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Endophytic Fungi Affect Root Characteristics of Tall Fescue Grown in Andisols

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Abstract: We assessed how *Neotyphodium coenophialum* (Morgan-Jones and Gams) Glenn, Bacon and Hanlin infection influenced root characteristics of tall fescue (*Lolium arundinaceum* [Schreb.] SJ Darbyshire, formerly *Fectuca arundinacea* Schreb.) ecotypes (Fukaura, Koiwai and Showa) grown under a high (Black Andisol: high in all nutrients but low in phosphorus) and a low (Red Andisol: low in all nutrients but high in phosphorus) nutrient status soil for 30 weeks. We measured root growth parameters as well as root nutrient acquisition of infected (E+) and uninfected (E-) plants. In Black Andisol E+ plants produced more root dry matter and had greater root volume as well as root dry mass density. In Red Andisol E- plants produced more dry matter and had greater root volume as well as root dry mass density. Infected plants tended to have lower root/shoot ratio regardless of ecotypes and soils. Phosphorus and calcium (Ca) concentrations in roots of E+ plants showed higher values irrespective of soil fertility status although the values were not always statistically significant. On the other hand, concentrations of potassium (K) and magnesium (Mg) showed higher values in E- plants. In case of P, K, Ca and Mg uptake, E+ plants showed higher values than those of E- plants regardless of ecotypes grown in Black Andisol. This trend was inconsistent in E+ plants grown in Red Andisol. In this study *Neotyphodium* infection seems to be beneficial to tall fescue ecotypes under soil condition that is comparatively low in P but high in other nutrients content (Black Andisol) and detrimental under soil, relatively high in P but low in other nutrients content (Red Andisol).

Key words: Andisol, endophyte, ecotype, root growth, nutrient acquisition, tall fescue

INTRODUCTION

Tall fescue (*Lolium arundinaceum* [Schreb.] SJ Darbyshire), is very popular long-lived, branch forming, upright-growing cool-season forage grass with a deep root system. The massive root structure of tall fescue is frequently attributed to its wide adaptation and growth on the many different soil types (Miller, 1984; Sleper and Buckner, 1995). Tall fescue is an important cool-season perennial forage for many cattle producers in humid regions throughout the world. In recent, tall fescue has become valuable as grass cover on play areas, athletic fields, airfields, parks, highway rights-of-way and industrial sites and public institutions. Earlier reports suggest that tall fescue pastures are infected with a fungus, *Neotyphodium coenophialum* (Shelby and Dalrymple, 1987; Saiga *et al*., 2003a). Fungal endophyte-*Neotyphodium coenophialum* live for a significant part of their life cycle internally and asymptomatically in plants. They are unbiquitous in vascular plants, usually occurring in aboveground organs, but occasionally in roots, where they differ from mycorrhizae in that they lack external hyphae or mentels (Wilson, 1995; Saikkonen *et al*., 1998). It is well known that the *Neotyphodium*-tall fescue association is one of the mutualism. Tall fescue provides *Neotyphodium* with energy, nutrients, shelter

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and a means of propagation through the seed, while *Neotyphodium* provides mechanisms for improving tall fescue persistence to over grazing and insect pressure. The *Neotyphodium coenophialum* also confers greater drought tolerance that could improve tall fescue productivity (Bouton *et al*., 1993; West *et al*., 1993). The drought tolerance mechanisms in endophyte infected tall fescue are due to a lower net photosynthetic rate, higher stomatal resistance (Belesky *et al*., 1987) and greater root proliferation under drought-stressed conditions (Richards *et al*., 1990).

In Japan Andisols cover one-sixth of the total land surface constituting 27% of the total arable soils and 51% of the soils used for upland crops and fruit frees. Andisols of Japan characterized by low pH, P content, bulk density and high porosity with high P retention capacity and organic matter content (Agricultural Production Bureau, 1980). Phosphorus deficiency, like nitrogen deficiency, leads to an increase in root/shoot dry weight ratio. Increasing the duration of P starvation increases root dry weight and root length in particular. An increase in root surface area in deficient plants can be considered as a strategy for enhancing P acquisition from soils (Marschner, 1999). Far less is known about the influence of *Neotyphodium* infections on wild populations of native grass especially grown in Andisols. Despite this, the mechanisms of mineral element stress tolerance in tall fescue infected by *Neotyphodium* sp. is not clearly understood. Therefore, we hypothesized that E+ plants of tall fescue should produce more root biomass as well as greater nutrient acquisition in roots than E- plants grown under nutrient limited conditions and this effect would be pronounced and/or reversed when nutrient status of growing medium was more limiting. In this study we assessed how *Neotyphodium* infection influenced root characteristics of tall fescue ecotypes under two contrasting nutrient status soils. We measured root dry matter, root volume, root dry mass density and root nutrient acquisitions (P, K, Ca and Mg).

