Article

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Life forms interactions in semiarid Mediterranean annual grassland community

Abstract

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Species interaction plays a central role in structuring plant communities. However, few studies have investigated the nature of species interaction among different life forms along a productivity gradient. The current study is aimed to investigate the nature of life forms interactions and its impact on production of annual grasses grown in semiarid Mediterranean areas. Competition treatments (absence/presence of neighbours) were applied in randomized complete block design over two growing seasons. Relative interaction index (RII) was used to measure competition intensity. RII standardizes the reduction in growth of one species due to presence of neighbour species. Competition reduced grass biomass production by approximately 15%. Competition role was eliminated under low productivity conditions. Results showed that competition may limit the direct effect of defoliation on dominant grass species. Further, competition effect on dominant annual grasses showed positive and negative effects in relation to site productivity and best explained by a sinusoidal model. This hypothesized sinusoidal model suggests that facilitation and competition are alternatively affecting grassland communities along productivity gradient. The nature of interaction changes with changing community productivity revealing a cyclic pattern. The reflection points where interaction switches from facilitation to competition may explain the mechanism of maintaining high species diversity at intermediate level of community productivity. The experimental defoliation exerted a pronounced effect on plant productivity and modified the nature of interaction between annual grasses and other growth forms. These mechanisms may explain the ability of *Avena* and *Hordeum* species to form persistent annual climax grasslands in semi-arid rangelands. These findings may suggest that *Avena* and *Hordeum* species may be used in revegetating degraded areas in the north-eastern part of Jordanian Mediterranean grasslands.

Key words: competition, relative interaction index, *Avena*, *Hordeum*.

Introduction

Middle Eastern Mediterranean grasslands have evolved 8000-9000 years before present (BP) (Harlan 1975; Hunt & al. 2004). These grasslands were prehistorically subject to persistent pressure from grazing domesticated animals (Noy-Meir & Seligman 1979; Perevolotsky & Seligman 1998; Alhamad 2006). Competition among plant spices is a key

player in structuring semi-arid grassland communities (Fowler 1986; Alhamad & Alrababah 2008), linking their maintenance, productivity, and management to biodiversity and livestock production.

Grace & Tillman (1990) showed that competition has a significant role in shaping the structure of terrestrial plant communities. Three mechanisms have been used to explain the relationship between site productivity and competitive interactions among plant species. The first of these mechanisms shows that competition can be intense in high-productivity locations and reduced in low-productivity environments (Grime 1979; Huston 1979; Keddy 1989). The second mechanism says that the intensity of competition does not depend on the productivity of the environment, but that the nature of competition changes according to the availability of growth resources. Where competition among plants is light or space in high-productivity environments, and when site productivity decreases, competition between plants becomes over water or soil nutrients (Newman 1973; Tilman 1982 & 1987). Taylor's theory of resource competition (Taylor & al. 1990) was used to explain the mechanism of competition between plants. This theory suggests that there is no causal relationship between productivity and competition, and that the primary determinant of competition is the ratio of supply of resources to demand it, and this ratio depends on the frequency of disturbance events such as drought and grazing.

Livestock production systems in the eastern part of the Mediterranean region depend on semi-arid grassland as the main fodder source for feeding grazing animals (Noy-Meir & Briske 2002; Alhamad 2006). The semi-arid grassland is found under an annual rainfall of 200-300 mm in the north-eastern part of Jordan (Alhamad & Alrababah 2008). The unsustainable grazing activities have led to a noticeable decline in biodiversity and a sharp decrease in the productivity of these lands (Alhamad 2006; Alhamad & Alrababah 2008). The prolonged uncontrolled grazing pressure led to successive degradation, in which the tallest perennial herbs were replaced by shorter perennial herbs and then later replaced by annual herbs to finally end up with barren land.

