

Role of nurse shrubs in restoration of an arid rangeland: Effects of microclimate on grass establishment

M. Jankju*

Department of Range and Watershed Management, Ferdowsi University of Mashhad, Azadi Square, Mashhad, Iran

ARTICLE INFO

Article history:

Received 4 April 2011

Received in revised form

5 September 2012

Accepted 11 September 2012

Available online 14 November 2012

Keywords:

Agropyron desertorum

Canopy facilitation

Competition

Iran

Rangeland

Soil moisture

ABSTRACT

A perennial forage grass, *Agropyron desertorum* was sown under the canopies of four shrub species or in open areas to test for facilitation during seedling establishment in an arid rangeland in Karnakh, Northeast Iran. Height, area and volume of shrubs were measured. Microclimate conditions and seedling establishment were assessed three times within two consecutive growing seasons. Near surface light intensity and air temperature were lower under shrubs, which led to initially higher soil moisture and grass establishment under the canopy of some shrub species. The leguminous shrub (*Astragalus gossypinus*) showed facilitation during moderate stress (summer 2009), but shifted to a negative effect during the severe drought (summer 2010). Competition, possibly for light, reduced the establishment of *Agropyron* seedlings under the cushion-like shrub (*Acantholimon prostegium*). *Salsola arbusculiformis* and *Artemisia kopetdaghensis* respectively showed a neutral and a facilitation effect in the first season, but a combined effect of allelopathy and drought led to the high mortality of *Agropyron* seedlings under their canopy. In conclusion in this arid rangeland, shrubs may facilitate establishment of understory plants under moderate drought stress, and for non-resource factors (light and temperature), but these positive effects are suppressed due to competition under severe drought conditions.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Arid rangelands are among the most sensitive ecosystems to global climate change (Maestre et al., 2012). High grazing pressures combined with repeated drought have pushed many arid rangelands toward desert conditions, so that the possibility of their natural recovery has significantly declined (Kefi et al., 2007). Hence, there is a vital need for restoration of these rangelands to attain more sustainable ecosystems, with a higher forage production and greater soil and water protection.

The most crucial stage in a restoration project is seedling establishment (Grubb, 1977). In arid rangelands, it can largely be limited by soil moisture deficiency, temperature fluctuation and herbivory (Smith et al., 1997; Valentine, 1989). Thus, there is a need for developing novel, low-cost and efficient restoration techniques (Hobbs et al., 2006; Ormerod et al., 2003), particularly in regard to timing and abundance of available soil water in drylands (Jankju and Griffiths, 2006; Reynolds et al., 2004).

When restoration fails because of stressful environmental conditions or intense herbivory, species that minimize these effects might be used to improve performance in nearby target species (Padilla and Pugnaire, 2006). Interaction effects by nurse plants can significantly increase or decrease seed germination and seedling establishment under their canopies (e.g. Soliveres et al., 2010). Several experiments in the Mediterranean regions have shown the successful use of nurse shrubs in restoration projects (e.g. Gómez-Aparicio et al., 2004; Rousset and Lepart, 2000; Sanchez-Velazquez et al., 2004). According to the “stress-gradient” hypothesis (Bertness and Callaway, 1994) shrub facilitation for understory plants should be more common in arid rangelands and desert ecosystems than semi-arid and Mediterranean climates. Nevertheless, there are debates on the role of shrubs in arid and desert ecosystems. Several authors have reported higher plant diversity, emergence and/or survival rate under the canopy of shrubs, compared with open areas (e.g. King, 2008; Padilla and Pugnaire, 2006), while others have reported contrasting results (e.g. Anthelme and Michalet, 2009; Huber-Sannwald and Pyke, 2005; Tielbörger and Kadmon, 2000). Therefore the primary aim of this experiment was to test the capability of shrubs as a restoration tool in an arid rangeland.

* Tel.: +98 511 8763234, +98 9155252538 (mobile); fax: +98 511 8788805.

E-mail addresses: mjankju@um.ac.ir, mjankju@ferdowsi.um.ac.ir.

Relationships between nurse-plants and their nearby species may be dependent on the ontogeny of the interacting species (e.g. Armas and Pugnaire, 2009; Quero et al., 2008; Soliveres et al., 2010), annual rainfall (Tielbörger and Kadmon, 2000), biomass of potential nurse plant species (Kitzberger et al., 2000), indices used for monitoring plant performance (i.e. emergence, survival, growth and density; Travis et al., 2006; Gomez-Aparicio, 2009), and resource vs. non-resource stress factors (Michalet, 2007). Therefore, the second aim of this research was to investigate these interactions during seedling establishment in terms of resource effects (soil moisture) versus non-resource factors (temperature and light), for the interaction between an aridland shrubs (acting as a benefactor) and a perennial grass (as beneficiary), during two consecutive growing seasons. Previous work has suggested that the type of plant interaction is dependent on the balance between resource versus non-resource factors (e.g. Maestre et al., 2009), and ontogeny of the interacting species (Soliveres et al., 2010). Therefore in this research, I expected to find strong facilitation in the early spring of the first growing season, when the beneficiary species was germinating and the main limiting factors were non-resources (light and temperature), but strong competition during summer of the second growing season, when the benefactor species, became a competitor and the main limiting factor was a resource (water or nutrients).

