Journal of Arid Environments 75 (2011) 487–493

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Role of competition in restoring resource poor arid systems dominated by invasive grasses

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ARTICLE INFO

Article history:
Received 23 June 2010
Received in revised form
14 December 2010
Accepted 3 January 2011
Available online 26 January 2011

Keywords:
Addition series
Bromus tectorum
Competition
Importance
Intensity
Restoration
Semi-arid steppe
Taeniatherum caput-medusae

ABSTRACT

Understanding the role competition intensity and importance play in directing vegetation dynamics is central to developing restoration strategies, especially in resource poor environments. We hypothesized 1) competition would be intense among invasive and native species, but 2) competition would be unimportant in explaining variation in target plant biomass and survivorship relative to other factors driving these variables. We performed a two year addition series field experiment to quantify competition intensity and importance. Densities of two invasive (cheatgrass and medusahead) and two native (Sandberg's bluegrass and bluebunch wheatgrass) species were arranged in monocultures and mixtures of two, three and four species, producing varying total densities and species proportions. Multiple linear regression models predicting individual plant biomass and survivorship were developed. Based on biomass, competition intensity coefficients ranged from −0.38 to 0.63 with $R^2 < 0.06$. All survivorship data produced poor fitting regression models ($R^2 < 0.05$). Our results suggest neither competition intensity nor importance influenced plant dominance in resource poor environments during the two years of establishment. Land managers may be more successful at restoration of resource poor ecosystems by overcoming abiotic barriers to plant establishment rather than focusing on plant–plant interactions.

1. Introduction

The role of competition in controlling plant dominance in resource poor environments remains poorly understood. Some authors have argued that competition is minimal or non-existent under conditions of high environmental stress (Grime, 1973, 1979), while others suggested that the strength of competition is of equal magnitude in habitats of both high and low productivity (Newman, 1973; Tilman, 1980; Wilson and Tilman, 1993). In spite of the development of refined conceptual frameworks of plant interactions occurring in varying environments (Goldberg and Novoplansky, 1997; Maestre et al., 2009) and quantitative syntheses of existing literature (Goldberg et al., 1999; Gomez-Aparicio, 2009), a unified understanding of the degree to which competitive interactions control plant dominance in resource poor environments has not emerged. This is because only limited empirical evidence exists supporting either hypothesis, and those data are not consistent.

Understanding competition intensity and importance is a central barrier to developing restoration strategies, especially in resource poor environments (Grace, 1991; Tikka et al., 2001; Sheley and Krueger-Mangold, 2003; Brooker and Kikvidze, 2008). Competition intensity refers to the degree to which resource competition by neighbors reduces target plant performance below a value when no neighbors are present (Welden and Slauson, 1986). In their original source article, Welden and Slauson (1986) indicated that importance of competition is the proportion of variation in target plant fitness that is accounted for by competition in relation to all other factors affecting plant fitness. A vigorous debate is occurring in the literature in an attempt to improve the concept of competition importance (Brooker and Kikvidze, 2008; Freckleton et al., 2009; Damgaard and Fayolle, 2010; Kikvidze and Brooker, 2010). Freckleton et al. (2009) argued that the definition of importance should provide an indication of long-term consequences of competition on the structuring of plant communities. This can be achieved by including the effects of plant interactions on other indicators of fitness, especially fecundity, in plant communities at equilibrium. In response, Kikvidze and Brooker (2010) suggested that the complexity of biotic interactions invites

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doi:10.1016/j.jaridenv.2011.01.002

