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## Ecophysiological Aspects of the Interactions between *Bromus kopetdaghensis* and Two Nurse Shrubs, *Astragalus meschedensis* and *Acantholimon raddeanum* in a Semiarid Rangeland

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**Abstract:** Plant-plant interactions are known as the main biotic drivers of the vegetation dynamics. Therefore, understanding such processes is beneficial for the applied vegetation management. The aim of this research was to investigate the type and intensity of plant-plant interaction during the time course of a growth season. We studied ecophysiological aspects of facilitation and competition between two aridland shrubs, *A. meschedensis* Bunge and *A. raddeanum* Czernjak and one perennial grass, *B. kopetdaghensis* Krasch. Soil and plant sampling were carried out for shrubs and the grass that were either growing alone or the grass was growing under the canopy of shrubs. In Spring (May), soil humidity weight was higher under the shrubs+grass than the grass-only site. By the beginning of Summer (July) grass consumed the common soil water and rapidly terminated its yearly growth. Therefore, in August and September, soil humidity weight was lower under the shrubs+grass than shrub-only sites. Photosynthesis rate of *B. kopetdaghensis* was sharply reduced from the beginning towards the end of growth season, but was not varied between the different plant combinations. Leaf proline measurement in July indicated higher stress for *B. kopetdaghensis* that were growing under shrubs than those of open areas. In conclusion, we found facilitation effects of shrubs on the grass at the early times of growth season, but it shifted into the competition for water during summer times. The outcome of plant interaction was positive for the grass but negative for the shrubs, especially *A. meschedensis*.

**Key words:** Nurse effect, rangeland shrub, photosynthesis, proline

### INTRODUCTION

Shrubs are the dominant plant life forms in vast areas of the arid and semi-arid rangelands in Iran. They may grow alone or contain other plants within their canopy. Shrubs and their understory plants may have both negative (competition) and positive (facilitation) interactions, for the environmental resources (Callaway, 1995). The interactions between shrubs and their understory largely determine the diversity and the structure of the aridland plant communities (Holzapfel *et al.*, 2006; Garcia *et al.*, 2007). Both competition and facilitation can simultaneously occur within a plant community, but their intensity and direction depend on the habitat's ecological conditions (Pugnaire and Luque, 2001; Dormann and Brooker, 2002), growth season (Armas and Pugnaire, 2005; Acuna-Rodriguez *et al.*, 2006; Kikvidze *et al.*, 2006; Jankju *et al.*, 2008) and the life strategies of interacting plants (Liancourt *et al.*, 2005; Michalet *et al.*, 2006; Maestre *et al.*, 2009).

The balance between competition and facilitation may also depend on the competitive-ability of the interacting

plants and/or their tolerance to the drought stress. If the nurse shrubs are stress tolerant they will have lower competitive effect, on their understory plants (Michalet *et al.*, 2006). In this case, facilitation will be the dominant interaction type under the less stressful condition and competition will be more important under the stressful end of the gradient (Choler *et al.*, 2001; Wang *et al.*, 2008).

Intensity of competition and facilitation may also vary during the time course of a growth season. For example, Eckstein (2005) studied plant interactions between the oak tree and three herbs, i.e., *Viola stagnina*, *V. elation* and *V. pumila*, in its understory. He found positive effects of Oak on the seedlings of the *Viola* sp. in the early stages of growth, but negative effects on the growth and reproduction of herbs at the later stages. Schultz *et al.* (2007) also indicated that the intensity of the interaction between *Pinus edulis* and the shrub *Fallugia paradoxa* was dependent on the soil moisture availability during different times of year.

Soil moisture is one of the most critical factors for the plant growth in the aridland communities; hence it does have a key role on the outcome of plant-plant interactions. While the seasonal changes in the soil moisture

availability may cause significant influences on the intensity and the outcome of plant-plant interaction (Novoplansky and Goldberg, 2001; Eckstein, 2005; Jankju and Griffiths, 2006), most of the current literature have studied the interaction between shrubs and their understory plants at only one stage of the growth season (Holmegren, 2000; Kikvidze *et al.*, 2006). Furthermore, most of the previous studies have only measured the effects of plant interaction on the ecological growth performances, e.g., diversity, richness and establishment, of the understory plants (Hacker and Bertness, 1999; Maestre *et al.*, 2001; Michalet *et al.*, 2006), which give us little information on the mechanism of plant interaction. Therefore physiological ecology are needed in order the soil moisture availability and the physiological performances of interacting plants during different times of the growth season and subsequently obtain detailed information on the mechanisms of plant-plant interaction for soil water.