Previous studies on the role of nurse plants as a restoration tool have shown that the nursing effects can be dependent on identity and composition of the nurse plants understory species (Facelli and Brock, 2000; Gómez-Aparicio et al., 2004), varying levels of shading created by nurse plants (Hastwell and Facelli, 2003; Sanchez-Velazquez et al., 2004) and morphological characteristics of the nurse shrubs (Callaway, 2007). Furthermore, nitrogen-fixing capability (e.g. Maron and Connors, 1996) and cushion-like canopy (e.g., Cavieres et al., 2007) may enhance positive interactions, whereas allelopathic shrubs (e.g. Gómez-Aparicio et al., 2004) may enhance negative plant–plant interactions. Accordingly, the third aim of this research was to compare nursing effects of four aridland shrub species, which were different in terms of canopy architecture (loose vs. dense), canopy size (large vs. small) and ecological impact (N-fixing, allelopathy, and salt accumulator) on seedling survival of a perennial grass species. I expected higher nursing effects for large and N-fixing shrubs, but negative effects for small and allelopathic shrubs, with the loose and dense canopies, being beneficial, respectively, earlier or later during the growing season.

2. Material and methods

2.1. Study area

The study site was located in Karnakh, Garmsar, Northern Khorasan, Iran (37° 21' 35.6"N and 56° 33' 35.2"E). Karnakh rangelands are located in the transition zone between temperate climate of Caspian Sea and harsh desert climate of Central Iran. Hence, it is affected by severe desiccating winds in early spring and early autumn, which can cause major problems for restoration projects (Jankju et al., 2008). Slope aspect was northern, slope degree 40–60%, soil texture sandy clay loam, maximum soil depth varied from 10 to 45 cm, EC was 0.66 ds/m and pH was 7.66. We used the ratio method (2 water: 1 soil) for estimating soil EC and pH (Jafari-Haghighi, 2003). The rainy season lasts four months during January–April. Although the average annual rainfall is 170 mm, the total precipitation in 2009 and 2010 was 200 and 145 mm, indicating relatively wet and dry years, respectively (www.weather.ir).

2.2. Plant species

I analyzed the potential nurse effect of four shrub species: a leguminous shrub with a wide and loose canopy structure, (*Astragalus gossypinus* Fisch Papilionaceae, hereafter *Astragalus*), a cushion-like shrub with a dense canopy (*Acantholimon prostratum* Czernjak, Plumbaginaceae, hereafter *Acantholimon*) and two different-sized shrubs with possible allelopathic effects *Artemisia kopetdaghensis* Krasch, Asteraceae (hereafter *Artemisia*) and *Salsola arbusculiformis* Drob., Chenopodiaceae (hereafter *Salsola*). Previous experiments have shown allelopathic effects for *Artemisia* (e.g. Behdad, 2009). *Salsola* is an accumulator of soil cations (Na, K, Mg) and it can increase soil EC more than 20 times under its canopy than the nearby open areas (Bagherzadeh, unpublished results). Desert wheatgrass (*Agropyron desertorum* Fisher ex Link) Schultes, Poaceae, (hereafter *Agropyron*) was the target species to be sown under the canopy of shrubs or in open areas. *Agropyron* is an introduced grass species, originally from central Asian steppe (Asay and Knowles, 1985). It is a competitive and perennial forage grass and relatively resistant to drought and grazing stresses. It has been planted in North America, ranging from south Alaska to California to south Texas (Asay and Knowles, 1985). In Iran, *Agropyron* is widely used for restoration of arid and semiarid rangelands (Azarnivand and Zare-Chahooki, 2008). This grass is most common on coarse or medium-textured soils, and can survive on extremely shallow, dry soils and is not tolerant of crust forming, finely textured soils and is not saline tolerant (Zlatnik, 1999).

2.3. Experimental design

The experiment was followed a completely randomized design and was performed in a relatively homogenous area (about 4 ha). There were five treatments i.e. each shrub species was considered as a separate treatment (four shrubs, four microhabitats), and “open areas” between shrubs was a control treatment (the fifth microhabitats). I selected 20 shrubs of each species and 20 open areas. Seeds were shown beneath the shrub canopies and in open areas. Small pits (30-cm width, 50-cm length and 15-cm depth), were dug out by shovel, to increase runoff accumulation and facilitate seedling establishment. Pitting is a typical restoration method for dry rangelands (Valentine, 1989). Twenty seeds of *Agropyron* were uniformly distributed within pits (area 1500 cm²) and sown at a depth of 1–3 cm from the soil surface. Seeds were sown shortly after the beginning of the rainy season (mid-January 2009). Seedlings survival was measured at three periods; seed germination was recorded one month after the beginning of growing season, i.e. 18 April 2009, seedling survival was recorded at the end of two consecutive dry seasons, i.e. 10 June 2009 and 5 June 2010.

