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Influence of phosphorus on the growth and ergot alkaloid content of *Neotyphodium coenophialum*-infected tall fescue (*Festuca arundinacea* Schreb.)

D.P. Malinowski[1], D.P. Belesky[1], N.S. Hill[2], V.C. Baligar[1] and J.M. Fedders[1]
[1]*USDA-ARS, Appalachian Soil and Water Conservation Research Laboratory, P.O. Box 400, Beaver, WV 25813-0400, USA*[*] *and* [2]*University of Georgia, Department of Crop and Soil Sciences, Athens, GA 30602, USA*

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Abstract

Tall fescue (*Festuca arundinacea* Schreb.) plants infected by the fungal endophyte *Neotyphodium coenophialum* (Morgan-Jones & Gams) (Glenn et al., 1996) often perform better than noninfected plants, especially in marginal resource environments. There is a lack of information about endophyte related effects on the rhizosphere of grasses. In a greenhouse experiment, four endophyte-infected (E+) tall fescue clones (DN2, DN4, DN7, DN11) and their endophyte-free (E−) forms were grown in limed (pH 6.3) Porter soil (low fertility, acidic, high aluminum and low phosphorus content, coarse-loamy mixed mesic Umbric Dystrochrept) at three soil P levels (17, 50, and 96 mg P kg^{-1} soil) for five months. Excluding the genotype effect, endophyte infection significantly increased cumulative herbage DM yield by 8% at 17 mg P kg^{-1} soil but reduced cumulative herbage DM yield by 12% at 96 mg P kg^{-1} soil. With increased P availability in the soil, shoot and root DM, and root/shoot ratio in E+ plants were significantly less when compared to E− plants. Endophyte infection increased specific root length at 17 and 50 mg P kg^{-1}soil. At soil P level of 17 mg P kg^{-1}soil, E+ plants had significantly higher P concentrations both in roots and shoots. Similar relationships were found for Mg and Ca. E+ plants had significantly higher Zn, Fe, and Al concentration in roots, and lower Mn and Al concentration in shoots when compared to E− plants. Ergot alkaloid concentration and content in shoot of E+ plants increased with increasing P availability in the soil from 17 to 50 mg P kg^{-1} but declined again at 96 mg P kg^{-1} soil. Ergot alkaloid accumulation in roots increased linearly with P availability in the soil. Results suggest that endophyte infection affects uptake of phosphorus and other mineral nutrients and may benefit tall fescue grown on P-deficient soils. Phosphorus seems also to be involved in ergot alkaloid accumulation in endophyte-infected tall fescue.

Introduction

Tall fescue is an important pasture grass in the eastern USA. Its widespread use is attributable in part to tolerance of poor soils, temperature extremes, drought, and varying management practices (Hanson, 1979). Tall fescue is often infected by clavicipitaceous fungi of the tribe Balansieae (Bacon and De Battista, 1991), belonging to the genus *Neotyphodium* (Morgan-Jones and Gams) (Glenn et al., 1996). Infected plants may express increased tolerance to biotic and abiotic stresses, which may result in better persistence (Bacon, 1993; Latch, 1993). The ecological significance of this symbiosis has been studied extensively in recent years (Clay, 1994; Latch et al., 1985; Marks et al., 1991) and considered in terms of host-endophyte association.

Positive effects of endophytes on dry matter allocation to roots of grasses are reported by numerous authors (Belesky and Fedders, 1995; De Battista et al., 1990b; Latch et al., 1985). The influence of endophyte on root architecture and mineral uptake efficiency, however, are not well understood. Studies on endophyte-related responses of tall fescue to nutrient