MATERIALS AND METHODS

Plant Materials

Three tall fescue (*Lolium arundinaceum* [Schreb.] SJ Darbyshire) ecotypes viz., Fukaura, Koiwai and Showa were chosen for this experiment. Tall fescue ecotypes of Fukaura, Koiwai and Showa infected with their naturally occurring strains of the endophytes species *N. coenophialum* were collected from Aomori, Iwate and Akita prefectures, respectively, in the northern part of Honshu Island. To maximize the likelihood of collecting different ecotypes, plants were collected 80-100 km apart. Endophyte-infected plants were divided into two groups and one group was then treated with benomyl fungicide (Latch and Christensen, 1982) to eliminate the endophyte fungus and other group was not treated. Fungicide-treated and non-treated plants were planted in a field at Iwate University. After a few months, the endophyte infection status was verified by staining plant tissue with rose bengal (Saiga *et al*., 2003b). Plants of the tall fescue clone for each ecotype infected with *N. coenophialum* (E+) and free of endophyte (E-) were selected for the experiment. Ramets of equal size and shape were prepared by cutting the shoots 5 cm above the crown and the roots 5 cm below the crown. To standardize the initial size and shape each ramet was selected from a single tiller with three adventitious roots.

Growth Condition

A pot experiment was conducted under controlled conditions since this is the first study under Andisol with tall fescue infected with endophyte and free of endophyte. Tall fescue plants with E+ and E- grown in two loamy Pumice and Haplic Andisols (Black Andisol and Red Andisol, respectively) of different fertility status. The Black Andisol was collected from the Uwadai field of Iwate University in the prefecture Iwate while the Red Andisol was collected from the Nikaho highland in the prefecture of Akita, northern Japan. The Black Andisol was characterized with pH 6.02 and naturally low P content (6.71 mg 100 g^{-1} soil) and high in other nutrients such as N (0.34%), K (39.6 mg 100 g^{-1} soil), Ca (316 mg 100 g^{-1} soil), Mg (31.8 mg 100 g^{-1} soil), Cu (1.42 µg 100 g^{-1} soil), Mn (29.4 µg 100 g^{-1} soil) and Zn (2.18 µg 100 g^{-1} soil). While the Red Andisol characterized with pH 5.00 and naturally high content of P (15.3 mg 100 g^{-1} soil) and low in other nutrients such as N (0.12%), K (20.3 mg 100 g^{-1} soil), Ca (0.91 mg 100 g^{-1} soil), Mg (1.18 mg 100 g^{-1} soil), Cu (0.36 µg 100 g^{-1} soil), Mn (3.20 µg 100 g^{-1} soil) and Zn (0.10 µg 100 g^{-1} soil). Despite Black Andisol was higher in P-retention capacity (1962) with higher organic matter content (184 g kg^{-1}) compared to Red Andisol having lower in P-retention (604) and organic matter content (94 g kg^{-1}). After removing plant debris the air-dried soils were passed through a 4 mm sieve and the pots were filled with this soil (2 kg pot^{-1}). Water was then added to bring the soil to Field Capacity (FC). The tops of the pots were covered with a black polyethylene film to prevent evaporation and the soils were allowed to equilibrate at glasshouse temperature. The pots were weighed prior to transplanting the plants into them. The plants were grown in a control condition (Rahman and Saiga, 2005; Rahman *et al*., 2006) for 30 weeks without application of any chemical fertilizers. Pots were maintained at field capacity (p^F 2) throughout the experiment by adding tap water as required.

Harvest and Mineral Analysis

The plants were allowed to grow for 30 weeks and then plants were separated from soil, by washing the soil over a screen surface. The roots were separated and stored at low temperature until the measurement of root volume. Roots and shoots were dried at 80°C for 48 h in a forced-air oven and weighed to obtained dry yield. Root/shoot ratio and root dry mass weight were calculated. Dried root samples were digested with HNO_3-$HClO_4$ acid (2:1) and concentrations of K, Ca and Mg were measured by atomic absorption spectrophotometry (Perkin Elmer-3300). The concentration of P was measured colorimetrically using a vanadomolybdate-phosphoric yellow color method (Jasco Ubest-30 UV/VIS spectrophotometer) as described by Jackson (1973). From the concentration of different nutrients in roots, nutrients uptake per plant were calculated.

