Factors Affecting Carbon Exudate Levels for Andropogon gerardii in the Presence and absence of Mycorrhizal Fungus

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Introduction

The limited understanding of the mechanisms that govern the partitioning of photosynthate and mineral nutrients between different plant structures is a major factor restricting the development of process-based models of whole plant growth (Marschner et al. 1996). The distribution of biomass among plant structures is a key variable that affects the survival, competitive ability, and performance of single plants. Plant dry matter is largely determined by the partitioning of photosynthate among the various sink organs. The distribution of recently assimilated carbon into structures that contribute to growth in photosynthetic capacity is critical for optimal growth. However, sufficient C must be allocated to roots and other non-photosynthetic structures that supply nutrients and water to the shoot. Hence, a delicate balance exists in partitioning of photo-assimilate between autotrophic leaves and non-autotrophic roots and associated mycorrhizal fungi. We suggest that a knowledge of how the mycorrhizal fungus

responds to changes in host C allocation and soil nutrient supply rates is required to make predictions about whole plant responses to a changing environment.

It has been suggested that plants that are normally nonmycorrhizal compensate for a lack of colonization by enhancing the release of organic exudates into the rhizosphere as a means for acquiring P (Diaz et al.1993). Plants that are normally mycorrhizal when grown in the nonmycorrhizal condition also appear to respond to nutritional deficiency in a similar manner, by increasing the amount of organic exudate. Furthermore, mycorrhizal plants appear to exuded less organic acids than their nonmycorrhizal counterpart.

Objective

The goal of this study was to determine those host and mycorrhizal fungus traits that influence the amount of exudate C, as measured by extractable organic C, for the tallgrass prairie plant Andropogon gerardii when grown with and without mycorrhizal fungi and in low and high P supply soils.

Materials and Methods

Study System

Species: A. gerardii

Treatments:

* Arbuscular mycorrhizal fungi inoculation
* Two levels of soil phosporus fertility
* Three levels of nitrogen addition

Harvesting: Sequential harvests at: 60, 75 and 90 days after planting

Parameters Measured

* Plant height
* Number of leaves
* Numbers of stems
* Leaf area
* Shoot weight
* Root weight
* Root length
* Mycorrhizal colonization
* Tissue Nitrogen, Phosphorus, and Potassium
* Soil Nitrogen and Phosphorus
* Tissue non-structural carbohydrates
* External hyphal length
* Photosynthesis and C gain
* Extractable soil C and Microbial Biomass Carbon

Preparation of Growth Media

* Soil samples were collected from Fermilab, Batavia IL, and Manhattan KS
* Samples were then sieved (6.35 mm), pasteurized and mixed with sand and calcinated clay in a ratio of 3:1:1 (soil : sand : clay)
* Low (KCl solution) or high (KH_2PO_4 30μg P/g soil) phosphorus treatments were given to samples.
* Soils were also subjected to three levels of nitrogen availability. NH_4NO_3 was added to weekly watering and plants received: deionized water (no nitrogen), dI water + NH_4NO_3(at an estimated "ambient" concentration, [X]), or dI water + NH_4NO_3 at a [10X] - "high" concentration.

Measurement of Extractable Organic Soil Carbon

Preparation of Soil samples

* Soil samples were stored at -20°C until needed.
* Samples were thawed at 4°C and passed twice through a 4mm (No 5) sieve to remove root material.
* Representative subsamples were then taken from the seived soil and dry and wet weights of the subsamples were used to calculate the moisture content of each soil mixture.
* Subsamples of the moist soil - equivalent to 10g dry weight were then taken and dI water was added to bring the moisture content of each sample to 60% of the soil water holding capacity.
* Subsamples were then incubated for 27hrs at 22°C and 100% relative humidity

Carbon Extraction

* Incubated subsamples were extracted with 50 ml of K_2SO_4 (0.5M) for 1 hour using a wrist-action shaker.
* The extract mixture was then filtered through Whatman 42 ashless filters.
* Filtered extract was then stored at -20°C.