[*] FAX No.: +1 304 256 2921. E-mail: dbelesky@asrr.arsusda.gov

acquisition have focused upon the influence of nitrogen inputs, since this element is a constituent of alkaloids in infected plants (Arechavaleta et al., 1992; Lyons et al., 1990). Infected plants of a heterogenous population of cv. KY-31 tall fescue produced significantly more biomass than noninfected plants at each applied nutrient level (Cheplick et al., 1989). Arachevaleta et al. (1989) observed higher efficiency of nitrogen utilization in one genotype derived from cv. KY-31 tall fescue. The nature of this phenomenon might be related to greater activity of glutamine synthetase in endophyte-infected tall fescue, an enzyme which is responsible for reassimilation of ammonia within plants (Lyons et al., 1990). Reports of endophyte-mediated, nonmycorrhizal responses of forage grasses to phosphorus (P) nutrition are scarce (Azevedo, 1993). However, recent research suggests an involvement of *N. coenophialum* in P dynamics in tall fescue (Azevedo and Welty, 1995). Mycelium of *N. coenophialum* colonizes intercellularly in leaf sheaths, emerging culms, and finally seeds (Siegel et al., 1987), but has not been found in roots of soil-grown fescues and ryegrasses (Hinton and Bacon, 1985). Epiphytically growing hyphae, observed on roots of tall fescue plants grown in agar media and sterile coarse sand, contained high amounts of P in the cytoplasm, which may benefit endophyte-infected plants when grown in soils with low P availability (Azevedo and Welty, 1995). Similar P containing structures in cytoplasm of mycorrhiza have been reported (Lapeyrie et al., 1984; White and Brown, 1979) and were related to enhanced P uptake ability by infected plants. The ability of endophyte to influence P accumulation would affect uptake dynamics of P and possibly other mineral nutrients by roots of tall fescue.

The objective of our experiment was to determine if P nutrition influenced growth, mineral content, and ergot alkaloid production of *N. coenophialum*-infected tall fescue. Results of this study will provide a better understanding of the mechanisms involved in tolerance of endophyte-infected grasses to conditions of mineral nutrient stress.

Material and Methods

Tall fescue genotypes chosen for this experiment were selected from a wild population and differed in morphological and chemical features as described by Belesky and Fedders (1995). In a greenhouse experiment, four mycorrhiza-free tall fescue clones (DN2, DN4, DN7, DN11) infected with their naturally occurring *N. coenophialum* strains (E+) and their endophyte-free (E−) forms were multiplied from plantlets with 3 tillers and similar weights (0.45−0.48 g DM) and grown for 4 weeks in compartmented (5×5 cm) plastic trays to ensure establishment. On 27 June 1996, plantlets with 5 tillers were replanted into pots (11 cm diam., 0.82 L volume) filled with Porter soil (coarse-loamy mixed mesic Umbric Dystrochrept) and placed in a greenhouse with day/night temperatures of 25/15 °C. The untreated Porter soil had pH 4.2 (H_2O), 535 mg kg^{-1} Al (1 *M* KCl extractable) and 1.7 P, 40 K, 111 Ca, 8.1 Mg, and 300 mg kg^{-1} Na (1 *M* ammonium acetate extractable). Each pot contained 1 kg of soil and 0.35 kg water needed to achieve field capacity of the soil.

Three soil P treatments were achieved by addition of P to the soil in form of KH_2PO_4 solution at three levels: 25, 50, and 100 mg P kg^{-1} soil corresponding to 50, 100, and 200 kg P ha^{-1}. These three soil P treatments represented low, medium, and high P fertilization rates of acid soils (Wright et al., 1987). All soil P treatments received additional K as KCl to bring the K level to 125 mg K kg^{-1}, 75 mg N kg^{-1} as $(NH_4)_2SO_4$ and micronutrients at the rate of 0.1 Mo, 1.0 B, 5.0 Cu, and 5.0 Fg Zn kg^{-1} soil. Soil was incubated for 1 week with dolomitic lime (James River Lime, Buchanan, VA 24066*) at the rate of 10 g kg^{-1} to achieve a final pH of 6.3 (H_2O). At the end of incubation, the Bray 1 (Olsen and Sommers, 1982) extractable P was 17, 50, and 96 mg P kg^{-1} soil, respectively in the three soil P treatments. During the experiment, additional N was applied to the pots each week as NH_4NO_3 solution, corresponding to 12 mg N pot^{-1}.

