turfgrasses. It may be possible to reduce this damage by identifying grass genotypes that increase host plant protection. This study examined the impacts of plant genotype, endophyte infection, and plant ontogeny on host plant and insect responses during whole-plant feeding by *T. paludosa*. A series of no-choice greenhouse trials were conducted with third instar crane flies to determine 1) host plant tolerance in terms of reductions to above- and belowground plant biomass, 2) antixenosis resistance impacting insect behavior (emigration), and 3) antibiosis resistance impacting insect growth. Results showed that insect infestation level was the primary factor influencing plant biomass reductions. Belowground tissues were more tolerant to feeding than were aboveground tissues, with tall fescues, *Festuca arundinacea* Schreber, being most resistant to aboveground biomass reduction. Host plant associations with intercellular fungal endophytes (E+) decreased insect weight gain and decreased insect movement, but did not increase host plant tolerance. Plant ontogeny affected this response with insect weight gain significantly decreased on young (28 d) growth E+ grasses but not on old (90 d) growth E+ grasses, however. Host plant genotype and plant ontogeny can have significant impacts to host plant tolerance and insect physiology for *T. paludosa* larva. Furthermore, plant-endophyte associations have apparent sublethal effects that impact insect fitness and may further enhance host plant protection.

**KEY WORDS** antibiosis, antixenosis, insect behavior, crane fly, endophytes

Grasses grown for turf are faced with numerous insect pests that impact both above- and belowground plant tissues. With few exceptions, insects that feed on turfgrasses rarely cause direct feeding damage to both sets of tissues during a particular stage of their development (Vittum et al. 1999). Previous work has indicated that the crane fly (Diptera: Tipulidae) *Tipula paludosa* Meigen is primarily a pest through belowground feeding activity (Blackshaw and Coll 1993, Dawson et al. 2002), but active feeding also occurs on aboveground tissues. Peck et al. (2010) documented extensive direct aboveground biomass loss through crane flies feeding and indicated that 50–75% of tine holes on golf course greens exhibited larval chewing damage. This unique case where active feeding takes place on both above- and belowground tissues during each instar may mean that constitutive plant defenses restricted to particular plant tissues may not protect against feeding on other tissues.

Plant defenses that deter or reduce insect feeding are often restricted to particular sets of tissues, though linkages of above- and belowground defenses do exist (Bezemer and van Dam 2005). As a method of plant protection, selection of host plants that incorporate multiple lines of defense can greatly enhance integrated pest management (IPM) programs aimed at safeguarding grass-based systems (Reinert et al. 2004, Held and Potter 2012). Each type of host plant resistance, whether antixenosis (preference, behavior), antibiosis (insect physiological response), or plant tolerance can increase protection against the detrimental impacts of insect herbivory. In the context of managed turfgrass settings, understanding insect-plant interactions on both above- and belowground plant tissues will help to identify viable plant defenses and increase host plant protection against *T. paludosa.*

As host plants, grasses may have several simultaneously acting mechanisms that can increase plant resistance. Grasses typically counter herbivory through compensation that increases tolerance (Hawkes and Sullivan 2001). Changes in physiology, morphological defenses, and mutualistic associations may also occur (Strauss and Agrawal 1999, Hawkes and Sullivan 2001, Heng–Moss et al. 2006). Aboveground physical defenses including lignin and fiber content that impact texture and toughness can greatly increase plant protection (Hanley et al. 2007, Clissold et al. 2009). These physical defenses can also increase with plant age.

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Hong et al. (2012) showed that that several species of turfgrass increased in fiber and lignin content over time, resulting in a reduction in weight gain by *Agrotis ipsilon* Hufnagel. Mutualistic associations with intercellular fungal endophytes may also increase aboveground tissue protection through the production of alkaloids that serve as defensive compounds that can deter insect feeding (Popay et al. 1994, Potter et al. 2008).

While *T. paludosa* is known to feed on a wide range of plant genotypes, little is known about host plant preference or how plant defenses may impact feeding ecology. Pesho et al. (1991) found little impact of forage grass genotype on *T. paludosa* field infestation levels, while in turfgrasses ryegrasses were less infested than bluegrasses, fescues, and bentgrasses. Mechanisms of direct feeding have only been investigated for belowground plant tissues. Dawson et al. (2002) supported the work of Ramsell et al. (1993) in showing that plant genotype and root physical structure can influence *T. paludosa* feeding, with larvae greatly reducing *Trifolium repens* (L.) root length but having no effect on *Lolium perenne* L. root length. *T. paludosa* feeding was also shown to decrease biomass and root:shoot ratios in *T. repens* but not in *Agrostis capillaris* (L.); however, the rate of root appearance for *A. capillaries* was significantly reduced (Dawson et al. 2004). Little work has examined the extent to which aboveground tissue defenses impact *T. paludosa* feeding success. Lewis and Vaughan (1997) showed no impact of *T. paludosa* feeding on host plants associated with intercellular fungal endophytes, though this study was limited to only three varieties of *L. perenne.*

This study was designed to examine the impacts of host plant factors on the feeding ecology of *T. paludosa.* Understanding the roles of host plant, antixenosis and antibiosis resistances are needed for whole plant feeding insects such as *T. paludosa.* Here, we used controlled no-choice feeding experiments with several cool-season (C3) grass species and cultivars commonly grown as turf to evaluate both plant and insect responses. Our main objectives were to identify the factors that affected the protection of above- and belowground biomass and to examine the degree to which either sets of plant tissues were more susceptible to feeding damage. To do this, we used a host plant feeding trial to examine the effects of plant species, host plant morphology and endophyte infection on 1) plant biomass change and 2) insect survival and behavior (i.e., emigration). We then studied the role of plant ontogeny and endophyte infection on 3) insect weight gain through a set of independent insect feeding trials.

