Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Applied Soil Ecology 32 (2006) 111–117

Applied Soil Ecology

www.elsevier.com/locate/apsoil

Defoliation effects on arbuscular mycorrhizae and plant growth of two native bunchgrasses and an invasive forb

Sara Z. Walling [1], Catherine A. Zabinski *

Land Resources and Environmental Sciences, Montana State University, 334 Leon Johnson Hall, Bozeman, MT 59717, USA

Received 6 February 2004; received in revised form 11 November 2004; accepted 28 February 2005

Abstract

Centaurea maculosa, an invasive forb in western North American grasslands, dominates more than 4 million ha of rangeland in the Rocky Mountain region. Our research examined the effects of herbivory and arbuscular mycorrhizae (AM) on the growth of *C. maculosa*, and two native grasses, *Festuca idahoensis* and *Pseudoroegneria spicata*. Plants were grown for 11 weeks, with or without AM, prior to simulated herbivory. We removed 75% of aboveground biomass from half of the plants, and harvested all plants 4 weeks later. All species increased their growth rate after clipping, but clipped plants were smaller than unclipped plants. The difference in biomass between clipped and unclipped plants was smaller for *C. maculosa* (clipped:unclipped = 0.62) than for the native grasses (0.42 and 0.52). Plants with AM were smaller than non-AM plants across all species, with the greatest reduction in *F. idahoensis* (77% versus 18% in *C. maculosa* and *P. spicata*). Levels of AM colonization were minimal in *F. idahoensis* (<1% of root length colonized), intermediate in *P. spicata* (13% colonization) and highest in *C. maculosa* (20%). Extra radical hyphae (ERH) lengths were highest for *C. maculosa*, and equal between the two grasses. Because of the lower biomass, plant tissue N concentrations were higher in AM plants, but P concentrations increased in AM plants for only *C. maculosa* and *P. spicata*. The superior competitive ability of *C. maculosa* may be the result of greater compensatory growth after herbivory and higher amounts of ERH, both of which result in greater resource capture.

Keywords: *Centaurea maculosa*; Herbivory; Arbuscular mycorrhizae; Extra radical hyphae; Invasive species; Compensatory growth

1. Introduction

Herbivory can be a strong selective pressure on plants (Stowe et al., 2000) resulting in compensatory growth or tolerance to herbivory (Strauss and Agrawal, 1999), in which plants replace tissue lost to herbivores. Plants able to avoid or escape herbivory often have a competitive advantage, which may partially explain the success of invasive species introduced to habitats that lack a full compliment of herbivores (Elton, 1958; Siemann and Rogers, 2003). A plant's response to herbivory will also be affected by nutrient availability (Paige, 1992; Crawley, 1997), and empirical studies suggest that species differ in ability to take advantage of a high nutrient environment, in response to herbivory (Wallace and Macko, 1993; Hicks and Reader, 1995). High nutrient concentrations do not always allow the plant species to overcompensate (Meyer, 2000; Schmid et al., 1990), as slow growing species may need only a slight increase in growth rate to replace lost biomass (Hilbert et al., 1981).

Arbuscular mycorrhizae (AM) influence plant nutrition (Smith and Read, 1997) and could affect

---

* Corresponding author. Tel.: +1 406 994 4227; fax: +1 406 994 3933.

E-mail addresses: swalling@purdue.edu (S.Z. Walling), cathyz@montana.edu (C.A. Zabinski).

[1] Present address: National Soil Erosion Research Laboratory, 275 South Russell Street, West Lafayette, IN 47907-2077, USA. Tel.: +1 765 496 6585.

0929-1393/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.apsoil.2005.02.017

plant compensation after herbivory (Newingham, 2002). As obligate symbionts, AM fungi form a symbiotic relationship with plants and assist the host plant in P uptake (Sanders and Tinker, 1971; Kothari et al., 1991). In return, the plant allocates photosynthetically derived carbon to the fungus. In nutrient-limiting environments, AM benefit the host plant by foraging for nutrients beyond the rhizosphere, often accessing nutrients in soils unexplored by the host plant's root system (Friese and Allen, 1991; Jakobsen et al., 1992). In fertile systems, the benefits of AM are often negated by the carbon cost to the plant by the fungi, and by the abundant nutrients available to the plant directly through their root systems (Johnson et al., 1997). Because 85% of terrestrial plants form this symbiosis (Smith and Read, 1997), many plants impacted by grazing are mycorrhizal. Increased soil nutrient acquisition inherent to the plant–fungal mutualism can assist in plant compensation for herbivore losses. However, when soil nutrient availability is high, the carbon drain by the fungus could reduce regrowth (Eom et al., 2001).