Plants were cut once a month to 5 cm and the clippings were dried (60 °C) and weighed for herbage yield. Three destructive harvest were performed at 3, 4, and 5 months after planting. Root and shoot (herbage + stubble) dry matter, tiller number, root length, and mineral concentrations were determined. Root length was measured with a root length scanner (Comair, Commonwealth Aircraft Corporation Limited, Melbourne, Australia) and the results presented on the basis of root DM as specific root length (SRL). Phosphorus and other mineral elements in plant tissues were analyzed using the method of Kingston and Jassie (1988). Ergot alkaloid content in root and shoot tissues was determined by extracting lyophilized tissues of E− and E+ plants with phosphate buffer (1:80 w/v), reacting

* Trade names are used for the convenience of the reader and do not imply endorsement by USDA over comparable products.

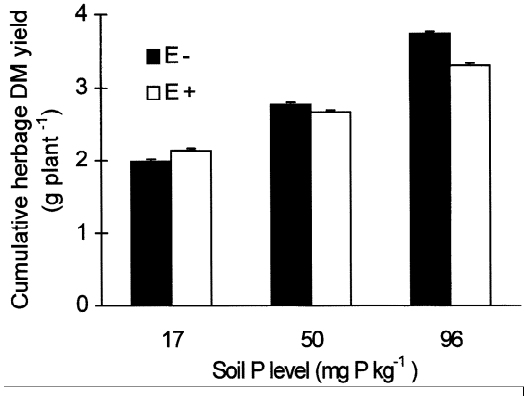

Figure 1. Cumulative herbage DM yield of endophyte-infected (E+) and noninfected (E−) tall fescue plants in relation to soil P level, averaged over four genotypes. Bars indicate standard errors (n = 16).

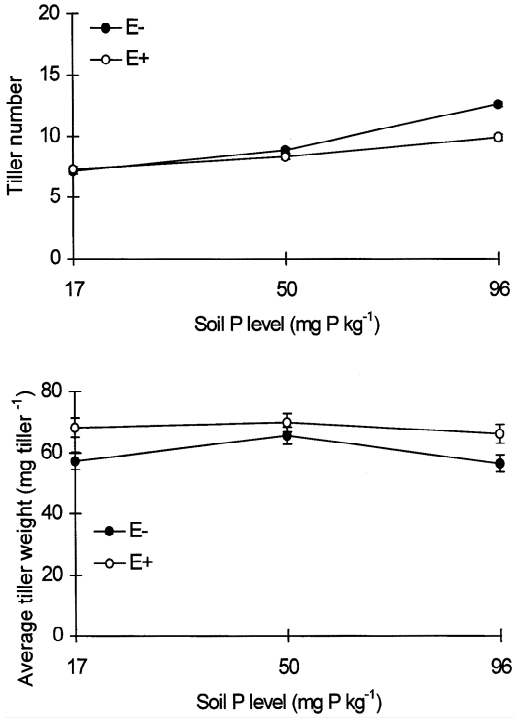

Figure 2. Tiller number and average tiller weight of endophyte-infected (E+) and noninfected (E−) tall fescue plants in relation to soil P level, averaged over five harvests and four genotypes. Bars indicate ± standard errors (n = 80).

the extract with monoclonal antibody (15F3.E5), and analyzing by ELISA procedure using lysergic acid as standards (Hill and Agee, 1994).

The experiment was set up as a split plot design with P fertilization level (main plot) considered fixed and endophyte-tall fescue genotype associations (split-plot) as random effects replicated four times for a total of 96 pots. Analysis of variance was performed using the SAS statistical package (SAS Inst., Cary, NC). Plant measurements at each harvest were based on four replicates. Means among P fertilization levels or tall fescue genotypes were compared by the Duncan multiple range test (P = 0.05). Means between plants with different endophyte status were compared by the pairwise multiple comparison test (LSD) (P = 0.05).