## Materials and Methods

**Plant Material.** All grass species and cultivars used in these studies were commercially available (Preferred Seed, Buffalo, NY). One endophytic (E+) and one endophyte-free (E-) cultivar were included for each of fine fescue, tall fescue, and perennial ryegrass. Grass species and cultivars included fine fescues 'Chewings fescue' (E-; *Festuca rubra* L. ssp. *fallax* (Thuillier) Nyman) and 'Creeping red' fescue (E+; *Festuca rubra* L. ssp. *arenaria* (Osbeck) Aresch); tall fescues (*Festuca arundinacea* Schreber) 'Rhambler' (E+), 'K31′ (E-), Kentucky bluegrasses (*Poa pratensis* L.), 'Brilliant' (E-), and 'Kenblue' (E-); perennial ryegrasses 'Protégé GLR' (E-) and 'Revenge GLX' (E+); and creeping bentgrass (*Agrostis stolonifera* L.) 'Penncross' (E-). All seed was stored under controlled conditions (4°C) before, and throughout the duration of this work. The presence of endophytic fungi, *Epichloë*/*Neotyphodium* spp. (Ascomycetes: Clavicipitaceae), was assessed at the time of seeding for all trials with a Phytoscreen seed endophyte detection kit (Agrinostics Ltd. Co., Watkinsville, GA). Endophyte infection was calculated based on the percentage of infected seeds ($n = 100$) detected for each cultivar. Cultivars with >50% endophyte infection rate were considered E+. Cultivars with a 0% endophyte infection rate were considered E-, with the exception of Chewing's fescue that had low infection (10%) across both years and was classified as E-.

For the host plant trials, individual round 9 cm diameter plastic pots were filled to 1 cm of the pot rim with a sterilized soil mix (90% sand, 10% peat moss). Seeding rates were established to reflect commercially suggested rates: Kentucky bluegrasses 9.8 g/m$^2$ (recommended 4.8–9.8 g/m$^2$), perennial ryegrass 34 g/m$^2$ (29–39 g/m$^2$), fine fescues 29 g/m$^2$ (24–34 g/m$^2$), tall fescues 44 g/m$^2$ (39–48 g/m$^2$), and creeping bentgrass 4.8 g/m$^2$ (4.8–9.8 g/m$^2$). Seeding occurred for the first trial (2010) on 1 March 2010 and the trial was initiated on 30 April 2010. For the second trial (2011), seeding occurred on 04 March 2011 and the trial was initiated on 06 May 2011. After seeding for either trial, pots were arranged on greenhouse benches in a randomized complete block design with an equal number of infested to uninfested control pots for each grass cultivar. Each pot was initially fertilized with 6 g of Osmocote (The Scotts Company, Marysville, OH) controlled release fertilizer (18–6-12). Pots were maintained and grasses allowed to germinate and develop before trial initiation under controlled greenhouse conditions at a mean temperature of 15°C (12–19°C) and a photoperiod of 14:10 (L:D) h. The greenhouse was equipped with an automated overhead irrigation system that delivered 5 cm of irrigation every other day. Grasses were trimmed weekly to a height of 8 cm until trial initiation, after which they were not trimmed. One week before trial initiation, potted grasses were moved from the greenhouse to an environmental chamber that reduced variation in temperature (15°C and photoperiod of 14:10 [L:D]) h. At this time all plots were enclosed in clear, bottom-sealed Plexiglas tubes (15 cm internal diameter [i.d.], 40 cm tall) to ensure that larvae, once placed in the pots, could not move among replicates.

For the insect feeding trial, a separate set of grasses were established to assess the impact of grass genotype and plant ontogeny on insect fitness. In the first trial (2010) replicated ($n = 20$) 30 ml plastic cups were filled with the standard soil mix and seeded on 2 April

2010 with a pinch of grass seed for each cultivar. A set of cups without seeding served as a control. Cups were maintained under controlled conditions (15°C and a photoperiod of 14:10 [L:D] h). Cups were watered twice weekly (5 ml), or as needed. At the initiation of the trial on 30 April 2010 grasses had developed for 28 d and were considered young growth plants. A second trial (2011) was conducted on older plant material that was allowed to establish for 90 d. Replicated ($n = 10$) plastic pots (9 cm diameter) were seeded on 1 February 2011 and maintained as in the host plant trials until trial initiation on 2 May 2011.

**Source of Test Insects.** Active third instar T. *paludosa* were used in all trials. This growth phase was selected because the third instar represents the life-stage where insect feeding causes the greatest damage to host plant material in northeastern United States (Peck et al. 2010). Larvae for all trials (2010, 2011) were collected from a multipurpose mixed grass (Kentucky bluegrass/tall fescue/perennial ryegrass/creeping bentgrass) field in Lockport, NY, through several collections made on 10–20 April 2010 and 08–19 April 2011. After collection, larvae were held under controlled conditions at 15°C and fed organic green leaf lettuce until the initiation of trials. Two days before infestation larvae were separated and held in soil without food. To account for low field collections of larvae that occurred in 2011, we supplemented field insect collections with lab-reared larvae. Lab colonies were reared from eggs taken from adults collected at the same research field used for larval collections. Lab colonies were maintained at 10°C on sterile sand and reared on organic leaf lettuce. Lab-reared crane flies where third instars at the time of the trial. Instar determination was made through measurements of head capsule width based data collected from previously reared larvae (unpublished data).

**Host Plant Trials.** Trials in 2010 and 2011 were conducted to evaluate insect behavior and plant response. In the 2010 trial a total of 10 potted replicates per grass cultivar (5 infested × 5 uninfested controls; 180 pots total) were used at one infestation level (four larvae per pot). In the 2011 trial the number of replicates were increased (10 infested × 10 uninfested; 20 pots per cultivar; 260 total pots) and two infestation levels (four or seven larvae per pot) were used. An infestation of four larvae corresponded to an economic threshold of 493 larvae/$m^2$ (40 larvae/$ft^2$). This threshold was established to reflect the findings of Peck et al. (2010) who found a higher threshold than that established in the pacific northwest United States (Antonelli and Campbell 1989). Larval densities at seven larvae per pot (80 larvae/$ft^2$, 889 larvae/$m^2$) nearly doubled these threshold levels. Larvae were weighed before infestation and grouped into sets of four (2010, 2011) or seven (2011) with equal total larval weights assigned for each group to ensure that equal infestation rates were applied to each pot. At the start of the trial, sets of larvae were placed on the soil surface of each test pot. Larvae that did not enter the soil after one day were replaced with live larvae. The infested and control pots were maintained for 28 d. During the trials, the Plexiglas tubes were checked every other day for larvae occurring outside of the pots (i.e., insect emigration). All larvae found outside of pots were counted and returned to the corresponding pot. Insect mortality was measured at the end of each set of trials. At the end of both trials, all potted replicates were destructively sampled. Above- and belowground biomass were separated, washed and held for 2 wk at 38°C and 5% humidity before being weighed. Before drying, the mean tiller diameter and tiller weight for each cultivar were determined based on measurements of 10 tillers from each control pot. Measurements were taken only from control pots to eliminate any bias that may have been caused because of larval feeding activity.