Simulated or natural herbivory may affect AM colonization levels if the host plant shifts carbon allocation away from or to the fungal symbiont. Gehring and Whitham (1994) found that in 23 of 37 studies (60%), AM colonization levels decreased after simulated or natural herbivory events. The authors speculate that decreases in AM colonization may have profound effects on plant competitive interactions, reducing plant competitive abilities with reduced AM colonization.

Centaurea maculosa Lam. (spotted knapweed), a plant species native to Eurasia, was introduced to the United States in the early 1900s. Since its introduction, *C. maculosa* has invaded over 4 million ha in the Rocky Mountain region of the United States (Boggs and Story, 1987). *C. maculosa* is characterized by its ability to outcompete neighboring plants for nutrient and water resources, forming dense monocultures in areas once dominated by native bunchgrasses (Boggs and Story, 1987). With increased awareness of the short- and long-term effects of herbicide application, biological controls have been used to decrease *C. maculosa*'s abundance (Boggs and Story, 1987). Grazing management to control *C. maculosa* infestations hinges on grazing effects being more detrimental to the invasive species than to native neighboring species (Olson, 1999). While cattle preferentially graze grasses over *Centaurea* (Kennet et al., 1992), small ruminants such as sheep and goats readily graze *C. maculosa* (Olson and Wallander, 1997).

The objectives of our study were to evaluate the effects of AM on plant response to herbivory and to assess the effects of herbivory on AM structure and function. We hypothesized that AM would increase plant N and P concentration and compensatory growth for all plant species, and that herbivory would not affect AM colonization levels or ERH production.

2. Materials and methods

2.1. Experimental design

Our experiment was a randomized, complete block design with 3 plant species, 2 mycorrhizal treatments, and 2 herbivory treatments, and 10 replicates of each treatment combination. Replicates were divided into blocks placed in a grid pattern to account for variations in temperature, light level, and humidity in the greenhouse. Plants were grown individually in 38 cm tall by 10 cm diameter PVC pots. An 8:1 mix of sand (masonry grade silica sand, 20:30 grit) and field soil was used. The field soil was taken from rangeland on Red Bluff Research Ranch in southwestern Montana (45.60°N, 111.50°W), and is classified as a fine-loamy, mixed, frigid Calcidic Argiustoll.

Two native bunchgrasses, *Festuca idahoensis* Elmer (Idaho fescue) and *Pseudoroegneria spicata* [Scribn. & Smith] A. Love (bluebunch wheatgrass), and the invasive forb, *C. maculosa* (spotted knapweed) were used in this study. These cool season grasses are common in plant communities invaded by *C. maculosa* in the western United States (Tyser and Key, 1988). Four seeds of a single species were seeded into each pot, with 1/2 cm of sterilized sand applied over the seeds. *F. idahoensis* seeds take longer to germinate so were planted 7 days earlier than *P. spicata* and *C. maculosa*. Pots were watered twice daily for the first 2 weeks after germination, and daily for the remainder of the experiment. Fifty milliliters of 1/8-strength modified Hoagland's solution (minus P) were added twice during seedling establishment to reduce potential nutrient stress. Plants were supplemented with 0.0168 mmols N pot^{-1} day^{-1} and P fertilizer addition of 0.0607 g pot^{-1} triple super phosphate (TSP; 46% available P_2O_5).

The greenhouse was maintained at 21 and 16 °C during the day and night respectively, with a photoperiod of 16 h for the first 8 weeks of plant growth, after which time the natural day lengths reached approximately 16 h. Lighting was supplemented with 10 GE Multi-Vapor MVR1000/C/U (GE Lighting, General Electric Company, Nela Park, Cleveland, OH 44112).