Results and Discussion

Developmental characteristics

Significant interactions between soil P level and tall fescue genotype as well as soil P level and endophyte status suggest that P availability in the soil influenced cumulative (the sum of herbage yield harvested every month) herbage dry matter (DM) yield (Table 1). Regardless of soil P level and endophyte status, upright growing genotype DN2 produced the greatest cumulative herbage DM yield (3.12 g plant $^{-1}$), followed by DN7 (2.92) and the short-leaf genotypes DN 4 (2.72) and DN 11 (2.37). Dry matter production is a genetically controlled trait in tall fescue (Wilhelm and Nelson, 1978), and our results of cumulative herbage DM yield agreed with those reported by Belesky and Fedders (1995) in a separate experiment. Excluding genotypic effects, endophyte infection significantly increased cumulative herbage DM yield at 17 mg P kg^{-1} soil by 8% but reduced cumulative herbage DM yield by 12% at 96 mg P kg^{-1} soil relative to E− plants (Figure 1). The increase in cumulative herbage DM yield of E+ plants at 17 mg P kg^{-1} soil could be a function of significantly greater average tiller weight (107 mg) than in E- plants (98 mg). Endophyte infection had no effect on tiller number at soil P levels of 17 and 50 mg P kg^{-1} soil (Figure 2). Although tiller number is often shown to be positively influenced by endophyte infection when plants are well supplied with nutrients (Arachevaleta et al., 1989; De Battista et al., 1990b; Schmidt, 1993), in our experiment E+ plants produced significantly fewer tillers (10) than E− plants (13) at a very high soil P level of 96 mg P kg^{-1} soil. This contributed to significantly lower cumulative herbage DM yield of E+ plants at the highest soil P level. Growth of two of the tall fescue clones used in our experiment (DN7 and DN11)

Table 1. Analysis of variance summary of soil P level (P), tall fescue genotype (G), and endophyte (E) effects upon developmental features

Source	Tiller No.	Tiller weight	Cumulative herbage DM	Shoot DM	Root DM	Root/Shoot ratio
P	*	*	*	*	*	*
G	*	*	*	*	*	*
E	NS	NS	NS	*	*	NS
P×G	NS	NS	*	NS	NS	NS
P×E	*	*	*	*	*	NS
E×G	*	NS	NS	*	*	*
P×G×E	NS	NS	NS	NS	NS	NS

*, significant at $P < 0.05$; NS, not significant.

was analyzed by Azevedo (1993) under a range (0.0–2.0 ppm) of very limited available soil P. The clones differed in responses to increased soil P in terms of tillering, leaf biomass and leaf area. Leaf biomass of clone DN7 was reduced in response to endophyte infection when P concentration in the soil was greater than 1.0 ppm. Reduced cumulative herbage DM yield of E+ plants versus E− plants at the high soil P level in our experiment agrees with results presented by Azevedo (1993). Thus, we suggest that endophyte-infected tall fescue is not responsive to high soil P. Differences in DM could also be attributable to differing quantities of root exudates; however, we did not quantify nor characterize root exudates in this experiment. Flores et al. (1996) noted that organic acids exuded by roots of plants growing in resource-limited environments were very effective at mobilizing P from sparingly soluble Fe and Al complexes. Further research should reveal the mechanism of nutrient acquisition present in roots of endophyte-infected tall fescue.

Regardless of endophyte infection, tiller number significantly increased with increasing soil P while tiller mass was reduced at 96 mg P kg^{-1} soil (Figure 2). Endophyte status interacted with soil P level in terms of tiller characteristics (Table 1). At 96 mg P kg^{-1} soil, E+ plants produced significantly fewer but heavier tillers than E− plants, regardless of the genotype. This agrees with results reported by Belesky at al. (1989), Hill et al. (1990), and Maclean et al. (1993) in selected tall fescue genotypes. Endophyte-related effects on tiller number of tall fescue, however, are often reported as inconsistent. A positive effect of endophyte infection on tillering was reported by De Battista et al. (1990b) and Hill et al. (1991a) while in some cases endophyte infection did not influence tiller number (Belesky and Fedders, 1995, 1996; White et al., 1992). The mechanism controlling tiller expression in endophyte-infected grasses is not known. *Neotyphodium* endophytes are able to produce auxin in vitro (De Battista et al., 1990a). This suggests that genotype specific endophytes could also influence the level of auxin and other hormones in infected plants, thereby altering tillering patterns as well as root development and resource allocation among tissues in infected grasses (Belesky et al., 1987; Joost, 1995). Similarly, yield per tiller was also inconsistent across tall fescue genotypes. Average tiller weight can increase or decrease in response to endophyte infection (Hill et al., 1990; Richardson et al., 1990; West et al., 1993), suggesting specifity of grass/endophyte associations in terms of tiller characteristics.