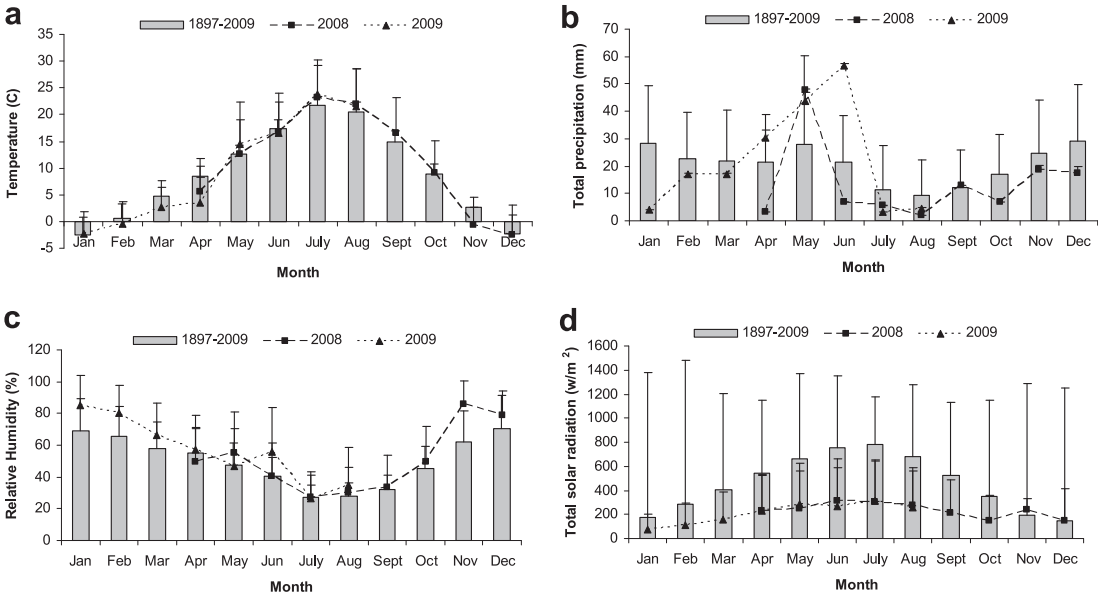

Fig. 1. Monthly precipitation (a), temperature (b), solar radiation (c) and relative humidity (d) at the study site. Long-term monthly precipitation, temperature, solar radiation and relative humidity also were determined at a weather station near the study site (monitored daily, National Climate Data Centre (NCDC), 2009).

a range of approaches in determining competition importance, but should be consistent with Welden and Slauson (1986).

Even though Welden and Slauson (1986) were clear that the two measures of competition are not necessarily correlated, the bulk of empirical work focuses on how intensity of competition changes along resource gradients with the underlying assumption that intensity of competition will be proportional to its importance (Grace, 1991; Mitchell et al., 2009). However, competition could range from non-existent to being intense and unimportant to being very important. For example, if the target plant biomass is affected only by competition, this interaction may have a low or high intensity but is very important (Briones et al., 1996). If the target plant biomass is determined by other factors (e.g. abiotic stress, disturbance, herbivory, parasitism) than the competition could be of low or high intensity but is unimportant (Welden and Slauson, 1986; Briones et al., 1996). In resource poor environments resources are limited and competition could be intense (Fowler, 1986), but abiotic factors could have an overriding role in influencing plant biomass and survival (Ackerman, 1979; Gutterman, 2002) This may be directly linked to the ability to tolerate drought and temperature extremes (Went, 1949; Mulroy and Rundel, 1977).

A better understanding of competition intensity and importance may allow advancements in ecology that could be particularly important in identifying how we link ecology to management and restoration of resource poor systems. For example, invasion by exotic annual grasses such as cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* L. Nevski), have been identified as the greatest ecological threat to the native vegetation of the semi-arid steppe of the North America (Mack, 1989; Pellant, 1990; D'Antonio and Vitousek, 1992; Sheley and Petroff, 1999; Duncan et al., 2004; Germino et al., 2004; Sheley et al., 2008). Each year several billion dollars are spent to control invasive plant species (Westbrooks, 1998; Pimentel et al., 2005), but long-term success is rare. While competition is assumed to play an important role in limiting success, harsh abiotic conditions such as drought and cold stress also influence restoration outcomes (Allen, 1989; Padilla and Pugnaire, 2006). Although several studies have indicated that invasive annual grasses are more competitive than grass species native to North America (Sheley and Larson, 1995; Humphrey and Schupp, 2004; Krueger-Mangold and Sheley, 2008; Vasquez et al., 2008), most information was derived from studies conducted on relatively productive grassland sites or under optimal environmental conditions. Therefore, a more complete understanding of competition intensity and importance may be a useful step in helping managers understands how to prioritize restoration efforts in resource poor environments within the semi-arid steppe.

The objectives of this study were to: 1) quantify the intensity of competition among invasive annual grasses and native perennial bunchgrasses, and 2) determine the importance of competition in explaining variation in target plant biomass and survivorship in an arid, resource poor system. We used an addition series competition design that allows quantification of the intensity and importance of competitive interactions (Spitters, 1983; Welden and Slauson, 1986). Intensity was measured as the slope of linear regression equations (Spitters, 1983), while importance was calculated as the percentage of the variation explained by the regression equation (i.e., R^2; Welden and Slauson, 1986). The analysis is confined to the natural and un-known heterogeneity of biotic and abiotic factors present at the study site. There are also possible measurement errors and genotypic differences between individuals apart from the controlled density of species in competition. The specific hypotheses tested were 1) competition would be intense among invasive and native plant species but 2) competition would be unimportant in explaining variation in target plant biomass and survivorship relative to all other factors driving variation in these two parameters. Our rationale for these hypotheses was based on the theory that in resource poor environments resources are limited (by definition) and competition may be intense among species, but because there are a number of other factors determining plant fitness, competition may not be important.

2. Material and methods

2.1. Study site and environmental conditions

The study was conducted at a Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* [Beetle & A. Young] S. L. Welsh)- steppe community type in southeastern Oregon (43° 32′ N,