Plant biomass change for each cultivar was measured as the change in above- and belowground biomass in relation to the mean above- and belowground biomass of the corresponding uninfested controls. Proportional plant biomass change was determined as: $(WT_{infested} - WT_{control})/WT_{control}$, where $WT_{infested}$ is the end tissue specific weight for each infested pot and $WT_{control}$ is mean end tissue specific weight for the corresponding control group. A larger value of Δ indicated increases in biomass in relation to the control, while a lower value of Δ indicated larger reductions to biomass in relation to the controls.

**Insect Feeding Trials.** Trials in 2010 and 2011 were conducted to assess the impact of plant ontogeny on insect weight gain. Insect weight gain was measured on young (28 d) growth grasses in 2010 and on older (90 d) grasses in 2011. In both years, active third instar *T. paludosa* were held without food for 24 h pretrial, weighed, and added one per replicate. In both years, each replicate was enclosed to prevent insect escape. Larvae were removed at the end of the 14 d, held without food for 24 h, and reweighed. To account for differences in initial weights among larvae, the final weight change of each larva was measured as the proportional insect weight change: $(WT_{end} - WT_{start})/WT_{start}$, where $WT_{start}$ is the starting insect weight and $WT_{end}$ is the end insect weight.

**Data Analysis.** Plant response data from the two host plant trials were analyzed separately by trial, as randomized complete block experiments. All analyses were performed in R (R Development Core Team 2009). The impact of larvae feeding on the change in above- and belowground biomass in relation to uninfested controls within grass cultivars were compared using a paired *t*-test for the first trial, and by a one-way analysis of variance (ANOVA) with infestation level as a main effect for the second trial. Significant differences among infestation levels for cultivars in the second trail were determined using Fisher least significant difference (LSD) test. All differences were determined significant at $P < 0.05$.

Insect (cumulative emigration, and mortality) and plant (Δ Above, Δ Below) responses measured during the 2011 host plant trail were modeled using generalized linear model analyses. A model selection procedure was conducted using Akaike's Information Criterion, adjusted for small sample size (AICc)

**Table 1. Mean (±SE) belowground biomass change (g) of select grass species and cultivars after 28 d of feeding by *T. paludosa* at low (four) and high (seven) infestation levels**

| Species/cultivar | 2010 | | 2011 | | |
|---|---|---|---|---|---|
| | 0 larvae (g) | 4 larvae (g) | 0 larvae (g) | 4 larvae (g) | 7 larvae (g) |
| Fine fescue | | | | | |
| Chewings | 2.21 ± 0.16a | 1.80 ± 0.16a | 0.83 ± 0.05a | 0.79 ± 0.06a | 0.73 ± 0.06a |
| Creeping red | 2.32 ± 0.27a | 1.66 ± 0.27a | 0.67 ± 0.04a | 0.61 ± 0.05a | 0.66 ± 0.05a |
| Tall fescue | | | | | |
| K31 | 2.46 ± 0.17a | 1.54 ± 0.17b | 1.14 ± 0.15b | 1.50 ± 0.11a | 0.98 ± 0.13b |
| Rhambler | 3.63 ± 0.30a | 2.18 ± 0.27b | 0.96 ± 0.05a | 0.79 ± 0.07a | 0.96 ± 0.07a |
| Kentucky bluegrass | | | | | |
| Brilliant | 1.03 ± 0.22a | 0.81 ± 0.22a | — | — | — |
| Kenblue | 3.19 ± 0.38a | 2.55 ± 0.38a | 0.68 ± 0.04a | 0.59 ± 0.05a | 0.64 ± 0.05a |
| Perennial ryegrass | | | | | |
| Protégé GLR | 2.10 ± 0.16a | 1.45 ± 0.16b | 1.19 ± 0.07a | 1.24 ± 0.09a | 0.84 ± 0.09b |
| Revenge GLX | 2.08 ± 0.32a | 1.39 ± 0.32a | 0.77 ± 0.06a | 0.67 ± 0.07a | 0.75 ± 0.07a |
| Creeping bentgrass | | | | | |
| Penncross | 4.24 ± 0.55a | 2.10 ± 0.61b | 1.17 ± 0.08a | 0.97 ± 0.09a | 1.16 ± 0.10a |

Means within a row followed by a different letter are significantly different ($P < 0.05$; *t*-test [2010]; LSD test [2011]).

(Burnham and Anderson 1998). All possible models, including intercept only models, were evaluated for each analysis using the MuMIn package (Bartón 2011) in R (R Development Core Team 2009). The best-fit models were selected as the model(s) having the lowest AICc value, with all models possessing ΔAICc values <2.0 additionally retained as equally good (Burnham and Anderson 1998). Parameter coefficient estimates ($\beta$) and Akaike weights (*W*i) for each variable were averaged across the set of best-fit models. Akaike weights averaged across all best models provided a value of the relative variable importance (RVI) of each factor. Predictor variables used to explain plant change (Δ Below, Δ Above) and insect response (emigration, mortality) included: grass species (SP), larval infestation at the start of the trial (ST), percent mortality (MT), fungal endophyte status (EN), mean tiller mass (TM), mean tiller diameter (TD), and grass growth habit (i.e., bunch or lateral growth) (BC). Mortality data were expressed as percent mortality recorded for each pot. Cumulative insect emigration data were expressed as the total insect escapes, with replacement, for each pot. All data were checked for normality before analyses. Cumulative emigration data were square root transformed and mortality data were arcsine square root transformed before analyses. Model significance was determined through a likelihood-ratio test comparing all best models to the intercept-only model. Only the second year of data (2011) was used in these analyses because of the confounding effects of a single infestation level used in the first year.