2.4. Shrub morphology measurements

Shrubs' morphology was studied on 50 random samples of each species. A preliminary field survey indicated canopy surface of all four shrub species to be very close to a rounded shape. Therefore, the longest diameter of each shrub was measured, for estimating maximum canopy area (according to Cavieres et al., 2006). Further, height of tallest branch of each shrub was measured, for estimating maximum height and volume.

2.5. Microclimate measurements

Microclimate conditions were simultaneously measured on 5 replicates of each shrub species and open areas. Near surface light and temperature were respectively measured using a Light Meter (Lurton, Taiwan) and a Digital Timer Thermometer (LTD France).

Relative water content was measured in the top 10 cm of the soil layer, using a Moisture Probe Meter (MP Kit, ICT, Australia). Recording time of each parameter was about 1 min. Data recording was repeated three times during 9–11 a.m. Average values of the repeated records were used. Measurement season was concurrent with the time of seedling survival assessment in April and June 2010. For measuring soil samples, 4 samples (1 kg each) were taken from 0 to 20 cm depth in open areas; pH and EC were measured from a saturated soil paste (Jafari-Haghighi, 2003).

2.6. Data analysis

Generalized Linear Modeling (GLM), with repeated measures, was applied on the data for grass survival, using SPSS 16 statistical program. For this, measurement date (spring 2009, summer 2009, and summer 2010) was considered the random factor and microhabitat (understory of four shrub species and open areas) was considered as the main factor. Mean values for soil moisture, near surface temperature and light intensity, and seedling establishment were compared by Tukey's test. Relative interaction index (RII) was used for measuring negative or positive effects of shrub species on the survival rate of the target grass, using following formula (Armas et al., 2004).

$$RII = (Bw - Bo)/(Bw + Bo)$$

Where Bw is number of *Agropyron* seedlings under the canopy of each shrub and Bo the mean number of *Agropyron* seedlings established in open areas.

3. Results

3.1. Effects of main treatments

Results of GLM analysis (Table 1) revealed significant effects of growing season (date) and microhabitat (shrubs) on the survival rates of *Agropyron* seedlings. Furthermore, the interaction between factors was also significant, which indicated changes in shrub effects at different dates during the experiment (i.e. spring 2009 till summer 2010).

3.2. Grass establishment

At the beginning of the first growing season (spring 2009), there were significant differences between numbers of established seedlings under the shrub canopies and those in open areas (Fig. 1a). At this date, grass establishment was highest under *Artemisia* and *Astragalus* species, whereas the number of established seedlings under the canopies of *Salsola* and *Acantholimon* was similar to that of open areas. However at the end of the first growing season, all shrubs had similar effect on *Agropyron* survival (Fig. 1b). Most *Agropyron* seedlings were dead under the canopies of the two allelopathic shrubs, *Artemisia* and *Salsola*, by the end of the second growing season (summer 2010). Furthermore, the number

of established seedlings under the canopies of *Astragalus* and *Acantholimon* were significantly lower than in open areas (Fig. 1c).

3.3. Shrub morphology

The widest canopy crown was for *Astragalus* and the smallest for *Acantholimon*, with those of *Artemisia* and *Salsola* being intermediate (Fig. 2a). Differences in shrub heights were similar to those for canopy area (Fig. 2b).

3.4. Light intensity

All shrubs significantly reduced soil irradiation under their canopy compared to open areas. Light intensity was higher under *Astragalus* canopy than under the canopy of any other shrub species (Fig. 3a).

3.5. Temperature

Instantaneously measured air temperature near the soil surface was generally lower under the canopy of shrubs than in open areas (Fig. 3b). The warmest understory was for *Astragalus* and the mildest for *Artemisia*.

3.6. Soil moisture

Shrubs also differed in their effects on soil moisture. Early in the season (Fig. 3c) (April) a significantly higher soil moisture was found under canopy of *Salsola* and *Artemisia*. At this date, *Acantholimon* and *Astragalus* retained slightly higher (non-significant difference) soil moisture under their canopies compared with nearby open areas. By the end of the second growing season (Fig. 3d), the available soil moisture was reduced under canopies of all shrubs and also in open areas. At this date, the differences between the available soil moisture of the various treatments almost vanished; the only significant difference was higher soil moisture under the canopy of *Acantholimon* compared to *Astragalus*.

4. Discussion and conclusions

4.1. Shrub effects along the growing season

The interaction between the shrub species and the target plant (*Agropyron*) changed markedly during two years after seed sown of *Agropyron* seedlings. Such shifts can be shown by comparing the relative interaction index (Armas et al., 2004) for each shrub species during spring 2009, summer 2009 and summer 2010 (Fig. 4). Although there were differential effects between contrasting shrub species (Fig. 4b), which will be discussed in the following sections, the average trend of all shrubs (Fig. 4b) showed neutral effects at the beginning of the first growing season, which changed to a slight negative effect by the end of the first growing

Table 1

Results of repeated measurements GLM where measurement date is the random factor, microhabitat (shrub species and open area) is the main factor and survival of *Agropyron* seedlings the dependent variable.