Experimental Design

The experiment was set up as a split plot design with two soil fertility levels (main plots) and endophyte/tall fescue ecotype associations (split plots) as random effects replicated three times.

Statistical Analysis

A three-way analysis of variance (ANOVA) was employed to determine whether endophyte infection affected root growth and nutrient concentration as well as uptake. The ANOVA model included endophyte, soil and ecotype as the mail source of variation and three pairwise: endophyte x soil, endophyte x ecotype and soil x ecotype and one three-way: endophyte x soil x ecotype interaction. Multiple range tests were conducted using the method of RYAN-EINOT-GABRIEL-WELSCH (Ryan, 1960) to compare results for endophyte infection with the variables at a 5% level of significance. The Statistical Analysis System, Version 6 (SAS Inst., Cary, NC, USA) was used for all analysis. Means between plants grown in various soils were also compared by Least Significant Difference (LSD) test ($p<0.05$).

RESULTS AND DISCUSSION

Analysis of variance revealed that the root dry weight was significantly affected by endophyte infection, soil fertility, plant ecotype, endophyte × soil, endophyte × ecotype and soil × ecotype but the interaction of endophyte × soil × ecotype was not statistically significant (Table 1). Significant effect of endophyte infection, soil fertility, plant ecotype, endophyte × soil, endophyte × ecotype and

Table 1: ANOVA test for the root characteristics of tall fescue

Source of variations	df	Dry weight MS	Dry weight F	Dry weight Pr>F	Root volume MS	Root volume F	Root volume Pr>F	Root mass density MS	Root mass density F	Root mass density Pr>F	Root/shoot ratio MS	Root/shoot ratio F	Root/shoot ratio Pr>F
Endophyte	1	8.08	15.06	0.0007	386.8	6.35	0.0188	1.62	14.31	0.0009	0.257	10.97	0.0029
Soil	1	274.23	510.96	0.0001	22500.0	369.36	0.0001	55.63	492.22	0.0001	0.080	3.43	0.0764
Ecotype	2	6.16	11.49	0.0003	98.6	1.62	0.2191	1.32	11.64	0.0003	0.183	7.81	0.0024
Endophyte× Soil	1	39.90	74.34	0.0001	2336.1	38.35	0.0001	8.34	73.82	0.0001	0.130	5.54	0.0271
Endophyte× Ecotype	2	3.18	5.92	0.0081	213.2	3.50	0.0464	0.67	5.93	0.0081	0.019	0.81	0.4580
Soil×Ecotype	2	7.13	13.29	0.0001	1164.1	19.11	0.0001	1.52	13.42	0.0001	0.288	12.29	0.0002
Endophyte× Soil×Ecotype	2	0.38	0.71	0.5027	52.7	0.87	0.4338	0.07	0.66	0.5258	0.009	0.40	0.6762

Table 2: Root characteristics of tall fescue ecotypes as affected by endophyte infection in different Andisols

Ecotype	Soil	Root dry weight g plant^{-1} E+	Root dry weight g plant^{-1} E-	Root volume cc plant^{-1} E+	Root volume cc plant^{-1} E-	Root mass density mg mL^{-1} plant^{-1} E+	Root mass density mg mL^{-1} plant^{-1} E-	Root/shoot ratio E+	Root/shoot ratio E-
Fukaura	Black Andisol	7.28a*	5.82a	69.00a	59.00a	3.31a	2.65a	0.51b	0.81a
	Red Andisol	1.17b	3.11a	10.00a	26.00a	0.54a	1.44a	0.73b	1.08a
	LSD**	1.662	1.995	19.759	16.371	0.755	0.931	0.362	0.623^{ns}
Koiwai	Black Andisol	10.24a	6.37b	91.67a	66.00b	4.65a	2.89b	0.69b	0.92a
	Red Andisol	0.61b	1.44a	5.67b	9.33a	0.28b	0.67a	0.46a	0.58a
	LSD	2.216	1.026	12.380	11.257	1.003	0.476	0.279^{ns}	0.236^{ns}
Showa	Black Andisol	10.06a	6.23b	79.33a	46.67b	4.57a	2.83b	0.55b	0.77a
	Red Andisol	2.93a	3.64a	26.00a	35.00a	1.36a	1.69a	0.59a	0.51a
	LSD	1.350	1.420	26.254	15.812	0.619	0.657	0.123^{ns}	0.234

*Values within the rows and parameters for each variable with the same letter(s) are not significantly different at $p<0.05$; **LSD ($p<0.05$) between Black Andisol and Red Andisol (columns)

soil × ecotype on root volume as well as root dry mass density was observed but the interaction of endophyte × soil × ecotype was not statistically significant. Root/shoot ratio was significantly affected by all the sources of variations except interaction of endophyte × ecotype and endophyte × soil × ecotype.