Natural annual grasslands communities occur in heterogeneous patches dominated by one or two annual grass species (George & al. 1992; Alhamad & Al-Rababah 2013). Where annual grass seedlings have competitive advantages over the development of perennial plant seedlings, in such patchy communities (Harris 1977). The biological inertia prevents the transforming of annual-dominated grasslands showed community into perennial-dominated grassland (George & al 1992). However, the shift between dominant annual species has been observed. Mechanisms that involved in plant community change are grazing impact, establishment, and competition beside seed banks (Westboy 1980; Walker 1988).

A fuller understanding of the relationship between site productivity and plant species competition, may help to develop sustainable grazing strategies to revegetate degraded arid rangelands and maintain the biological diversity in these areas (Fowler 1986; Alhamad 2006; Alhamad & Al-Rababah 2013). Therefore, this study was initiated to establish experimentally the foundation to understand the relative effects of site productivity on competition, and their interaction to reliably interpret the direct effects of defoliation (Noy-Meir & Briski 1996).

The present study was conducted to answer the following questions (1) what is the effect of competition from neighboring plants on the competitive performance of annual grasses under semi-arid conditions? (2) Is the nature of interaction modified by growth resources?

Materials and methods

Site description

The experimental site is located at Jordan University of Science and Technology (JUST) campus, in northeastern semi-arid grasslands of Jordan. The site is located 18 km to the east of Irbid city (32° 34' N, 36° 01' E). The campus was established in 1986. The site is characterized by a flat to gently rolling topography with less than 8% slope located at 520 m above sea level. The soil of the experiment site consists of deep silty clay soils and generally contains a low percentage of soil organic carbon (1.0%).

The plant community is a typical semi-arid Mediterranean annual grassland that is dominated by wild oat (*Avena sterilis* L.), and wall barley (*Hordeum murinum* L.). Companion species include *Senecio vernalis* Waldst. & Kit.*, Vicia peregrina* L.*, Trigonella arabica* Delile, *Erucaria hispanica* (L.) Druce, *Anthemis palestina* Reut. (see Alhamad & Alrababah 2008).

Climate

The locality is characterized by semi-arid Mediterranean conditions of mild rainy winters and dry hot summers. The long-term average annual precipitation is 230 mm. The site received a total rainfall of 208 mm during the 2003/2004 season and 226 mm during the 2004/2005 season .

Experimental design

The experiment was carried out in the 2003/2004 and 2004/2005 growing seasons. Eight replicated blocks were located in a natural grass community, dominated by wild oat (*Avena sterilis*) and wild barley (*Hordeum murinum*). The ground cover was generally continuous and little bare soil was exposed. Two 2 × 2 m plots were arranged within each block. These plots were allocated to two competition treatments in a complete block design. The two competition levels were: (i) no competition (all non-grass species were removed from the stand); (ii) full competition from neighboring plants (all native species in the stand including grass and non-grass species were allowed to grow). Under no competition treatment, all non-grass species were clipped down to soil surface in early February. Further clipping was performed as needed to eliminate interspecific competition between grasses and other species.

Above- ground biomass productions were collected from the center of each experimental plot using the 0.25 m^2 quadrat. The clipped material within each quadrat was separated into grasses and other species. Harvesting was performed when flag leaves and awns were dry. The harvested material was weighed oven dry to obtain the final biomass production of grasses.

Statistical analysis

A two-way analysis of variance (ANOVA) was used to assess the effects of competition and year on final and cumulative biomass production of grasses. The experimental error term was used as the denominator for constructing the F-test. 95 % confidence intervals (CI) were constructed around the main means of competition. Student's t-test (α=0.05) test was used to compare competition treatment means. ANOVA, CI, and Student's t-test were performed using JMP 5.1 software (JMP 1989-2004).

Intensity of competition

Competition intensity were measured on the basis of the relative interaction index (RII) proposed by Armas et al. (2004) as follows:

$RII = (B_{+neighbor} - B_{-neighbor})/(B_{+neighbor} + B_{-neighbor})$, where

$B_{+neighbor}$ = grasses biomass in presence of competitor neighbor plants

$B_{-neighbor}$ = grasses biomass in absence of competitor neighbor plants

To explore the relationship between competition intensity and graminoids biomass, we have plotted the RII against herbaceous biomass (the biomass of plots in the presence of neighbor species) for all levels of defoliation first and then for each of the three levels of defoliations separately. The relationship was then fit to various models using CURVEFIT software (CurveExpert 2001).