Test types	Sources of variation	SS	df	MS	F	Sig.
Within-subjects	Date	51,094.809	2	25,547.404	172.769	.000
	Date × Microhabitat	3034.587	8	379.323	2.565	.011
	Error	28,095.307	190	147.870		
Between-subjects	Intercept	95,469.352	1	95,469.352	484.251	.000
	Microhabitat	3444.162	4	861.040	4.367	.003
	Error	18,729.101	95	197.148		

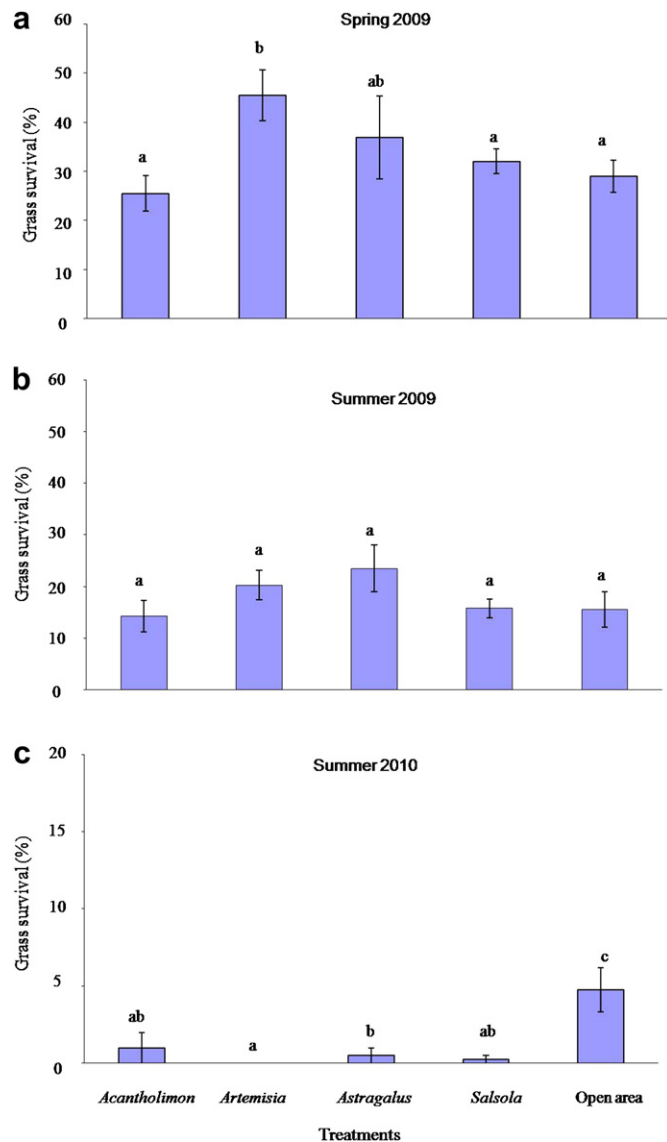


Fig. 1. Seedling establishment and survival rates for *Agropyron desertorum*, measured at three different dates during two consecutive growing seasons. Mean values \pm standard errors are shown, different alphabetic letters indicate significant differences by Tukey test ($P < 0.05$, $df = 19$).

season (i.e. summer 2009) and strong negative effect at the end of the second growing season (i.e. summer 2010).

The shifts in the type and intensity of plant–plant interaction can be related to the temporal changes in the type and severity of abiotic stresses, for the following reasons. First, low temperature and severe winds in the Karnakh area is a major constraining factor for seedling establishment in the early growing season (Jankju et al., 2011). Second, an increase in the severity of drought stress occurred from spring to summer 2009, which was shown as a significant reduction in soil moisture (Fig. 2a & b), indicating a change in the type of limiting factor from non-resource (cold and wind) to the resource (water) factors. Third, drought stress became more severe during the second growing season, which was found as a marked reduction (27%) in annual precipitation from 2009 (200 mm) to 2010 (145 mm). Accordingly, the slight facilitation effects by some shrubs (*Astragalus* and *Artemisia*) in spring 2009 were probably due to providing a favorable microclimate (against low temperature and severe winds) for establishment of *Agropyron*