The main questions that we aimed to answer in this research were: (1) Can the shrubs' canopy preserve the soil moisture availability and consequently enhance the physiological performance of the understory plants? (2) Do the direction and severity of the interaction between shrubs and their understory plants change during the time course of a growth season? (3) Can the understory herbs impose any positive or negative effect on the nurse shrubs?

## MATERIALS AND METHODS

**Study area:** The study was carried out during spring and Summer 2007 under both field and laboratory conditions. Soil samples, leaf water potential and leaf photosynthesis rates were measured in Baharkish Rangeland, Quchan, Iran. Leaf proline was measured in the Botany Laboratory, Ferdowsi University of Mashhad.

**Soil moisture measurements:** Soil sampling was conducted three times within the growth season; 25th of May, 5th of July and 5th of September. Four separate soil profiles were dug in (1) open space, or (2) under canopy of lonely growing *Acantholimon*, (3) where *A. raddeanum* had contained *B. kopetdaghensis* under its canopy (AcaBr), (4) under the canopy of lonely growing *A. meschedensis* (Ast), (5) where *A. meschedensis* included *B. kopetdaghensis* under its canopy (AstBr) and (6) under the canopy of lonely growing *B. kopetdaghensis* (Br). Soil samples of 1 kg weight were taken from 10, 20 and 35 cm depths of each soil profile. Samples were kept within the tightly packed containers and sealed with plastic bags, to minimize the moisture loss, then immediately transferred into the laboratory,

where the samples were immediately weighed. Relative humidity weight of each soil sample was calculated by using data of soil samples before and after 72 h drying in a 75°C oven.

**Photosynthesis measurement:** CO<sub>2</sub> assimilation rate of *B. kopetdaghensis* leaves were measured in 9-11 h, under the field conditions. Measurements were conducted at both vegetative (25th of June) and flowering (5th of July) growth stages of *B. kopetdaghensis*. Four replications were randomly selected from the following plant combinations: BrAst, BrAca and Br. One healthy and fully grown leaf blade of *B. kopetdaghensis* was selected and put within the gas exchange chamber of L.C.Licore5 (Lincoln, USA). CO<sub>2</sub> assimilation rates were manually recorded after 2-5 min.

**Leaf proline measurement:** Proline was measured on leaves of *B. kopetdaghensis*, that were naturally growing in the field. Proline concentration in plant leaves is an indication of drought stress; therefore it was measured during the Summer time (5th of July), when *B. kopetdaghensis* was in the flowering stage. Four replications were randomly selected from the following plant combinations: BrAst, BrAca and Br. Leaf samples were sealed in the plastic bags, kept at 4°C field fridges, then transferred into the lab. Leaf proline calculated based on the micromole per weight of fresh leaves. It was primarily extracted by using 1: 50 ratio sulfosalicylic acid and then processed according to Bates *et al.* (1973).

**Data analysis:** Soil and plant samples were taken in a randomized block design within a relatively homogenous small site (500 m<sup>2</sup>). Effects of time of measurements, plant combinations and soil depths were assessed on dependent variable, i.e. soil moisture, leaf photosynthesis rate and leaf proline concentration, by a two way ANOVA using a SPSS 10 (SPSS, 1997). Means were compared by Tukey HSD test within the 95% confidence limits.

## RESULTS

**Soil moisture:** A comparison of data on the soil relative humidity weight revealed significant reductions in the soil moisture availability from May to September. Soil moisture was reduced under the canopy of all plant combinations, i.e., Br, AstBr, AcaBr, Aca, Ast and in open areas. However, amount of the moisture reduction was greater for soil samples taken from the surface than the deep soil layer. It was also more severe under shrubs that included the grass in their canopy (i.e., AstBr and AcaBr) as compared with the lonely growing shrubs or grass (Fig. 1-3).