Results and discussion

The ANOVA analysis indicates a significant difference ($p < 0.01$) between the growing season 2003/2004 and 2004/2005, therefore, each year were analyzed separately (Table 1). During the growing season 2003/2004, grasses from competition-free plots produced significantly higher biomass compared to plots where competition from non-grass plants exist (Table 2). Similar results were observed during the 2004/2005 growing season (Table 2). However, productivity in the second growing season was higher than the first season, reflecting the favorable growth condition during the 2004/2005 season (Tables 2 and 3). The reduction in biomass production of grasses was 13.8 and 14.6, for the successive growing seasons, respectively (Table 2).

Competition intensity using relative interaction indexes showed a complex pattern. This pattern was best explained by the sinusoidal model (Fig 1) combined with a significant level of correlation coefficient of 0.65 (Table 3). In a previous study, Alhamad & Alrababah (2008) reported that competition showed significant interaction with different defoliation intensities in annual Mediterranean grasslands. The competition was a key player in the productivity of these grasslands under no defoliation or light defoliation. Competition reduced the biomass production of grasses in both growing seasons (Table 2).

Table 1. Analysis of variance (ANOVA), F values and significance levels for grass biomass production (g m^{-2}) randomized complete block design experiment over 2 years in semi-arid Mediterranean grassland (n=32).

Source		DF	Biomass production
Model		9	65.4**
	Year	1	265.6**
	Replicate	7	6.4**
	Competition	1	29.3**
Error		23	288.8
Total		32	

Table 2. Mean biomass production (g m^{-2}). Standard error (SE) and lower and upper 95 % confidence Interval (CI) and Percent Change in biomass production of grasses as affected by competition treatment.

Competition level	Mean	Lower. 95% CI	Upper. 95% CI	% change
First year				
- neighbor	100.71 a	96.77	104.64	
+neighbor	86.84 b	82.91	90.77	-13.8
SE	1.94			
Second year				
- neighbor	162.15 a	154.97	169.37	
+neighbor	138.48 b	131.26	145.70	14.6
SE	3.56			

Mean values (g m^{-2}) within competition level and defoliation intensity that are followed by the same letter are not different according to Student's t-tests (α=0.05).

These results are in agreement with previous research findings (Pacala & Crawley 1992; Rodriguez & Brown 1998). However, Del-Val & Crawley (2011) found that clipping a neighboring species did not improve the growth of target species. Neighbor removal approaches have been the most successful approach to study competition in plant communities. It may include the removal of all plant species except the target species or functional group species (Aarssen & Epp 1990).

The study results indicated that the impact of competition on plant growth is not linear linked to site productivity. Also, the study found clear evidence of the cyclical interaction between competition intensity and site productivity under semi-arid grassland environments. Further, the results showed the positive effect of declining competition from neighboring species on grass production. This response agreed with previous research results (Fonteyn & Mahall 1981; Fowler 1986). The competitive fitness is largely depending on the relative tolerance of annual grasses to grazing as compared to their competing neighbors (Anderson & Briske 1995).

Table 3. Fit Sinusoidal model (y=a+b*cos (cx+d) parameters, standard error (SE) and correlation coefficient (R) between relative competition intensity (y) and herbaceous biomass (x) (g m^{-2}).