The relationship between above- and belowground biomass was further examined by regressing Δ Above against Δ Below for each of the two infestation levels from the host plant trial in 2011. A linear regression was conducted to determine the relationship between the two factors.

Differences among grass species and cultivars during insect feeding trials were determined using a one-way ANOVA. Tukey's mean separation was used to test for differences among cultivars. Insect weight gain on plants at 28 and 90 d growth were analyzed separately. For grass species with endophyte expression (fine fescue, perennial ryegrass, and tall fescue), the effects of grass species, endophyte infection, and their interaction on insect weight gain were determined using multiple regressions. All differences were determined significant at $P < 0.05$. Analyses were performed in R (R Development Core Team 2009).

## Results

**Host Plant Trials.** *Plant Tolerance. T. paludosa* larvae were observed to readily feed on and impact both belowground (Table 1) and aboveground (Table 2) plant tissues. During the 2011 trials, Brilliant Kentucky bluegrass experienced extensive powdery mildew infection across a majority of pots and was excluded from further analyses. There was a significant reduction in K31 ($t = -3.88$; df = 7.73; $P < 0.01$) and Rhambler ($t = -3.49$; df = 5.92; $P = 0.01$) tall fescues, Protégé GLR perennial ryegrass ($t = -2.87$; df = 7.86; $P = 0.02$), and 'Penncross' creeping bentgrass ($t = -2.16$; df = 6.08; $P = 0.05$) belowground biomass in 2010. In 2011 belowground biomass significantly increased for K31 tall fescue at the low infestation level ($F = 4.05$; df = 2; $P = 0.03$) and significantly decreased for Protégé GLR perennial ryegrass at the high infestation level ($F = 5.81$; df = 2; $P = 0.01$). Aboveground biomass was a significantly reduced for K31 ($t = -2.55$; df = 6.70; $P = 0.04$) and Rhambler GLX ($t = -2.16$; df = 5.4; $P = 0.05$) tall fescues; 'Kenblue' Kentucky bluegrass ($t = -3.10$; df = 7.21; $P = 0.02$) and Revenge GLX perennial ryegrass ($t = -2.10$; df = 5.87; $P = 0.05$), in 2010. In 2011, at low infestation there was a significant reduction for all cultivars (df = 2; $P < 0.05$) except Creeping red fine fescue and Kenblue Kentucky bluegrass. At high infestation there was a significant reduction in all cultivars (df = 2; $P < 0.05$) except Penncross creeping bentgrass, Protégé GLR perennial ryegrass, and K31 tall fescue.

Model selection resulted in a set of three best models for proportional belowground biomass change (Δ

**Table 2. Mean (±SE) aboveground biomass change (g) of select grass species and cultivars after 28 d of feeding by *T. paludosa* at low (four) and high (seven) infestation levels**

| Species/cultivar | 2010 | | 2011 | | |
|---|---|---|---|---|---|
| | 0 larvae (g) | 4 larvae (g) | 0 larvae (g) | 4 larvae (g) | 7 larvae (g) |
| Fine fescue | | | | | |
| Chewings | 1.80 ± 0.16a | 1.66 ± 0.16a | 1.05 ± 0.06a | 0.77 ± 0.08b | 0.58 ± 0.08b |
| Creeping red | 1.65 ± 0.07a | 1.36 ± 0.07a | 1.05 ± 0.06a | 0.90 ± 0.08ab | 0.73 ± 0.08b |
| Tall fescue | | | | | |
| K31 | 1.31 ± 0.05a | 1.12 ± 0.05b | 1.03 ± 0.09a | 0.68 ± 0.11b | 1.07 ± 0.11a |
| Rhambler | 1.82 ± 0.08a | 1.51 ± 0.09b | 1.53 ± 0.07a | 1.15 ± 0.09b | 1.16 ± 0.09b |
| Kentucky bluegrass | | | | | |
| Brilliant | 1.11 ± 0.14a | 1.03 ± 0.14a | — | — | — |
| Kenblue | 1.61 ± 0.08a | 1.14 ± 0.06b | 1.14 ± 0.06a | 0.95 ± 0.07ab | 0.79 ± 0.07b |
| Perennial ryegrass | | | | | |
| Protégé GLR | 1.82 ± 0.11a | 1.60 ± 0.11a | 1.14 ± 0.15a | 0.75 ± 0.12b | 0.84 ± 0.12b |
| Revenge GLX | 1.67 ± 0.17a | 1.16 ± 0.17b | 1.12 ± 0.09a | 0.65 ± 0.10b | 0.41 ± 0.10b |
| Creeping Bentgrass | | | | | |
| Penncross | 1.92 ± 0.09a | 1.78 ± 0.09a | 1.29 ± 0.09a | 0.88 ± 0.11b | 1.19 ± 0.12ab |

Means within a row followed by a different letter are significantly different ($P < 0.05$; *t*-test [2010]; LSD test [2011]).

Below) (Table 3) and a set of five best models for proportional aboveground biomass change (Δ Above) (Table 4). All best models were significantly better ($P < 0.05$) than the intercept only model. Highest average Akaike weights recovered a positive relationship between Δ Below and cumulative insect mortality (RVI = 1.00; $\beta = 0.16$). Starting infestation level, endophyte infection, species identity, tiller diameter, and tiller mass had marginal or no measurable impacts on Δ Below. Highest Akaike weights recovered a negative correlation between Δ Above and the high infestation level (RVI = 1.00; $\beta = -0.08$). Grass species identity strongly impacted Δ Above (RVI = 1.00), with tall fescues ($\beta = 0.34$) having higher biomass than other species.

Host plants showed strong variation in the relationship between Δ Above and Δ Below according to larval infestation level (Fig. 1). At low infestation there was no relationship between Δ Above and Δ Below ($F = 0.09$; df = 1; $P = 0.76$); however, at the high infestation there was a significant positive correlation ($F = 13.47$; df = 1; $P < 0.05$).