In Black Andisol, root dry weight was higher in E+ plants than in E- plants (Table 2). The opposite was observed in Red Andisol. Although in Black Andisol, ecotype Fukaura and in Red Andisol, ecotype Showa did not show any significant differences on root dry weight between E+ and E- plants. Endophyte infection reflected positive effects on root volume as well as root dry mass density in Black Andisol while it was negative in Red Andisol for all forage tall fescue ecotypes although the values were not always statistically significant. Malinowski and Belesky (1999) observed that endophyte infection increased 57% root dry matter as compared to non-infected tall fescue grown in Al-free nutrient solution while Al in growth medium depressed dry matter accumulation in roots by 40% of E+ plants and 3% of E- plants. Lui *et al*. (1996) found that E+ fine fescues (*Festuca* sp.) had relatively less reduction in root DM than did E- plants when grown in an acidic soil or sand and that endophyte infection had no effect when plants were grown in nutrient solutions. Malinowski *et al*. (1998) also found that with increased P availability in soil, root dry matter in E+ plants of tall fescue were significantly less when compared to E- plants. They inferred that endophyte-infected tall fescue is not responsive to high soil P indicating that an interaction between endophyte infection and abiotic factors exists.

All tall fescue ecotypes showed significantly lower root/shoot ratios for E+ plants than that of E- plants under Black Andisol. While under Red Andisol ecotype Fukaura and Koiwai showed lower values and Showa showed higher values in E+ plants indicating ecotype behaved differently with soil fertility. Regardless of ecotype, E+ plants showed 18.33% higher root/shoot ratios as compared to E- plants. This increase is attributable to the higher rates of development of roots as compared to shoots in E+ plants than that of E- plants. Malinowski and Belesky (1999) observed that endophyte infection did not affect root/shoot ratio of plants grown in Al- nutrient solution. In contrast, E+ plants tended towards a reduced root/shoot ratio when compared to E- plants in Al^{+} growing conditions.

With a few exceptions mineral concentration and accumulation in roots was strongly influenced by endophyte status, soil and tall fescue ecotype (Table 3). Phosphorus, K and Ca concentrations in roots of forage tall fescue were affected endophyte × soil × ecotype interactions.

Table 3: ANOVA test for the root nutrient elements in tall fescue

		Root nutrient					
		P			K		
Source of variations	df	MS	F	Pr>F	MS	F	Pr>F
Concentration							
Endophyte	1	0.018	22.62	0.0001	902.30	32.73	0.0001
Soil	1	1.243	154.31	0.0001	1728.20	62.70	0.0001
Ecotype	2	0.016	19.68	0.0001	923.47	33.50	0.0001
Endophyte×Soil	1	0.000	0.58	0.4527	14.84	0.54	0.4703
Endophyte×Ecotype	2	0.001	1.69	0.2064	108.72	3.94	0.0330
Soil×Ecotype	2	0.030	37.69	0.0001	523.95	19.01	0.0001
Endophyte×Soil×Ecotype	2	0.000	4.82	0.0173	107.64	3.90	0.0340
Accumulation							
Endophyte	1	8.20	43.24	0.0001	41.60	0.05	0.8248
Soil	1	128.22	676.21	0.0001	648320.00	780.52	0.0001
Ecotype	2	2.77	14.62	0.0001	5665.60	6.82	0.0045
Endophyte×Soil	1	10.39	54.79	0.0001	39713.84	47.81	0.0001
Endophyte×Ecotype	2	1.01	5.31	0.0123	10187.43	12.26	0.0002
Soil×Ecotype	2	4.32	22.76	0.0001	33847.97	40.75	0.0001
Endophyte×Soil×Ecotype	2	0.59	3.12	0.0626	2147.55	2.59	0.0962