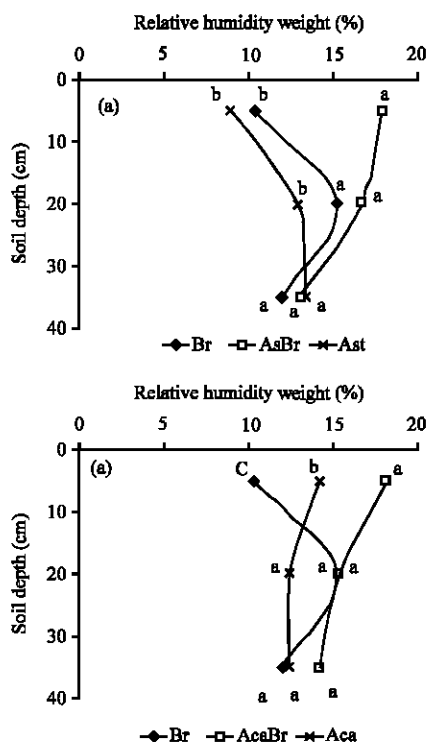


Fig. 1: Relative soil humidity weight measured at the three soil depths in late May, a: Under canopy of lonely *B. kopetdaghensis* (Br), lonely *A. meschedensis* (Ast), or *A. meschedensis* + *B. kopetdaghensis* (AstBr), b: under canopy of lonely *B. kopetdaghensis* (Br), lonely *Acantholimon* (Aca), or *A. raddeanam* + *B. kopetdaghensis* (AcaBr).

Comparison of data taken at the late May revealed significant ( $p < 0.05$ ) effects of soil depth and plant combinations on the relative soil humidity weight (Fig. 1). Moisture level of the upper soil layer (5-15 cm deep) was higher where *A. meschedensis* and/or *A. raddeanam* that contained the perennial grass within the canopy, as compared with the isolated shrubs. Nevertheless, soil moisture of the middle soil layer (20-25 cm deep) was significantly lower under the lonely growing *A. meschedensis* than AstBr or lonely growing *B. kopetdaghensis* (Fig. 1). But for the *A. raddeanam* combinations, there was not any significant difference in the soil moisture of middle layer between Aca, AcaBr and Br. Finally, for the samples taken from the lowest soil depth, there was not any significant difference between the soil moisture of the all plant combinations.

For the soil samples taken at the early July (Fig. 2), the relative humidity weight in the surface soil layer was similar between the all plant combinations. However in the

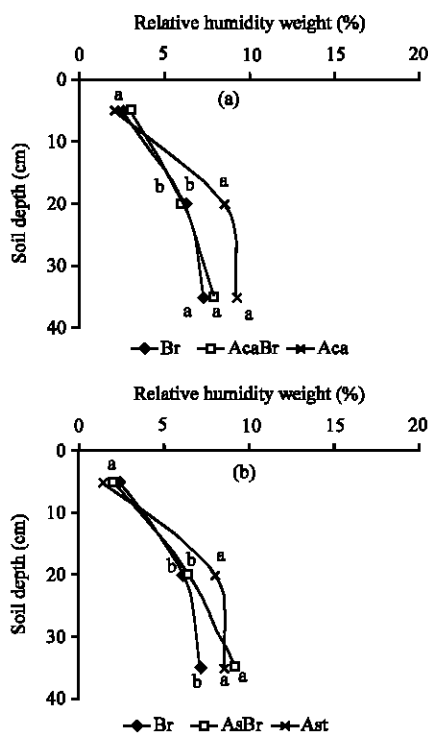


Fig. 2: Relative soil humidity weights of different plant combination in early July. a: Under canopy of lonely *B. kopetdaghensis* (Br), lonely *A. meschedensis* (Ast), or *A. meschedensis*+*B. kopetdaghensis* (AstBr), b: under canopy of lonely *B. kopetdaghensis* (Br), lonely *Acantholimon* (Aca), or *A. raddeanam*+*B. kopetdaghensis* (AcaBr)

middle soil layer, soil moisture was higher under the canopy of lonely growing shrubs (Ast and Aca) than those of shrubs + *B. kopetdaghensis* (AstBr and AcaBr). In the lowest soil depth, *B. kopetdaghensis* individuals that were growing under the canopy of *A. meschedensis* favored more soil moisture than those growing under the canopy of *A. raddeanam* or those growing alone.

For the soil samples taken at the early September (Fig. 3), grass presence did not cause any significant changes in the relative humidity weight under the canopy of *A. raddeanam*, i.e., soil moisture was similar under canopy of Aca and AcaBr. On the other hand, *A. meschedensis*, soil moisture was significantly lower under AstBr than Ast.