*Emigration and Mortality.* Insect emigration and mortality were both higher in the 2011 trials (Table 5). Cumulative emigration ranged from 0.20 to 2.60 escapes per pot in 2010, and 0.45–4.00 (four larvae) and 1.30–4.90 (seven larvae) escapes per pot in 2011. Mortality per potted replicate ranged from 13–40% in 2010, and 25–58% (four larvae) and 34–78% (seven larvae) in 2011.

The influence of grass and trial factors on cumulative insect emigration was explained by a set of three best models (Table 6). The influence of grass and insect factors on percent mortality was explained by two best models (Table 7). All best models were significantly better ($P < 0.05$) than the intercept only model. Cumulative insect mortality had a negative correlation with cumulative insect emigration (RVI = 1.00; $\beta = -0.63$) and the presence of fungal endophytes (RVI = 1.00; $\beta = -0.48$). Insect emigration was positively correlated with the high rate of insect infestation (RVI = 1.00; $\beta = 0.14$). Grass species identity also impacted emigration (RVI = 0.77), with all species having a negative effect on mortality relative to Kentucky bluegrass. Cumulative insect mortality had a negative correlation with the amount of insect emigration (RVI = 1.00; $\beta = -0.11$), the presence of fungal endophytes (RVI = 1.00; $\beta = -0.30$) and grass tiller diameter (RVI = 1.00; $\beta = -1.49$). A positive correlation between mortality and tiller mass was recovered (RVI = 1.00; $\beta = 1.03$).

**Table 3. Model selection table showing best models and relevant factors affecting host plant proportional belowground biomass change**

| Models | Model components[a] | | | k | ΔAICc | Wi[b] | Adj. $R^2$ |
|---|---|---|---|---|---|---|---|
| | ST | MT | EN | | | | |
| 1 | | + | | 3 | 0.00 | 0.54 | 0.05 |
| 2 | + | + | | 4 | 1.00 | 0.25 | 0.05 |
| 3 | | + | + | 4 | 1.52 | 0.21 | 0.04 |
| $\beta$[c] | <0.01 | 0.16 | <0.01 | | | | |
| RVI[d] | 0.29 | 1.00 | 0.23 | | | | |

The most appropriate model is model 1. All other models with Akaike information criteria adjusted for small sample sizes (AICc) <2.00 are also presented within the best model set.

[a] Only factors with model contribution are shown: ST, starting infestation; MT, mortality; EN, endophyte present.

[b] Akaike wt.

[c] Parameter estimates averaged across all best models.

[d] Relative variable importance as sum of *Wi* across all best models.

**Insect Feeding Trials.** Larvae were found to actively feed and gain weight on all tested grass species and cultivars. Larval weight gains were generally higher on young (28 d) growth grasses (Fig. 2). Final larval weights in the young growth trial were significantly greater than that of the control ($F = 113.58$; df = 10; $P < 0.05$) and there were significant differences among grass species ($F = 4.9$; df = 1; $P < 0.05$) with larvae gaining significantly more weight on Kentucky bluegrass, tall fescue, and perennial ryegrass than on creeping bentgrass. Mortality was nil (0%) across all cultivars except for Penncross creeping bentgrass (25%) and Creeping red fine fescue (10%). Among turfgrass species with endophyte expressing cultivars (fine fescue, perennial ryegrass, and tall fescue),

**Table 4. Model selection table showing best models and relevant factors affecting host plant proportional aboveground biomass change**

| Models | Model components[a] | | | | | | k | ΔAICc[b] | *Wi* | Adj. $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | SP | ST | MT | EN | TD | BC | | | | |
| 1 | + | - | | | - | | 8 | 0.00 | 0.31 | 0.22 |
| 2 | + | - | + | | - | | 9 | 0.66 | 0.22 | 0.23 |
| 3 | + | - | | - | | - | 9 | 0.69 | 0.22 | 0.22 |
| 4 | + | - | + | - | | - | 10 | 1.63 | 0.14 | 0.04 |
| 5 | + | - | + | | | | 8 | 1.90 | 0.12 | 0.08 |
| $\beta$[c] | * | −0.08 | 0.04 | −0.04 | −1.03 | −0.09 | | | | |
| RVI[d] | 1.00 | 1.00 | 0.48 | 0.35 | 0.53 | 0.35 | | | | |

The most appropriate model is model 1. All other models with Akaike information criteria adjusted for small sample sizes (AICc) <2.00 are also presented within the best model set.

[a] Only factors with model contribution are shown: SP, species; ST, starting infestation; MT, mortality; EN, endophyte present; TD, mean tiller diam.; BC, bunch growth.

[b] Akaike wt.

[c] Parameter estimates averaged across all best models.

[d] Relative variable importance as sum of *Wi* across all best models.

* $\beta$ values for species: creeping bentgrass = −0.11; fine fescue = −0.12; Kentucky bluegrass = 0.00; perennial ryegrass = 0.09; tall fescue = 0.34.

weight differences by grass species were not detected ($F = 1.49$; df = 2; $P = 0.23$). Larval growth on E+ cultivars was significant lower than growth on E- cultivars ($F = 5.68$; df = 1; $P = 0.02$). No interaction between endophyte presence and grass species was detected ($F = 0.02$; df = 1; $P = 0.98$). Mean weight of larvae was 0.21 g (1.17 proportional weight increase) on E- cultivars and 0.19 g (1.00 proportional weight increase) on E+ cultivars.