Model parameter	value
a	-0.04894
b	0.169894
c	0.018701
d	-2.3921
SE	0.15
R	0.65*

* significant at the 0.05 level
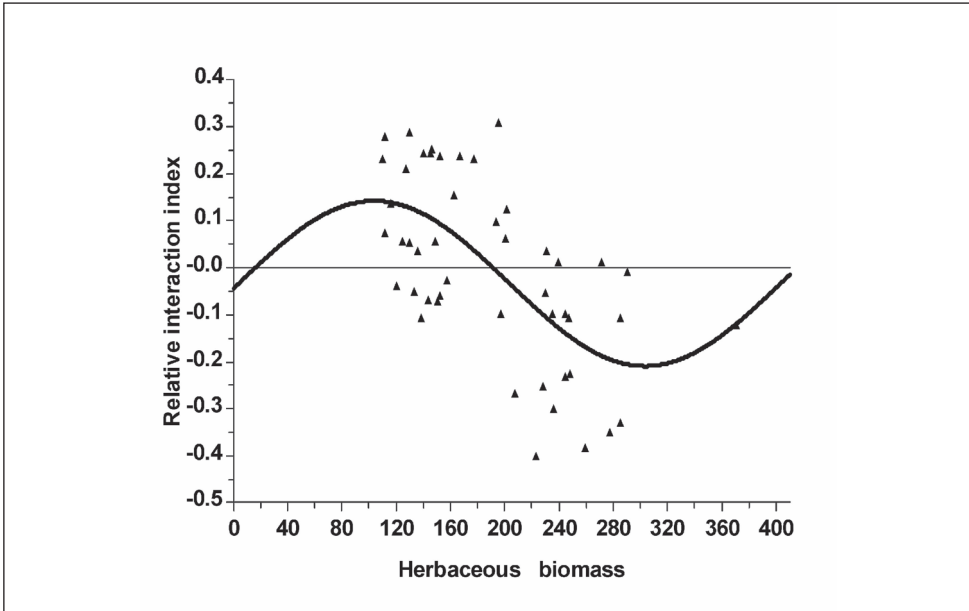
Fig 1. Curve fitting model between competition intensity (RII) and herbaceous biomass (g m^{-2}).

RII has defined limits that are symmetrical around 0. This index measures the perform-ance of target species or functional group species in the presence and absence of neighbors. RII ranges from -1 to 1 with positive values indicating facilitation and negative values indi-cating competition (Armas & al. 2004). The normalized nature of RII, makes it a more suit-able index to compare the changes of competition intensity among different environmental gradients or level of defoliations than absolute measures of competition intensity. RII is 0 when neighbors do not affect performance. When RII becomes negative, then competitive exclusion exists. Positive values of RII indicate facilitation and usually occur in harsh environmental conditions (Bertness & Hacker 1994).

In the present study, neighbor removal showed positive and negative effects on remain-ing grass species as indicated by the sinusoidal model (Fig 1). The nature of the interaction between grass growth form and other non-grass species changed as site productivity changed (Fig. 1). The presence of competition and facilitation interactions among multiple plant species has a profound effect on community organization (Lortie & al. 2004). The results showed the presence of a reflection point corresponding to primary productivity of about 200 kg /ha at which the nature of interaction switches from facilitation to competi-tion (Fig. 1). These results are in agreement with Grime (1979) theory on plant competi-tion. These changes in the nature of plant interaction from facilitation to competition at intermediate levels of community productivity may give a mechanistic explanation to the peaking of species diversity at moderate levels of productivity (Grime 1973). The nonequi-librium interactions of different growth forms of competing plant populations allow a com-munity of competitors to coexist (Huston 1979).

Conclusion

The present study detected a considerable non-equilibrium interaction between annual grass species and other growth forms. The nature of interaction changes with changing community productivity revealing a cyclic pattern as explained by the sinusoidal model. The reflection points where interaction switches from facilitation to the competition may explain the mechanism of maintaining high species diversity at intermediate community productivity. These mechanisms may explain the ability of *Avena* and *Hordeum* species to form persistent and closed annual climax grasslands in arid and semi-arid Mediterranean rangelands even under grazing pressure. These findings may suggest that *Avena* and *Hordeum* species may be used in re-vegetating degraded areas in the north-eastern part of Jordanian Mediterranean grasslands.

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