**Photosynthesis rate:** Photosynthetic rates were highly affected by the time of growth season (Fig. 4). For all plant combinations (Br, AcaBr and AstBr) photosynthetic rate of *B. kopetdaghensis* was significantly ( $p < 0.05$ ) higher in

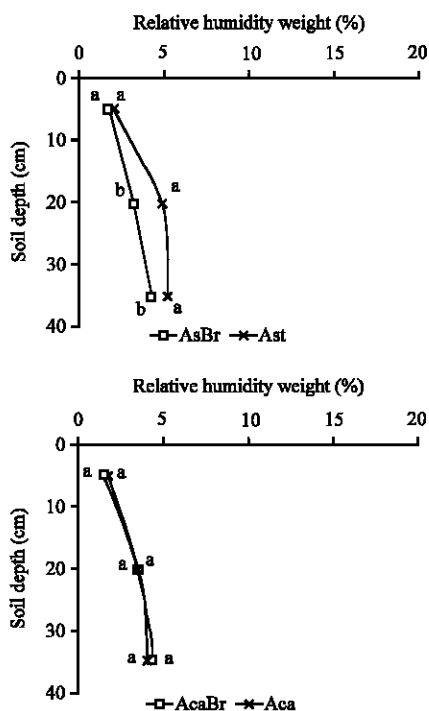


Fig. 3: Relative soil humidity weights of different plant combinations in early September. a: Under canopy of lonely *A. meschedensis* (Ast) or *A. meschedensis* + *B. kopetdaghensis* (AstBr), b: Under canopy of lonely *Acantholimon* (Aca), or *A. raddeanum* + *B. kopetdaghensis* (AcaBr).

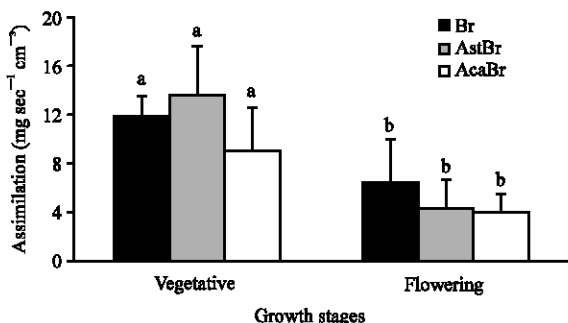


Fig. 4: Photosynthesis rate of *B. kopetdaghensis* under different plant combinations in the vegetative and flowering stages (May and July); under canopy of lonely *B. Kopetdaghensis* (Br), *A. meschedensis* + *B. kopetdaghensis* (AstBr) and *A. raddeanum* + *B. kopetdaghensis* (AcaBr).

the late May than in the early July. Comparing average photosynthesis rate of different plant combinations in the late May revealed higher values for *B. kopetdaghensis*

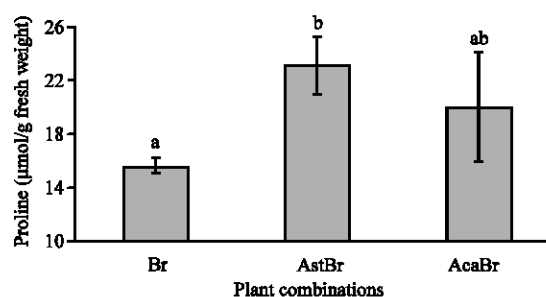


Fig. 5: Proline concentration in leaves of *B. kopetdaghensis* under different plant combinations in the flowering stages (May and July); under canopy of lonely *B. kopetdaghensis* (Br), *A. meschedensis* + *B. kopetdaghensis* (AstBr) and *A. raddeanum* + *B. kopetdaghensis* (AcaBr).

individuals growing under the canopy of *A. raddeanum* than those growing under the canopy of *A. meschedensis*, however the difference was not statistically significant. Similarly in the early July, concurrent with the flowering growth stage of *B. kopetdaghensis*, there were not significant differences in the photosynthetic rate between *B. kopetdaghensis* individuals growing alone or under canopy of shrubs.

**Proline:** Comparison of proline concentrations in leaves of *B. kopetdaghensis* indicated significant differences between the plant combinations. Total proline was significantly higher in leaves of *B. kopetdaghensis* individuals growing under canopy of *A. meschedensis* than those growing alone. Leaf proline of *B. kopetdaghensis* growing under the canopy of *A. raddeanum* was intermediate between those of other two combinations, but the difference was not statistically ( $p < 0.05$ ) significant (Fig. 5).

## DISCUSSION

**Shrubs facilitate soil moisture for grass:** Results of the relative soil humidity weight, measured at the late May, indicated higher soil moisture availability under the canopy of shrubs than in open areas. Accordingly, *B. kopetdaghensis* conferred more favorable microclimate conditions under the canopy of *A. meschedensis* and *A. raddeanum* than in open areas. Kitzberger *et al.* (2000) and Jankju (2009) also found lower sunlight radiation and higher soil moisture under the canopy of shrubs than in open areas. Cavieres *et al.* (2007) indicated that cushion-like shrubs increase the growth and survival rates of understory plants by preserving soil moisture availability. Joffer *et al.* (1989), Belsky *et al.* (1989), Ko

and Rich (1993), Mordelet and Menaut (1995) and Ludwig and Menaut (1995) reported significant effects of nurse plants on soil and microclimate conditions of their canopy, which accordingly enhanced water potential of the understory plants. They argued that the shade created by shrubs' canopy lowers the air temperature and hereby reduces evapo-transpiration rate and drought stress, but increases soil moisture storage and water use efficiency for the understory plants.