On older plants, larval weights were greater than those of the control ($F = 19.80$; df = 9; $P < 0.01$). Because of powdery mildew infection, Brilliant Kentucky bluegrass was removed from this trial. There were significant differences among grass species ($F = 6.4$; df = 6; $P < 0.01$) with larvae gaining significantly more weight on perennial ryegrass than on tall fescue or fine fescue. Mortality was higher on old plants (mean = 38%), being highest in creeping bentgrass (74%) and K31 tall fescue (67%) and lowest in Kenblue Kentucky bluegrass (14%), Revenge GLX perennial ryegrass (20%) and Creeping red fine fescue (0%). There was no correlation between mortality and larval weight change among species ($F = 0.02$; df = 2; $P = 0.81$). Among turfgrass species with endophyte expressing cultivars (fine fescue, perennial ryegrass, and tall fescue), species differences were found ($F = 9.85$; df = 2; $P < 0.05$) and larvae gained the most weight on perennial ryegrasses. Larval weights were not different between E+ and E- cultivars ($F = 0.07$; df = 1; $P = 0.80$) but there was a significant interaction between endophyte infection and grass species ($F = 3.9$; df = 2; $P = 0.03$). Mean weight of larvae was 0.08 g (0.33

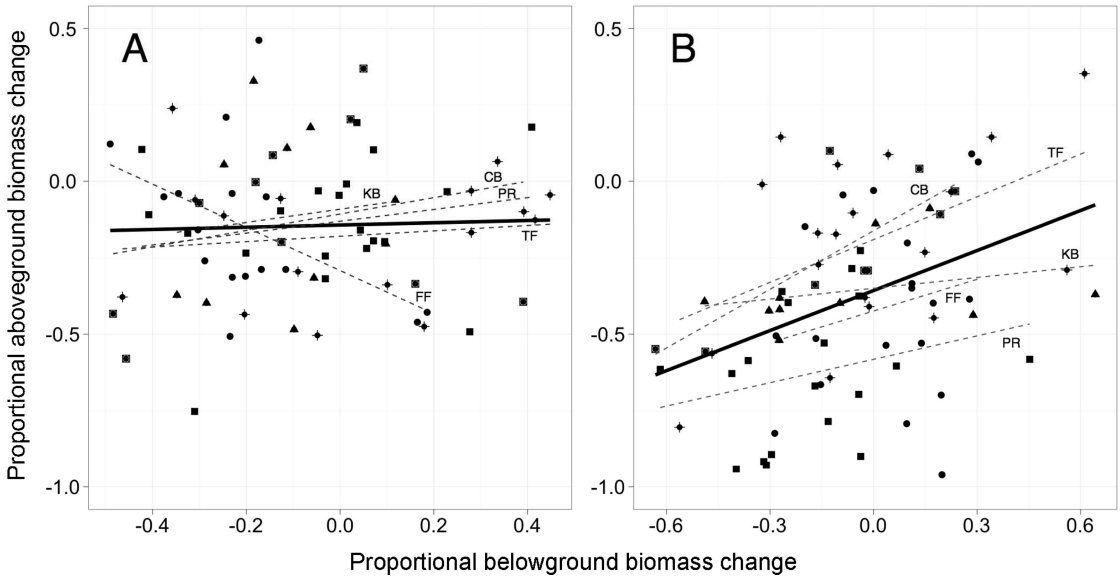


**Fig. 1.** Relationship between proportional below- and aboveground biomass at (A) four and (B) seven larvae per pot infestations. Linear regressions from pooled (solid line) and individual species (dashed lines) are shown (CB = creeping bentgrass; FF = fine fescue; KB = Kentucky bluegrass; PR = perennial ryegrass; TF = tall fescue).

**Table 5. Mean (±SE) emigration and mortality (%) response by larvae at low (four larvae) and high (seven larvae) infestation levels**

| Species/cultivar | 2010 | | 2011 | | | |
|---|---|---|---|---|---|---|
| | 4 larvae | | 4 larvae | | 7 larvae | |
| | Emigration | Mortality | Emigration | Mortality | Emigration | Mortality |
| Creeping bentgrass | | | | | | |
| Penncross | 2.60 ± 0.40b | 20 ± 13a | 1.60 ± 0.31ab | 48 ± 13a | 4.90 ± 0.36b | 61 ± 36ab |
| Fine Fescue | | | | | | |
| Chewings | 0.60 ± 0.40ab | 40 ± 13a | 1.20 ± 0.31b | 38 ± 13a | 4.00 ± 0.36b | 61 ± 36ab |
| Creeping red | 0.20 ± 0.40a | 15 ± 13a | 1.80 ± 0.31ab | 33 ± 13a | 1.30 ± 0.36a | 35 ± 36a |
| Kentucky bluegrass | | | | | | |
| Kenblue | 1.80 ± 0.40ab | 25 ± 13a | 4.00 ± 0.31a | 40 ± 13a | 3.40 ± 0.36ab | 47 ± 36ab |
| Brilliant | 1.00 ± 0.40ab | 31 ± 13a | — | — | — | — |
| Perennaial ryegrass | | | | | | |
| Protégé GLR | 0.20 ± 0.40a | 20 ± 13a | 1.66 ± 0.31ab | 25 ± 13a | 2.10 ± 0.36ab | 41 ± 36a |
| Revenge GLX | 0.25 ± 0.40ab | 13 ± 13a | 0.45 ± 0.31b | 48 ± 13a | 2.30 ± 0.36ab | 78 ± 36b |
| Tall fescue | | | | | | |
| K31 | 0.80 ± 0.40ab | 15 ± 13a | 1.44 ± 0.31b | 23 ± 13a | 3.40 ± 0.36ab | 34 ± 36a |
| Rhambler | 0.20 ± 0.40a | 15 ± 13a | 2.20 ± 0.31ab | 58 ± 13a | 1.90 ± 0.36ab | 43 ± 36a |

Means within a row followed by a different letters are significantly different ($P < 0.05$; LSD test).

proportional weight gain) on E- and 0.08 g (0.35 proportional weight gain) on E+ grasses.