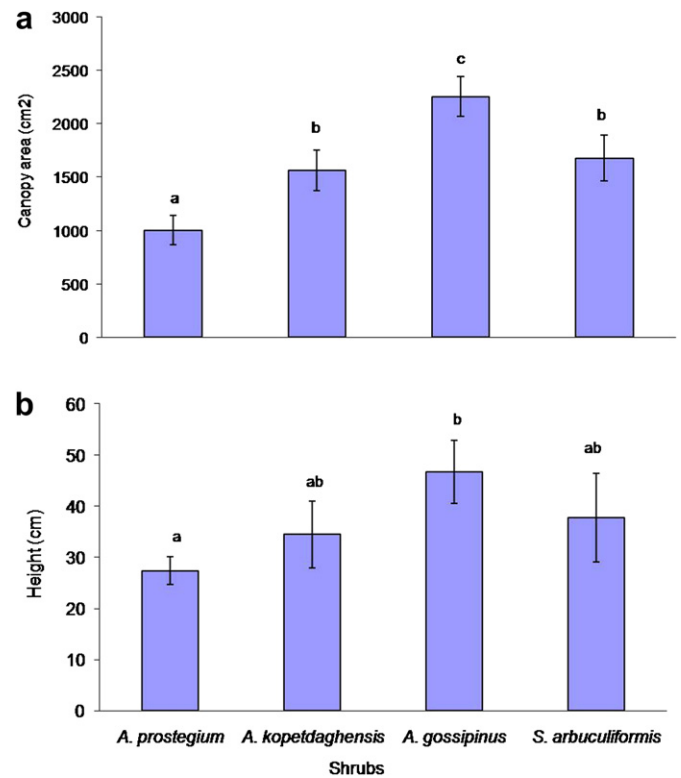


Fig. 2. Canopy area and canopy height of shrub species. Mean values \pm standard errors are shown, different alphabetic letters indicate significant differences by Tukey test ($P < 0.05$, $df = 4$).

seedlings. On the other hand, the negative interaction during summer 2009 and summer 2010 was probably associated with a gradual increase in the drought severity. These results are in accordance with a recent refinement of the Stress Gradient Hypothesis (SGH), which anticipates a shift in the type of plant–plant interaction from no effect (neutral) to competition (negative), when the limiting factor is a resource (here water) and the benefactor (here shrub species) and beneficiary (here *Agropyron*) plants are stress tolerant and competitive, respectively (Maestre et al., 2009).

The increases in severity of drought stress from spring 2009 toward summer 2009, led to the high mortality of *Agropyron* seedlings in all treatments, with the greater effects on the under-story plants than those growing in open areas (Fig. 1). Several experiments in dry areas have also shown increased germination and survival of understory plants before drought but no survival beyond the dry summer (Gasque and Garcia-Fayos, 2004; Tielbörger and Kadmon, 2000). In the Mediterranean region of Spain, the perennial grass *Stipa tenacissima* increased germination and survival of Kermes oak (*Quercus coccifera*) before the drought period, but all seedlings died during summer drought (Maestre et al., 2001). In the desert climate of Sahara, Niger, *Panicum turgidum* did not have any positive effect on *Acacia tortilis* seedlings, despite reducing atmospheric aridity within its canopy (Anthelme and Michalet, 2009).

4.2. Effects of different shrub species on *Agropyron* survival

The nurse species that impart greater micro-environmental benefits, such as increasing shade, reducing summer-time radiation load, increasing night-time winter temperature, increasing soil moisture and reducing herbivory, have a higher facilitation impact

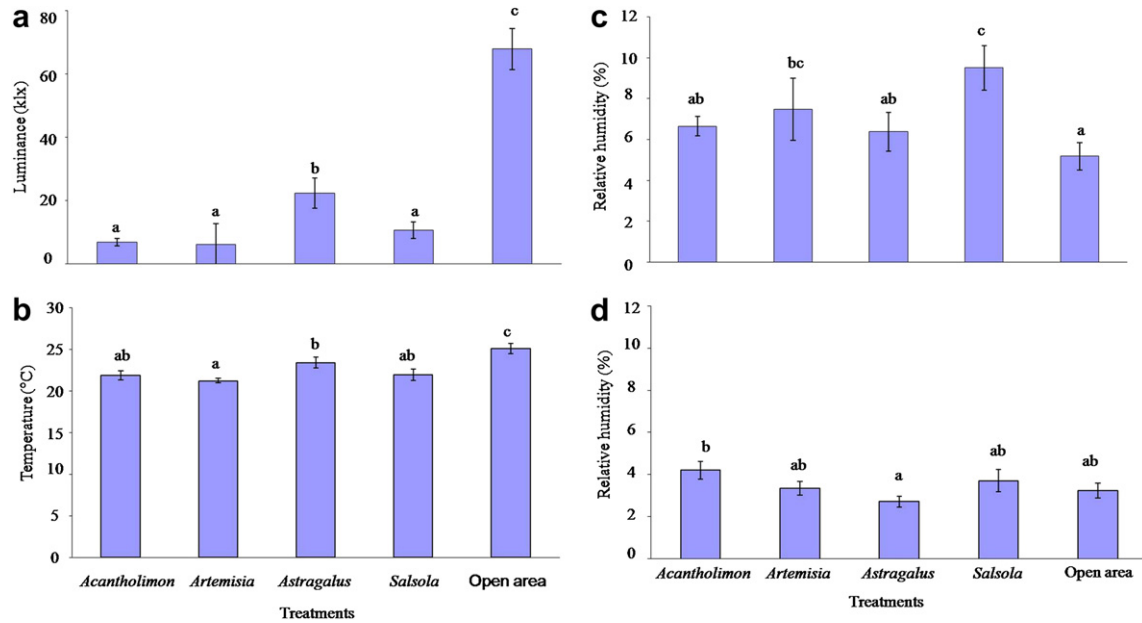


Fig. 3. Microclimate conditions under the canopy of shrub species or in open areas, light intensity (a), temperature (b) and relative soil moisture in the beginning (c) and the end (d) of growth season are compared. Mean values \pm standard errors are shown, different alphabetic letters indicate significant differences by Tukey test ($P < 0.05$, $df = 4$).