Carbon Concentration Measurement

* The organic carbon concentration of the extracts was measured by UV-persulfate digestions with a Dohrmann Carbon Analyzer.
* Samples were analyzed for both inorganic and total carbon content and the difference in these two measurements was then taken as the total organic carbon content.

Effects on Root exudates

We evaluated the amount of exudate C (extractable C) in the rhizosphere of *A. gerardii* roots at 60, 75 and 90 DAP. The four-way ANOVA showed a highly significant first order Time ($P < 0.0001$) and inoculation ($P < 0.0001$) effect for extractable C, where a reduction in exudation occurred over the period of the study. Similarly, the presence of AM fungi led to significant reduction in exudate C quantity (Table 1). The only nutrient effect on exudation quantity was the influence of P fertility, where the lower the soil P content of the soil the higher the extractable C ($P < 0.0005$). Furthermore, although an increase in extractable C was found with nonmycorrhizal plants, mycorrhizal plants' active and total colonization responded in a similar positive manner, whereas, external hyphae was negatively associated with the amount of extractable C in the soil (Table 2).

Table 1. A significant second order interaction effect was found for the relationship between inoculation with mycorrhizal fungi and the production of exudates (extractable C) in the Fermilab soil for the last three harvests ($P < 0.0358$).

Source	Mean (± SE) Extractable C (mg C/g soil)		
	60 DAP	75 DAP	90 DAP
Nonmycorrhizal	83.7 ± 1.2	73.3 ± 1.3	73.3 ± 1.2
Mycorrhizal	75.1 ± 1.3	71.1 ± 1.3	66.5 ± 1.3

Table 2. Association of extractable C with various host and mycorrhizal fungus parameters for mycorrhizal and nonmycorrhizal treatments (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *ns*, no statistical significance; *np*, not present; n=102).

Parameter	Pearson product-moment correlation coefficients (r)	
	Mycorrhizal	Nonmycorrhizal
Shoot N conc.	*0.46* ***	*0.48* ***
Root N conc.	*0.40* ***	*0.37* ***
Shoot P conc.	*0.22* *	*0.34* ***
Root P conc.	*0.26* **	*0.22* *
Plant P:N ratio	*-0.40* ***	*-0.51* ***
Root length	*-0.27* **	*-0.33* **
AMF Hyphal length	*-0.25* **	*np*
Active colonization	*0.32* **	*np*
Total colonization	*0.24* *	*np*
Total root carbohydrate	*-0.15 ns*	*0.33* **
Carbon gain	*0.31* **	*0.30* **

Table 3. Four-way ANOVA summary for treatment effects on extractable organic C (n = 202).

Source	df	F value	P > F	R^2
Time	2	28.37	***0.0001***	*0.43*
Inoculation	1	29.77	***0.0001***	
Time × inoculation	2	3.29	***0.0397***	
N	2	0.60	0.5527	
Time × N	4	0.80	0.5285	
Inoculation × N	2	0.41	0.6654	
Time × inoculation × N	4	0.12	0.9767	
P	1	12.09	***0.0006***	
Time × P	2	0.29	0.7461	
Inoculation × P	1	0.18	0.6677	
Time × inoculation × P	2	1.83	0.1637	
N × P	2	0.10	0.9078	
Time ×N × P	4	1.04	0.3882	
Inoculation × N × P	2	0.22	0.7993	
Time × inoculation × N × P	4	0.69	0.6014	

Conclusions

We find that with colonization and at low-soil P the amount of extractable C within the rhizosphere is reduced suggests that the nonmycorrhizal plants compensate for a lack of colonization by enhancing the release of organic exudates into the rhizosphere as a means for acquiring P. Although the amount of extractable C is less in quantity in inoculated soils, colonization levels were positively associated with extractable C. Furthermore, the amount of external hyphae was negatively associated with the amount of exudate C. These relationships suggest that both fungus and extractable C are related sinks.

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