## Discussion

The results of this study indicate host plant resistance to *T. paludosa* can be increased through a combination of more tolerant grass genotypes and host factors that increase antixenosis and antibiosis resistance. While we observed direct feeding on both above- and belowground plant tissues, it was apparent that aboveground biomass reductions were consistently greater than belowground reductions. Aboveground biomass was reduced on average by 25%, ranging from 13% in K31 tall fescue to 42% in Revenge GLX perennial ryegrass. By contrast belowground biomass was reduced on average by 11%, ranging from 2% in K31 tall fescue to 17% in Protégé GLR perennial ryegrass. While *T. paludosa* has been shown to significantly reduce belowground biomass (Dawson et al. 2002), our results do not confirm this. Therefore, our results are best interpreted as detecting tolerance directed at aboveground biomass. A promising result indicated that larvae gained less weight on grass genotypes that were also more tolerant of insect feeding (tall fescue) and had decreased emigration from pots of less tolerant species (perennial ryegrass). The insect-host plant relationship did change as a factor of both plant ontogeny and endophyte infection status, however. Insects feeding on older grasses, with the exception of Penncross creeping bentgrass, resulted in significantly decreased larval weight gain. Insects feeding on E+ cultivars had decreased weight gain on young plants, but this impact was decreased over plant ontogeny. These study results most clearly indicate a role for resistant grass genotypes, particularly tall fescue, in IPM programs for *T. paludosa*, but highlight the need for further research elucidating the impact of plant ontogeny and endophyte infection host plant protection.

Overall, aboveground tissues tended to be less tolerant to insect feeding than did belowground tissues. That is not to say aboveground tissues were fed on more by *T. paludosa*, but that the effects of feeding were more pronounced in above- over belowground

**Table 6. Model selection table showing best models and relevant factors affecting insect emigration during antixenosis trials**

| Models | Model components[a] | | | | | k | ΔAICc | *Wi*[b] | Adj. $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| | SP | ST | MT | EN | BC | | | | |
| 1 | + | + | - | - | | 8 | 0.00 | 0.56 | 0.18 |
| 2 | | + | - | - | - | 5 | 1.76 | 0.23 | 0.17 |
| 3 | + | + | - | - | - | 9 | 1.96 | 0.21 | 0.18 |
| $\beta$[c] | * | 0.14 | −0.63 | −0.48 | −0.10 | | | | |
| RVI[d] | 0.77 | 1.00 | 1.00 | 1.00 | 0.44 | | | | |

The most appropriate model is model 1. All other models with Akaike information criteria adjusted for small sample sizes (AICc) <2.00 are also presented within the best model set.

[a] Only factors with model contribution are shown: SP, species; ST, starting infestation; MT, mortality; EN, endophyte present; BC, bunch growth.

[b] Akaike wt.

[c] Parameter estimates averaged across all best models.

[d] Relative variable importance as sum of *Wi* across all best models.

* $\beta$ values for species: creeping bentgrass = −0.17, fine fescue = −0.25; Kentucky bluegrass = 0.00; perennial ryegrass = −0.46; tall fescue = −0.12.

**Table 7. Model selection table showing best models and relevant factors affecting insect mortality during antixenosis trials**

| Models | Model components[a] | | | | | k | ΔAICc | *Wi*[b] | Adj. $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| | ST | EM | EN | TD | TM | | | | |
| 1 | + | - | - | - | + | 7 | 0.00 | 0.69 | 0.20 |
| 2 | | - | - | - | + | 6 | 1.60 | 0.31 | 0.17 |
| $\beta$[c] | 0.01 | −0.11 | −0.30 | −1.49 | 1.03 | | | | |
| RVI[d] | 0.69 | 1.00 | 1.00 | 1.00 | 1.00 | | | | |

The most appropriate model is model 1. All other models with Akaike information criteria adjusted for small sample sizes (AICc) <2.00 are also presented within the best model set.

[a] Only factors with model contribution are shown: ST, starting infestation; EM, cumulative emigration; EN, endophyte present; TD, mean tiller diam.; TM, mean tiller mass.

[b] Akaike wt.

[c] Parameter estimates averaged across all best models.

[d] Relative variable importance as sum of *Wi* across all best models.

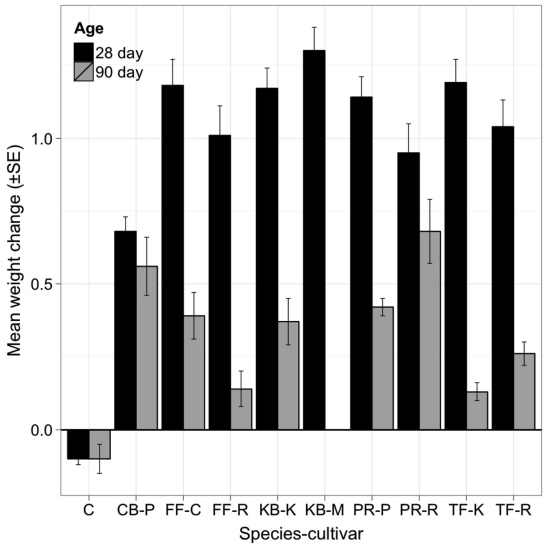


**Fig. 2.** Effect of plant ontogeny on the mean proportional weight gain (±SE) of *T. paludosa* feeding on grass cultivars at 28 (black) and 90 (gray) days of growth (C = sand only; CB-P = creeping bentgrass Penncross; FF-C, FF-R = fine fescue Chewings, Creeping red; KB-K, KB-M = Kentucky bluegrass Kenblue, Midnight; PR-P, PR-R = perennial ryegrass Protégé GLR, Revenge GLX; TF-K, TF-R = tall fescue K31, Rhambler).

biomass. Belowground feeding by insects can significantly reduce aboveground biomass (Müller–Schärer 1991) and this has been documented for numerous root-feeding turfgrass pests (Crutchfield and Potter 1995a,b; Bughrara et al. 2003). Furthermore, when belowground feeding is coupled with aboveground reductions the impact to aboveground biomass can be more severe (Van Staalduinen and Anten 2005). The observation of feeding on both above- and belowground plant tissues by *T. paludosa* could account for the more severe reductions to aboveground tissues observed here. The relationship between above- and belowground biomass is also clearly affected by insect pressure (Fig. 1), and may change according to feeding pressure.