on their understory plants (Callaway, 2007). In this experiment, the early differences between the effects of shrub (spring 2009) was possibly due to the differences in their canopy structure. On the other hand, the second season differences can be due to their different ecological impacts (i.e. N-fixing versus allelopathy). The general trends in the plant–plant interactions for allelopathic (*Artemisia* and *Salsola*) and the cushion-like shrub species (*Acantholimon*) was a directional reduction in facilitation and increase of competition during the time course of the experiment. However for the N-fixing shrub (*Astragalus*), it was a hump-backed shape, with negative effects at the both ends but positive under the moderate stress gradient (e.g. Maestre and Cortina, 2004).

***Astragalus*.** A loose canopy structure for *Astragalus* led to a brighter and warmer microclimate under its canopy as compared with other shrubs, in the early growing season (Fig. 3a–b). Furthermore, a taller stature and greater canopy area (Fig. 2) can provide a more stable microenvironment under the canopy, as compared to other shrub species (Gomez-Aparicio, 2009; Maestre and Cortina, 2004). Therefore, more favorable and stable microclimate conditions were the possible reasons for the higher grass establishment, under the canopy of *Astragalus* than in open areas,

as compared with the canopy of *Acantholimon* and *Salsola* species (Fig. 1). Nevertheless, the warmer and drier microhabitat under the canopy of *Astragalus* led to increased drought stress under its canopy as compared with other shrubs (Fig. 3d), which can be the reason for an increased facilitation effect of *Astragalus* on *Agropyron* seedlings during summer 2009 (Fig. 4). This result can also be related to the crucial role of early-season facilitation, which increases chances for seedling survival during the subsequent growth stages (Soliveres et al., 2010). Nevertheless, the nurse effect of *Astragalus* was not sufficient during the severe drought (summer 2010), when the mortality of *Agropyron* seedlings was higher under the canopy of *Astragalus* than in open areas.

***Acantholimon*.** This cushion-like shrub had negative effects on seedlings of *Agropyron*, throughout the all time periods of this experiment. At the beginning of the first growing season (spring 2009) seedling establishment was significantly lower under *Acantholimon* than other treatments. At this stage, soil moisture was not different (Fig. 2), but light intensity and near surface air temperature were lower under the canopy than in open areas (Fig. 3a–b). Therefore, the major limiting factor for early establishment of *Agropyron* seedlings under the canopy of *Acantholimon* was

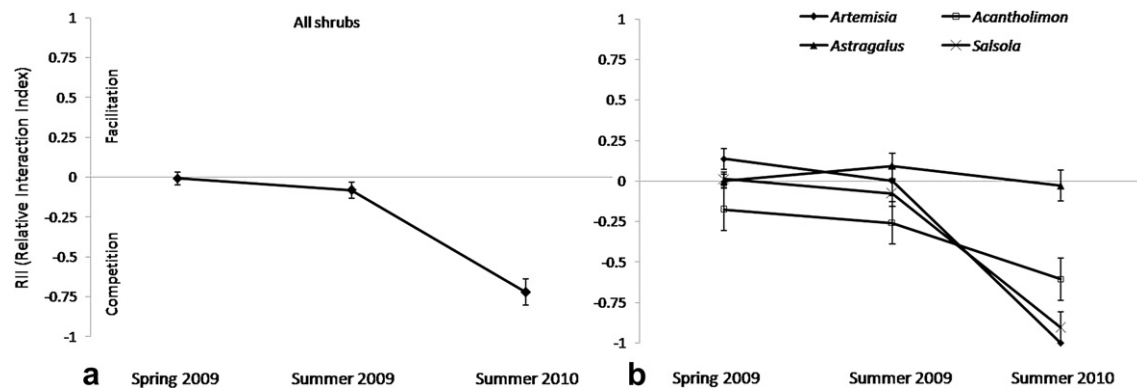


Fig. 4. Results of the intensity of the interaction, as measured with the RII index, from beginning toward the end of the experiment; effects of different shrubs on *Agropyron* seedlings (the target plant) are compared as the mean effects of all shrubs (a) or each shrub individually (b). Values of $RII < 0$ and $RII > 0$ respectively indicate net facilitative and competitive effects of the shrub on the grass.

possibly the lower light intensity. Several researchers have also shown the negative effects of varying levels of shading created by different nurse plants on seedling establishment of target species (e.g. Gómez-Aparicio et al., 2004; Sanchez-Velazquez et al., 2004). Plants growing under canopies of shrubs usually benefit from higher moisture, but at the cost of reduced light (Holmgren et al., 1997). For example, synthetic shading in the arid climate of South Australia reduced plant survival during winter and spring but had a strong facilitative effect during summer (Hastwell and Facelli, 2003). The severe drought in the second growing season intensified the negative effects of *Acantholimon*, which led to the death of all *Agropyron* seedlings under its canopy.