Comparison of soil relative humidity weight in the intermediate and deep soil layers revealed lower soil moisture under the canopy of shrubs than in open areas. Lower facilitation effect of *A. raddeanum* might be related to its denser canopy structure. Sanchez-Veasquez *et al.* (2004) suggested that shrubs with dense canopy structure negatively affect their understory plants; first by reducing available sunlight and second by absorbing lights rain. Accordingly, the difference in facilitation effects between *A. meschedensis* and *A. raddeanum* are partly explained by the differences in their canopy structure. Jankju (2008) observed higher establishment of *B. kopetdaghensis* seedlings under the canopy of *A. meschedensis* than *A. raddeanum* in the Baharkish rangeland.

#### **Competitive effects of shrubs on grass physiology:**

Whilst most of the current literature have compared type and intensity of plant-plant interactions between wet and dry years (Cavieres *et al.*, 2002; Castro *et al.*, 2004), here we have found that the type and intensity of plant-plant interaction may also vary due to changes in the seasonal soil availability. Soil moisture was gradually decreased from the beginning towards the end of growth season. Lower soil moisture led to significant reductions in the photosynthetic rates of all plant combinations, in early July than late May. Several researchers (Mooney, 1976; McAllister *et al.*, 1998; Shumway, 2000; Nagel and Griffin, 2004) have found positive relationships between photosynthetic rate and plant growth and development. Therefore the lower photosynthetic rate at the early July may have reduced growth rates for all plant combination in Baharkish rangelands.

A greater reduction in soil moisture under the canopy of AcaBr and AstBr than those of Aca, Ast or Br, can be due to the simultaneous consumption of soil water by shrubs and their understory grass. Nevertheless, lower soil moisture did not cause significant changes in the photosynthetic rate of *B. kopetdaghensis*, whereas it led to the higher leaf proline for *B. kopetdaghensis* individuals growing under canopy of *A. meschedensis* than those growing in the open areas. An increase in leaf proline concentration indicates higher drought stress (Strain, 1969; Moeini *et al.*, 2006; Tatar and Gevrek, 2008).

Furthermore, several researchers have shown that the seasonal changes in the soil moisture availability may alter the type and intensity of interaction between nurse plants and their understory plants (Armas and Pugnaire, 2005; Acuna-Rodriguez *et al.*, 2006; Kikvidze *et al.*, 2006). As a result for this experiment, competition for soil water led to a greater drought stress on *B. kopetdaghensis* individuals under canopy of *A. meschedensis* as compared to those in open areas.

**Indirect competition effects of grass on shrubs:** Soil water was lower where shrubs had contained *B. kopetdaghensis* under their canopy as compared with the lonely growing shrubs (Fig. 2, 3). The lower soil water can be due to the simultaneous consumption of soil water by the grass and shrub from the common water storage in the soil. *B. kopetdaghensis* is a drought escaping perennial grass. It rapidly consumes soil water during favorable condition of the early season and terminates its yearly growth by the beginning of the Summer drought (Sharifabad and Dorri, 2003). Melgoza *et al.* (1990) and Jankju (2009) found that the invasive annual grass, *B. tectorum*, could rapidly consume the common soil water and hereby impose competition effect on its overstory shrubs. Maestre *et al.* (2003) found that a decrease in soil moisture during late Summer led the indirect competition effect by *Stipa tenacissima* on its overstory shrub *Pistacia lentiscus*. Accordingly in this research, *B. kopetdaghensis* had imposed indirect competition effects on its nurse shrubs, by rapidly using the common soil water in Spring and leaving a dry soil for the nurse shrub throughout the Summer drought.

#### **CONCLUSIONS**

There were both facilitation and competition interactions between the two cushion-like shrubs and a perennial grass within their canopy. Soil water was the main source of plant-plant interaction. Facilitation was the dominant interaction type in the early growth season, whereas competition was dominant throughout the summer. Shrubs imposed both facilitative and competitive effects on the grass, whereas, the grass had only competitive effects on the shrubs. The shrub species that initially imposed greater facilitation effect, suffered more from the competition effect by its understory grass.

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