Direct feeding on both above- and belowground tissues highlights a need for increased research into host plant factors affecting the removal of each set of tissues. *T. paludosa* feeding ecology has largely focused on damage directed at belowground plant tissues. Removal of both lateral and primary root axes is affected by root morphology and grass species identity (Dawson et al. 2002, 2004). While this work does not identify the causative factors that may similarly affect aboveground feeding, it does indicate a role for grass texture in the measured response. Grass texture and toughness are known to differ among grass species and affect insect feeding activity (Richmond and Shetlar 1999; Reinert et al. 2004). Here, the range of negative to positive correlations for studied grass species closely resembles the range of plant textures expressed by each species (Pessarakli 2007). We found fine textured creeping bentgrass and fine fescues were negatively correlated with aboveground biomass while coarse textured tall fescues were positively correlated. While we did not directly quantify texture of toughness in these trials, these qualitative differences match well with other studies in which aboveground biomechanical factors affected insect feeding success (Hanley et al. 2007, Clissold et al. 2009, Keathley and Potter 2011, Hong et al. 2012). This study suggests the need for increased attention toward quantification of the aboveground factors impacting *T. paludosa* feeding.

Results suggested that emigration behavior by *T. paludosa* might be a reaction to both positive and negative stimuli. Model selection determined three mechanisms impacting insect movement: insect density, endophyte infection, and host plant identity. Given the positive correlation with infestation level and negative correlation with mortality, our results most clearly describe a density dependent response (Stilling 1988). It is not clear if such a response was because of interactions among individuals or was a consequence of increased populations in trial pots leading to the potential for more cumulative counts, however. We had initially hypothesized that emigration behavior would increase primarily as a response to suboptimal hosts. Our results partially supported this contention. *T. paludosa* gained significantly more weight on perennial ryegrass regardless of plant ontogeny, and emigration was decreased on this species. No species was found to greatly increase insect emigration, and similarly no grass species was a clear sub-optimal host. This suggests insect emigration response is decreased by positive stimuli (i.e., reduced movement from a preferred host). However, a negative stimuli was suggested through interactions with E+ grasses. Endophyte infection, which significantly decreased larval weight gain in young grasses, was correlated with decreased emigration. Increased emigration away from E+ plants has been detected with both chewing and sucking insects in turfgrasses (Richmond and Shetlar 1999, 2000, 2001), while avoidance of E+ plants is often associated with movement toward E- plants (Carriere et al. 1998, Clement et al. 2011, Shiba et al. 2011). Other turf feeding insects are not affected by endophyte-mediated defenses (Williamson and Potter 1997). The only other study on the effects of E+ grasses on *T. paludosa* showed no effect on survival (Lewis and Vaughan 1997). Our results suggest that E+ host plants can affect *T. paludosa* fitness and may decrease its movement. The role of host plant suitability on *T. paludosa* emigration needs to be further examined; however, it is possible that several simultaneous stimuli may be responsible for this response.

The significant impact of E+ cultivars on insect weight gain and movement support the role of fungal endophytes in decreasing insect fitness (Popay and Rowan 1994). A decrease in weight gain is commonly encountered across insect groups when feeding on E+ host plants (Clement et al. 2011). Proportional *T. paludosa* weight gain on E+ plants was reduced by 0.016

over the young grass growth trial, resulting in a 4.76-d lag in growth behind insects feeding on E- plants. This developmental delay, particularly when coupled with the indication of decreased larval movement, could be biologically important toward insect survival up to and beyond the third instar. Studies have shown alkaloid profile, rather than general endophyte infection alone, may better explain insect response (Potter et al. 2008, Baldauf et al. 2011). Here categorizing infection with different fungal endophyte-grass species associations as E+ did not allow us to identify the specific alkaloids produced by *Epichloë* and *Neotyphodium* spp. (pyrrolizidine, lolitrems, peramine, and ergot alkaloids) as the causative agent responsible for the measured results. Further work is needed to elucidate of the effects of specific alkaloid profiles on *T. paludosa* behavior and physiology, particularly how they interact with changing grass morphology over plant ontogeny.

Insect performance and the factors impacting insect weight gain changed over plant ontogeny. Larvae had a proportional weight gain of 104% (−23 to 109%) on young grasses. This figure decreased to 36% (−23 to 120%) on older plant material. This decrease would suggest *T. paludosa* larvae weight gain is affected by changing plant morphology. Plant lignin and fiber content can decrease the digestibility of removed tissues and decrease insect feeding by making tissue removal more difficult (Peeters et al. 2007, Clissond et al. 2009, Keathey and Potter 2011). Maturing grasses generally increase in toughness as structural factors needed to support the increased weight of the plant increase (Pessarakli 2007). Hong et al. (2012) recovered plant ontogeny as a factor influencing the growth of *A. ipsilon*, with older plants increasing plant fiber and leading to decreased insect weight gain. European corn borer larvae similarly reduce feeding on older aboveground tissues as the plant increases biomechanical properties with age (Bergvinson et al. 1995). A similar result of decreased insect fitness over plant ontogeny is shown here. Furthermore, the loss of significance shown for insect weight gain on E+ cultivars over plant ontogeny suggests the impact of E+ grass could be trumped by grass physical structure.

Plant biomass and larval survival did differ between the 2 yr of study. Although plant growth conditions were consistent between trials, variability in ambient air temperatures existed and may have caused the differences in plant biomass observed between years (Pessarakli 2007). Mean monthly temperatures in Geneva, NY, during the time of grass development were 0.70°C (March) and 3.67°C (April) greater in 2010 than in 2011. Similarly, larval growth conditions where consistent among years but mortality was clearly higher in the second year trials. Larval survival differences between years are unlikely to have affected the conclusions from model selection analyses, particularly because insect mortality was included in the model. It is possible that the decreased response in terms of plant biomass attributed to the decreased variance explained by our models, however. Additional studies will be needed to further confirm the results shown here.

Our results indicate that several mechanisms of host plant resistance are available toward increasing plant protection against *T. paludosa* in amenity turfgrass. Most prominent was the indication that tall fescues combined resistance mechanisms by conveying both increased plant tolerance and antixenosis resistance. Furthermore the wide selection of E+ tall fescue cultivars could additionally increase antixenosis resistance, particularly for newly established stands of turf. While these results provide a promising direction for host plant selection against *T. paludosa*, it should be stressed that it is unlikely that grass species, per se, is the causative agent eliciting these results. Additional field and laboratory studies will be needed to extract the causative factors responsible for the recovered response. In particular, the impact of biomechanical factors affecting aboveground biomass reduction need to be further examined.

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