Artemisia and Salsola. Plant–plant interaction becomes more complicated when the nurse plants have allelopathic effects (e.g. Gómez-Aparicio et al., 2004). Early in growing season, *Artemisia* facilitated establishment of *Agropyron* seedlings under its canopy. Such positive effects could be due to higher soil moisture (Fig. 3c), and a more stable microclimate conditions, under its canopy as compared with open areas. The microclimate conditions under canopy of *Salsola* were not significantly different as compared to those in open areas, hence this species only had a neutral effect on establishment of *Agropyron* seedling, in the early growing season (Fig. 4). Although lacking specific data, one might expect that the allelopathic effects of *Artemisia* and *Salsola* would be low early in the growing season. Consistent with this observation was a two-week lag at the start of growing season between the shrub species and *Agropyron*. During this time, *Agropyron* could benefit from the favorable microclimate and winter rains under the canopy of shrubs. Later in the growing season, an increasing effect of drought was probably intensified by the allelopathic effects of shrubs or salt load. As a result, seedling mortality rate was much higher under the canopy of allelopathic shrubs (*Artemisia* and *Salsola*) as compared with non-allelopathic (*Astragalus* and *Acantholimon*). Results of seedling establishment under *Artemisia* and *Salsola* warrant further attention in the study of multiple biotic interactions, when using aridland shrubs as nurse plants. Without having additional information on their allelopathy and salt accumulation, negative effects of *Artemisia* and *Salsola* are indirectly related to the competition effect for water or nutrients.

4.3. Conclusions

In arid ecosystems, water deficiency, herbivory, competition, allelopathy, temperature extremes, salinity and low soil fertility impose multiple stresses on plants, which make facilitation by nurse shrubs more appealing for restoration projects. An impact on light or temperature is not negative or positive per se. That is, the positive or negative impact is on the plant; in this study changes in light/temperature/soil moisture under the shrub story had both negative and positive impacts/effects on *Agropyron*. Although some facilitation effects on early establishment of a perennial grass were found by aridland shrubs in this study, such nurse effects may not be consistent. That is because (1) the facilitation effects by aridland shrubs were more important for non-resource factors (temperature and light) than resource factors (water) and (2) it was only found under mild drought stress. A severe summer drought changed the interaction from facilitation to competition, subsequently leading to high mortality of target plants. Also, contrasting nurse effects by aridland shrubs arising from different morphological or ecological traits, may be eliminated under a severe summer drought.

Acknowledgments

The financial support for this research was provided by Ferdowsi University of Mashhad, through a research grant to the author. Parts

of the traveling and field survey expenses were provided by Central Office of the Natural Resources Department, Northern Khorasan Province, Iran. Many thanks to Prof H. Griffiths, Prof C. Armas and two anonymous referees for their useful scientific comments, also to my students R. Lagzian, J. Gholami, H. Bagherzadeh, M. Taheri and M.S. Abbasi for their help in the field.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2012.09.008>.