Averaged over all harvests, root and shoot (herbage yield + stubble) DM was not influenced by endophyte infection at 17 mg P kg^{-1} soil, however, as P availability increased, E+ plants produced significantly less root and shoot DM than did E− plants (Figure 3). Not all of the tall fescue genotypes responded in the same way to endophyte infection as indicated by a significant interaction between genotype and endophyte status (Tables 1 and 3). Root DM of genotype DN2 was significantly less in E+ plants than in E- plants, regardless of soil P level. A similar relationship was observed for shoot DM of genotype DN2 at 50 and 96 mg P kg^{-1} soil. Root and shoot DM of genotype DN7 were also reduced in E+ plants, especially at 96 mg P kg^{-1} soil. In contrast, endophyte infection increased root DM of genotype DN4 at 17 mg P kg^{-1} soil. Root and shoot DM of genotype DN11 was not influenced by endophyte infection. Root/shoot ratio was not influenced by endophyte infection (Table 1) but was genotype specific (0.34, 0.54, 0.59, and 0.64, respectively for DN2, DN4, DN11, and DN7). Endophyte infection interact-

Table 2. Analysis of variance summary of soil P level (P), tall fescue genotype (G), and endophyte (E) effects upon mineral element concentrations in roots (R) and shoots (Sh)

Source	P		S		Mg		Ca		K		Mn		Fe		Zn		Al	
	R	Sh	R	Sh	R	Sh	R	Sh	R	Sh	R	Sh	R	Sh	R	Sh	R	Sh
P	*	*	*	*	*	*	*	*	*	*	*	*	NS	*	*	NS	*	*
G	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
E	*	*	*	*	*	*	*	*	NS	*	*	*	*	NS	*	*	NS	NS
P×G	*	*	*	*	*	*	*	*	*	*	*	*	NS	NS	*	*	NS	*
P×E	*	*	*	*	*	*	*	NS	NS	*	*	NS	*	NS	*	NS	*	*
G×E	*	*	*	*	*	*	NS	*	*	*	*	NS	NS	NS	*	NS	NS	*
P×E×G	*	*	*	*	*	*	*	*	*	NS	*	NS	NS	*	*	*	NS	*

*, significant at $P < 0.05$; NS, not significant.

Table 3. Root and shoot dry matter (DM) of tall fescue genotypes as influenced by soil P level and endophyte infection. Root and shoot DM data represent averaged values over three harvests

Soil P level (mg P kg^{-1})	Endophyte status	Root DM (g plant^{-1})				Shoot DM (g plant^{-1})			
		DN2	DN4	DN7	DN11	DN2	DN4	DN7	DN11
17	E−	0.50c	0.96b	1.19a	0.84b	1.32b	1.79a	1.77ab	1.56ab
	E+	0.32c	1.16a	1.08ab	0.91b	1.06c	1.96a	1.70ab	1.49b
	LSD[b]	*0.12*	*0.17*	*0.18*	*0.15*	*0.29*	*0.29*	*0.17*	*0.41*
50	E−	0.78c	1.32b	1.54a	1.19b	1.88b	2.36a	2.29a	1.91b
	E+	0.44c	1.28ab	1.39a	1.12b	1.28c	2.02ab	2.15a	1.75b
	LSD	*0.20*	*0.20*	*0.14*	*0.23*	*0.28*	*0.31*	*0.29*	*0.31*
96	E−	0.83c	1.52b	1.88a	1.37b	2.41b	3.04a	2.86b	2.44b
	E+	0.51b	1.40a	1.41a	1.30a	1.82c	3.01a	2.57b	2.24b
	LSD	*0.14*	*0.28*	*0.33*	*0.18*	*0.37*	*0.58*	*0.27*	*0.31*

[a] Means within rows with the same letters are not significantly different ($P > 0.05$).
[b] LSD ($P < 0.05$) between E+ and E- plants within a genotype (columns).

ed with tall fescue genotype, reducing root/shoot ratio of genotype DN2 irrespective of P applied to the soil (data not presented).

Specific root length (SRL) of E+ tall fescue plants was greater when compared to E− plants at soil P levels of 17 and 50 mg P kg^{-1} soil (Figure 4). This suggests an influence of endophyte infection on root morphology. A greater SRL of E+ plants might be related to more fibrous root structure and greater root surface area than found in E- plants. Therefore, greater SRL would increase root surface area and could enhance nutrient acquisition ability of roots for nutrients with restricted availability under certain limited conditions, such as low P. Specific features of root morphology are being investigated in a separate experiment.