		Root nutrient					
		Ca			Mg		
Source of variations	df	MS	F	Pr>F	MS	F	Pr>F
Concentration							
Endophyte	1	1.62	18.94	0.0002	0.3211	9.90	0.0044
Soil	1	6.50	75.94	0.0001	1.1025	33.99	0.0001
Ecotype	2	0.09	1.04	0.3674	0.0040	0.12	0.8842
Endophyte×Soil	1	0.12	1.46	0.2390	0.0040	0.01	0.9125
Endophyte×Ecotype	2	0.10	1.13	0.3397	0.0361	1.11	0.3445
Soil×Ecotype	2	0.45	5.25	0.0128	0.1564	4.82	0.0174
Endophyte×Soil×Ecotype	2	0.11	1.29	0.2947	0.0225	0.69	0.5090
Accumulation							
Endophyte	1	199.52	54.59	0.0001	1.37	0.65	0.4272
Soil	1	1890.10	517.16	0.0001	434.10	207.46	0.0001
Ecotype	2	12.01	3.29	0.0547	05.29	2.53	0.1008
Endophyte×Soil	1	302.58	82.79	0.0001	26.33	12.59	0.0016
Endophyte×Ecotype	2	3.13	0.86	0.4373	2.00	0.98	0.3975
Soil×Ecotype	2	3.09	0.84	0.4482	19.01	9.09	0.0012
Endophyte×Soil×Ecotype	2	0.60	0.16	0.8505	0.64	0.31	0.7388

Table 4: Metal macro-nutrient acquisition in root of tall fescue as affected by endophyte infection in different Andisols

		Nutrient							
		P		K		Ca		Mg	
Ecotype	Soil	E+	E-	E+	E-	E+	E-	E+	E-
Concentration ($mg\ g^{-1}$)									
Fukaura	Black Andisol	0.85a*	0.45a	53.03a	62.33a	2.89a	2.01a	1.13a	1.11a
	Red Andisol	0.18a	0.16a	31.04b	55.39a	1.45a	1.13a	0.78a	0.89a
	LSD**	0.029	0.035	18.123	16.016^{ns}	0.903	0.617	0.264	0.369^{ns}
Koiwai	Black Andisol	0.63a	0.61a	46.12a	50.78a	2.21a	1.66a	1.19a	1.39a
	Red Andisol	0.17a	0.10a	18.61a	24.78a	1.88a	1.35a	0.55b	0.83a
	LSD	0.058	0.129	13.369	5.792	0.932	0.316	0.291	0.269
Showa	Black Andisol	0.54a	0.42b	29.51b	41.73a	2.39a	1.88a	0.91b	1.28a
	Red Andisol	0.16a	0.14a	33.78a	36.96a	1.25a	1.19a	0.85a	1.01a
	LSD	0.026	0.043	6.311	3.550	0.557	0.360	0.594	0.533^{ns}
Accumulation ($mg\ plant^{-1}$)									
Fukaura	Black Andisol	5.81a	2.64b	385.73a	363.47a	20.72a	11.76b	8.19a	6.55a
	Red Andisol	0.21b	0.49a	38.43b	165.37a	1.72a	3.53a	0.91b	2.92a
	LSD**	0.627	0.219	87.705	75.430	2.477	3.329	2.086	1.543
Koiwai	Black Andisol	6.46a	3.95b	470.91a	323.07b	22.54a	10.82b	12.33a	8.86a
	Red Andisol	0.10a	0.15a	11.00b	35.57a	1.20a	1.95a	0.34b	1.15a
	LSD	1.801	1.201	79.148	35.972	5.263	1.383	5.353	1.501
Showa	Black Andisol	5.38a	2.66b	295.53a	259.91a	24.18a	12.35b	9.18a	7.98b
	Red Andisol	0.48a	0.52a	98.27a	134.61a	3.65a	4.36a	2.48a	3.73a
	LSD	0.761	0.373	35.840	58.131	7.559	2.947	3.524	2.843

*Values within the rows and parameters for each variable with the same letter(s) are not significantly different at $p<0.05$; **LSD ($p<0.05$) between Black Andisol and Red Andisol (columns)

Higher P and K uptake was observed in E+ plants grown in Black Andisol whereas lower was observed in E+ plants grown in Red Andisol (Table 4). Endophyte-infected plants had significantly higher root P concentrations than those of E- plants irrespective of soils whereas K concentration in root was substantially higher in E- plants than E+ plants grown in both the soils. Differences in Ca and Mg concentration between E+ plants and E- plants grown in both the soils were not statistically significant although higher amount of Ca was observed in E+ plants. Higher amount in root Ca concentration between E+ and E- plants could suggest an influence of the endophyte infection status upon the cell wall formation since Ca makes an electrical bridge between carboxyl group and pectin chain (Rahman, 1997) which may be responsible for wide adaptability of E+ plants in biotic and abiotic stress.

CONCLUSIONS

Our results indicated that, as compared to E- plants, E+ plants of tall fescue had better performance at high nutrients element level, but significantly lower performance at low nutrients element level, which presumably reflects the balance between the advantage of infection and the cost to the host supporting the endophyte. The variation in root characteristics of forage tall fescue ecotypes may be caused by chemical signaling system in E+ plants as *Neotyphodium* sp. are not exists in plant roots.

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