References

- Anthelme, F., Michalet, R., 2009. Grass-to-tree facilitation in an arid grazed environment (Air Mountains, Sahara). *Basic and Applied Ecology* 10, 437–446.
- Armas, C., Pugnaire, F.I., 2009. Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. *Journal of Vegetation Science* 20, 535–546.
- Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative index. *Ecology* 85 (10), 2682–2686.
- Asay, K.H., Knowles, R.P., 1985. Current status and future of introduced wheat-grasses and wildrye for rangeland improvement. In: Carlson, Jack R., McArthur, E. Durant (Eds.), *Range Plant Improvement in Western North America: Proceedings of a Symposium at the Annual Meeting of the Society for Range Management*; 1985 February 14, vol. 1–8. Society for Range Management, Salt Lake City, UT, Denver, CO, p. 4377.
- Azarnivand, H., Zare-Chahooki, M.A., 2008. *Range Improvement*. University of Tehran Press, Tehran, Iran, 354 pp.
- Behdad, A., 2009. *Allelopathic Effects of Nurse Plant Artemisia khorasanica on Seed Germination and Physiological Growth Characteristics of Bromus kopetdaghensis*. MSc dissertation, Ferdowsi University of Mashhad, Iran.
- Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9, 191–193.
- Callaway, R.M., 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., et al., 2006. Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist* 169, 59–69.
- Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Molina Motenogro, M.A., 2007. Microclimate modifications of cushion plants and their consequences for seedling survival of native and non-native herbaceous species in high Andes of Central Chile. *Arctic, Antarctic and Alpine Research* 39, 229–236.
- Facelli, J.M., Brock, D.J., 2000. Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of south Australia. *Ecography* 23, 479–491.
- Gasque, M., Garcia-Fayos, P., 2004. Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semi-arid Mediterranean areas. *Forest Ecology and Management* 189, 251–261.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant positive interactions to reforestation in Mediterranean mountains: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14, 1128–1138.
- Gomez-Aparicio, L., 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology* 97, 1202–1214.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities, the importance of regeneration niche. *Biological Reviews* 52, 107–145.
- Hastwell, G.T., Facelli, J.M., 2003. Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. *Journal of Ecology* 91, 941–950.
- Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., et al., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15, 1–7.
- Holmgren, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78, 1966–1975.
- Huber-Sannwald, E., Pyke, D.A., 2005. Establishing native grasses in a big sagebrush-dominated site: an intermediate restoration step. *Restoration Ecology* 13, 292–301.
- Jafari-Haghighi, M., 2003. *Methods of Soil Analysis, Sampling and Important Physical and Chemical Analysis "With Emphasis on Theoretical and Applied Principles"*. Neday Zahi Press, 236 pp. (In Persian).
- Jankju, M., Griffiths, H., 2006. Competition for pulsed resources: an experimental study of establishment and coexistence for an arid-land grass. *Oecologia* 148, 555–563.
- Jankju, M., Delavari, A., Ganjali, A., 2008. Seeding perennial forage grass, *Bromus kopetdaghensis*, in open space or under the canopy of four rangeland shrubs. *Rangeland. Journal of Iranian Society of Range Management* 2 (4), 314–328 (In Persian).

- Jankju, M., Mellati, F., Bozorgmehr, A., Tavakkoli, M., Azimi, R., 2011. Autecology of *Agropyron cristatum*, *Stipa turkestanika* and *Stipa barbata* in the rangelands of Northern Khorasan. *Journal of Range and Watershed Management* 4, 457–469.
- Kefi, S., Rietkerk, M., Alados, C.L., Puyo, Y., Papanastasis, V.P., ElAich, A., de Ruiter, P.C., 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449, 213–217.
- King, E.G., 2008. Facilitative effects of *Aloe secundiflora* shrubs in degraded semi-arid rangelands in Kenya. *Journal of Arid Environments* 72, 358–369.
- Kitzberger, T., Steinaker, D.F., Vebelen, T.T., 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81, 1914–1924.
- Maestre, F.T., Cortina, J., 2004. Do positive interactions increase with abiotic stress? A test from a semiarid steppe. *Proceedings of the Royal Society of London* 271, S331–S333.
- Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential of using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* 11, 1641–1655.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, F., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97, 199–205.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., Escurado, A., Ochoa, V., Delgado-Baquerizo, M., Garcia-Gomez, M.m., Bowker, M.A., Soliveres, S., Sclar, C., et al., 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335, 214–218.
- Maron, J.L., Connors, P.G., 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105, 302–312.
- Michalet, R., 2007. Highlighting the multiple drivers of changes in interactions along stress gradients. *New Phytologist* 173, 3–6.
- Ormerod, S.J., Marshall, E.J.P., Kerby, G., Rushton, S.P., 2003. Meeting the ecological challenges of agricultural change: editors' introduction. *Journal of Applied Ecology* 40, 939–946.
- Padilla, F.M., Pugnaire, F.I., 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and Environment* 4 (4), 196–202.
- Quero, J.L., Gomez-Aparicio, L., Zamora, R., Maestre, F.T., 2008. Shifts in the regeneration niche of an degraded tree (*Acer opalus ssp. granatense*) during ontogeny. *Basic and Applied Ecology* 40, 65–77.
- Reynolds, J.F., Kemp, P.R., Ogle, K., Fernandez, R.J., 2004. Modifying the pulse reserve paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194–210.
- Rousset, O., Lepart, J., 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). *Journal of Ecology* 88, 401–412.
- Sanchez-Velazquez, L.R., Quintero-Gradilla, S., Aragon-Cruz, F., Pineda-López, M.R., 2004. Nurses for *Brosimum alicastrum* reintroduction in secondary tropical dry forest. *Forest Ecology and Management* 198, 401–404.
- Smith, S.D., Monson, R.K., Anderson, J.E., 1997. *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin, Germany.
- Soliveres, S., DeSoto, L., Maestre, F.T., Olano, J.M., 2010. Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics* 12, 227–234.
- Tielbörger, K., Kadmon, R., 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81, 1544–1553.
- Travis, J.M.J., Brooker, R.W., Clark, E.J., Daytham, C., 2006. The distribution of positive and negative species richness across environmental gradients on a dual-lattice model. *Journal of Theoretical Biology* 241, 896–902.
- Valentine, J.F., 1989. *Range Improvement and Development*, third ed. Academic Press, San Diego, California, 524 pp.
- Zlatnik, E., 1999. *Agropyron desertorum*. In: *Fire Effects Information System* [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> (04.01.12.).