Mineral element concentration

Mineral element concentrations in roots and shoots were strongly influenced by soil P level, tall fescue genotype, endophyte status, and in part, by interactions of these factors (Table 2). Mineral concentration and DM accumulation are genetically controlled in tall fescue (Sleper et al., 1980). Phosphorus availability in the soil may also considerably affect uptake of other nutrients (Marschner, 1986). Since endophyte and soil P level interacted to influence root morphology, DM production, and allocation in our experiment, we focused upon endophyte-related effects on mineral composition of tall fescue. This was to determine if increases in growth or root characteristics influenced mineral acquisition patterns. At 17 mg P kg^{-1} soil, endophyte infection significantly increased P concen-

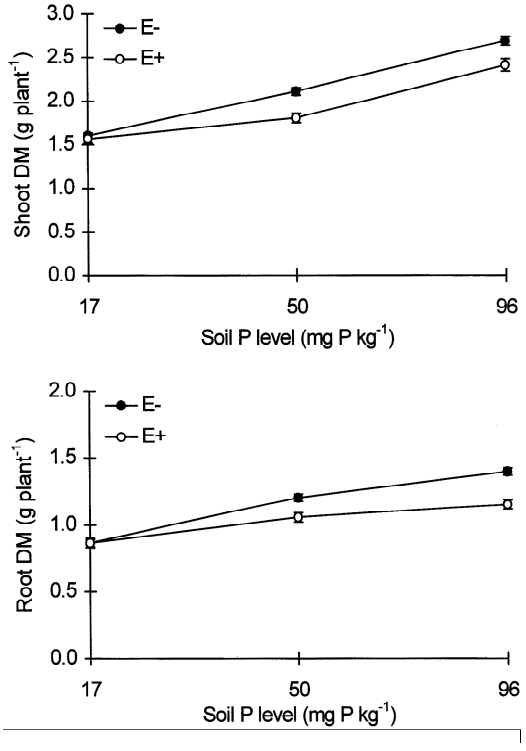

Figure 3. Root and shoot DM of endophyte-infected (E+) and non-infected (E−) tall fescue plants in relation to soil P level, averaged over three harvests and four genotypes. Bars indicate ± standard errors (n = 48).

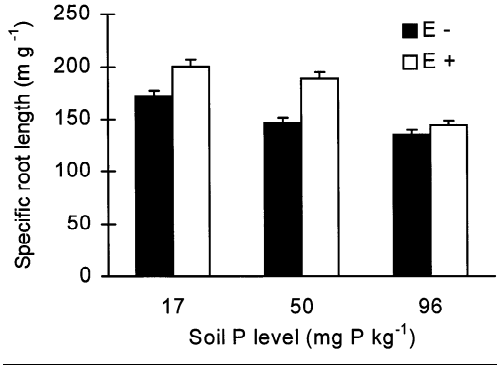

Figure 4. Specific root length of endophyte-infected (E+) and non-infected (E−) tall fescue plants in relation to soil P level, averaged over two measurements and four genotypes. Bars indicate standard errors (n = 16).

tration both in roots (10%) and shoots (20%) (Figure 5). An opposite effect was observed at 96 mg P kg^{-1} soil where P concentration was reduced by about 5% in E+ plants when compared to E- plants.

Endophyte-infected plants grown at 17 mg P kg^{-1} soil had greater concentrations of Ca, Mg, Zn, Fe, and Al in the roots, and Ca and Mg in the shoots than E− plants (Figures 5 and 6). Endophyte-related effects on mineral element concentrations were not related to a 'dilution effect' since there were no significant differences in root and shoot DM (averaged for three harvests) between E− and E+ plants grown at 17 mg P kg^{-1} soil (Figure 3). This is an important consideration, suggesting that enhanced mineral acquisition in endophyte-infected tall fescue occurred despite the endophyte being localized in the aerial portion of the plant. Unlike mycorrhiza, which can physically increase the effective surface area of roots as well as cause chemical modifications at the rhizoplane level, the endophyte of tall fescue may influence uptake of certain minerals quite likely due to production of root exudates (Peters and Zam, 1981). Enhanced uptake of P, Mg, and Ca by E+ plants when compared to E- plants suggests an altered root activity similar to that observed in plants grown in P-deficient soils (Marschner, 1986). At 17 mg P kg^{-1} soil, E+ plants had significantly higher Fe, Zn, and Al concentration in roots but lower Al concentration in shoot tissues when compared to E− plants (Figure 6). This suggested that E+ plants altered Al accumulation in shoots possibly by sequestering it in (on) the roots. This might be an important adaptive feature that enables endophyte-infected tall fescue plants to tolerate soil acidity associated with high levels of exchangeable Al.

Ergot alkaloid concentration and content

Ergot alkaloids were detected only in E+ plants. Genotypes differed in concentration and content of ergot alkaloids, both in root and shoot tissues, which agrees with previous reports by Hill et al. (1990, 1991a, b). After 20 weeks of growth (end of the experiment), ergot alkaloid concentrations increased more rapidly in response to P availability in the soil in the low ergot alkaloid content genotypes DN2 and DN4 by 2.1 and 3.2 times in roots, and 1.3 and 2.0 times in shoots, respectively (Table 4). In contrast, the high ergot alkaloid content genotypes DN7 and DN11 had 1.4 and 2.8 times greater ergot alkaloid concentration in shoots when grown at 50 mg P kg^{-1} soil when compared to 17 mg P kg^{-1} soil. Ergot alkaloid concentrations in shoots of genotypes DN7 and DN11 reached a clear peak with increased soil P level and declined with further increase in available soil P. In other reports, enhanced concentration of ergopeptine alkaloids in tall fescue was related to increased nitrogen fertilization (Arechavaleta et al., 1992; Belesky et

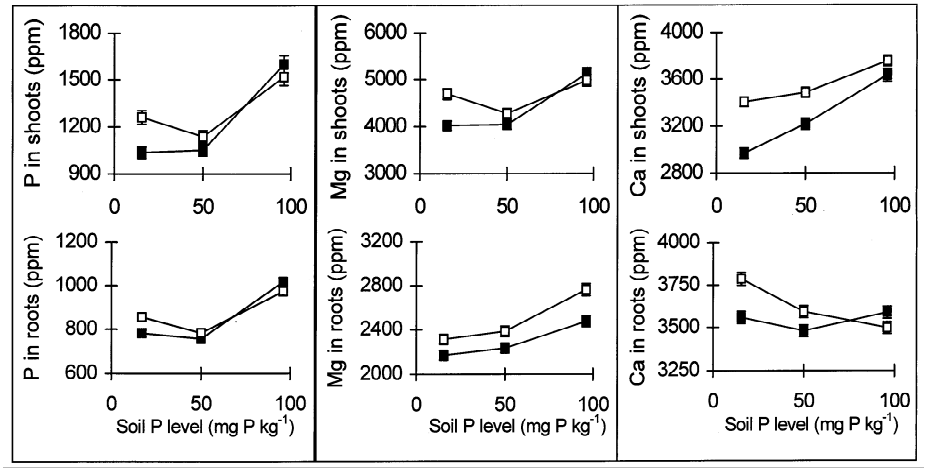

Figure 5. Concentrations of P, Mg, and Ca in roots and shoots of endophyte-infected (□) and noninfected (■) tall fescue plants in relation to soil to soil P level, averaged over three harvests and four genotypes. Bars indicate ± standard errors (n = 24).

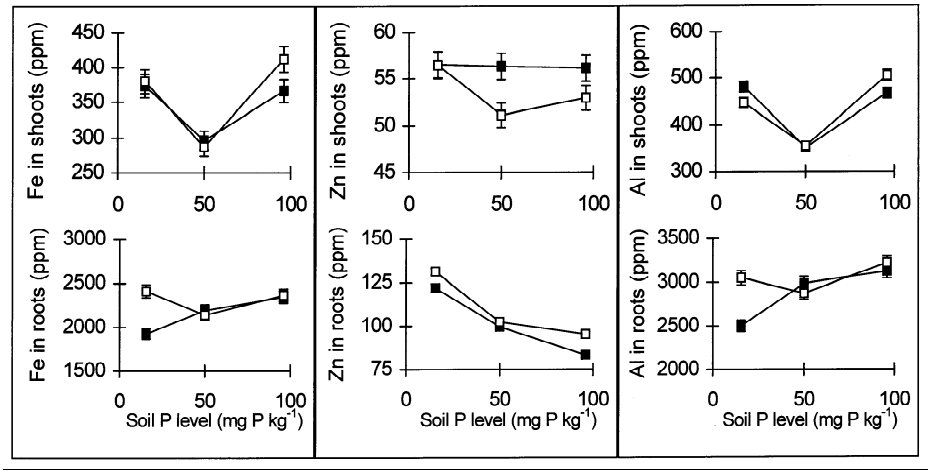

Figure 6. Concentrations of Fe, Zn, and Al in roots and shoots of endophyte-infected (□) and noninfected (■) tall fescue plants in relation to soil P level, averaged over three harvests and four genotypes. Bars indicate ± standard errors (n = 24).

Table 4. Ergot alkaloid concentration and content in root and shoot tissues of four endophyte-infected tall fescue genotypes in relation to soil P level after 20 weeks of growth

Soil P level	Ergot alkaloid concentration				Ergot alkaloid content			
(mg P kg^{-1})	DN2	DN4	DN7	DN11	DN2	DN4	DN7	DN11
(a) Roots	ppb				ng plant^{-1}			
17	64	90	332	712	18	126	398	691
50	104	248	364	470	63	479	631	709
96	136	290	222	992	81	543	381	1766
(b) Shoots					μg plant^{-1}			
17	7162	9992	14592	19192	7.08	21.16	22.52	28.37
50	5208	21200	21190	54152	6.18	51.26	45.03	113.77
96	9192	20462	8152	25592	16.38	72.47	23.30	63.61

al., 1988; Rottinghaus et al., 1991). Results presented in this experiment suggest that P availability in the soil might also influence ergot alkaloid accumulation in tall fescue. Moreover, classification of tall fescue into low and high ergot alkaloid content lines does not seem to be valid at high soil P level. In media-grown *Claviceps* spp., high P concentration in the growth medium depress the first enzyme in the biosynthetic pathway of ergot alkaloids (Flieger et al. 1991; Robbers, 1984). Apparently, a similar mechanism may regulate ergot alkaloid biosynthesis in certain endophyte-infected tall fescue associations (Garner et al., 1993).

We did not quantify the amount of mycelium in E+ plants, therefore the influence of soil P level on ergot alkaloid production might not be consider here in terms of a greater hyphae concentration in the plant or increased alkaloid production rate by the endophytes. Hill et al. (1990) reported differences in ergovaline concentration among selected tall fescue genotypes infected by their naturally occurring endophyte strains in a greenhouse experiment. In a subsequent study (Hill et al., 1991b), endophyte strains from two tall fescue genotypes known as a high (DN11) and a low (DN2) ergot alkaloid producer were reintroduced to noninfected individuals of tall fescue genotype DN2. The resulting symbionts were low alkaloid producers, irrespectively of endophyte strain. Plant genotype, therefore, appears to play a major role in controlling the expression of the genetic potential of endophytes for ergopeptine alkaloid production. Plants in those experiments were screened for presence of the endophytes, however, mycelium concentration was not quantified. Further study on endophyte-related tall fescue responses to phosphorus nutrition should consider both the effect of P on hyphae concentration in the host plant and the biosynthesis of ergot alkaloids.

Results of our study suggest an influence of endophyte on mechanisms associated with mineral nutrition of tall fescue when grown in P-deficient soils. Endophyte infection appears to influence allocation of photosynthates to roots which could contribute to better nutrient scavenging ability, benefiting tall fescue grown under limited nutrient input conditions. Phosphorus also appears to have a role in ergot alkaloid production in certain tall fescue/endophyte associations. The broad responses of tall fescue/endophyte associations to major resource gradients support the widespread occurrence of symbiotic plants under varied conditions. Further research needs to be conducted on the mechanisms involved in the ergot alkaloid biosynthesis regulation, root morphology, and the relationships, if any, to root exudates in endophyte-infected tall fescue.

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