Leaf conductance and transpiration of winterfat associated with 2 species of wheatgrass on disturbed sites

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Abstract

Competitive relations between a half-shrub and 2 wheatgrasses were determined on 2 disturbed sites in northwestern Colorado. Leaf conductance and transpiration of winterfat [*Eurotia lanata* (Pursh) Moq., also known as *Ceratoides lanata*] were measured in association with a neighboring plant of either winterfat, beardless bluebunch wheatgrass [*Pseudoroegneria spicata* subsp. *inermis* (Scribn. and Smith A. Löve], or western wheatgrass [*Pascopyrum smithii* Rydb.) A. Löve] and as affected by a shallow disturbance of soil to a depth of 30 cm or a deep disturbance of soil to a depth of 1 m. Reduced leaf conductance was associated with advancing phenology and plant water stress as soil water was depleted during the growing season. Leaf conductance and transpiration of winterfat was often lower when it was associated with the 2 grasses than when growing adjacent to another winterfat plant. Lowest transpiration rates of winterfat were found when it was growing adjacent to beardless bluebunch wheatgrass. Thus, the intensity of competition for soil water may be greater for winterfat when associated with wheatgrasses than when growing adjacent to another winterfat plant.

Key Words: soil-plant, water relations, competition, *Eurotia lanata, Pascopyrum smithii, Pseudoroegneria spicata* subsp. *inermis,* reclamation

Measurements of leaf conductance to water vapor and carbon dioxide exchange have been used to determine plant responses to water stress and disturbance (DePuit and Caldwell 1973, White 1976, Eissenstat and Caldwell 1988, Trlica and Biondini 1990). Stomatal aperture affects photosynthetic carbon dioxide flux when photosynthesis is limited by carbon dioxide diffusion. Furthermore, reduced photosynthesis during water stress has been correlated with stomatal closure in some plants (El-Sharkawy and Hesketh 1964, Van den Driessche et al. 1971, Larcher 1980).

Net photosynthesis has been observed to vary seasonally in big sagebrush [*Artemisia tridentata* (Nutt.)] (DePuit and Caldwell 1973). Air temperature, vapor pressure deficit, soil water, and phenological status of the plant also affect photosynthetic and transpiration rates (Larcher 1980, Trlica and Biondini 1990). For example, Moore et al. (1972) found that under field and laboratory conditions, vapor pressure deficit (VPD) and water stress were significant factors influencing transpiration in winterfat [*Eurotia lanata* (Pursh) Moq., also known as *Ceratoides lanata*] and shadscale [*Atriplex confertifolia* (Torr. and Frem.)]. However, little work has focused on the effects of neighboring plants on individual plant responses.

The objectives of this study were to test the effects of soil disturbance and competition on leaf conductance and transpiration of winterfat in associations with beardless bluegrass wheatgrass [(*Pseudoroegneria spicata* subsp. *Inermis* (Scribn. and Smith) A. Löve] and western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve].

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Materials and Methods

This study was conducted in the Piceance Basin in northwest Colorado at an elevation of 2,020 m. Average annual precipitation at this site is between 250 and 300 mm with approximately half of the amount received as snow. Soils were formed in alluvium derived from shale and are moderately deep and well drained. They were medium-textured loams *(Cumulic cryoborolla)* on the surface, underlain by moderately fine to fine textures to a depth of 60 cm (BLM 1984). The study site is gently sloping and has a northeast exposure.

Two plots designed to investigate secondary succession were disturbed and seeded in 1976. The present study used these 2 plots that had been modified by excavation and mixing of the top 1 m of soil to represent deep disturbance and shallow disturbance where the site was scraped and then soil mixed to a depth of 30 cm (Doerr and Redente 1983). Both disturbed sites were seeded with the same mixture of native and introduced species of grasses, forbs, and shrubs (Redente et al. 1984). Only winterfat, beardless bluebunch wheatgrass, and western wheatgrass were selected for the present study. Plants were selected in subplots that received no supplemental fertilizer or irrigation.

Pair-wise combinations of individuals of winterfat (EULA), beardless bluebunch wheatgrass (PSIN), and western wheatgrass (PASM) were selected and identified in May 1985. An individual of a species and its nearest neighbor, made up of another winterfat plant (EULA/EULA) or 1 of the western wheatgrass plants (e.g., EULA/PASM), were randomly selected in pairs to specifically test the effects of competition with winterfat. Two plants of the same species were identified as a pure-stand pair for each of the 3 species. Plants identified as nearest neighbors were within 20 cm of each other. Other plants were removed if they occurred within a radius of 20 cm of the selected pair. Each combination pair for each of the 2 levels of soil disturbance was repeated 6 times.

Leaf conductance and transpiration rates were measured 7 times during the 1985 growing season: 7 June, 27 June, 9 July, 27 July, 15 August, 9 September, and 3 October. Measurements of ambient air and leaf temperature (C°), conductance (mmol • m^{-2} • s^{-1}), and transpiration (mmol • m^{-2} • s^{-1}) were taken with a steady-state porometer (Licor Model LI-1600) 5 times during the day on each sample date for each species. Diurnal porometer measurements were taken at 7 a.m., 10 a.m., 1 p.m., 4 p.m., and 7 p.m. MST on pure-stand pairs of winterfat, beardless bluebunch wheatgrass, and western wheatgrass. No significant variations in conductance and transpiration were observed between 10:00 a.m. and 4:00 p.m. MST during a day; therefore, measurements were made throughout this time period. The 2 uppermost, fully expanded leaves from each plant were sampled. Both leaf surfaces (upper and lower) were measured independently, and an average value for conductance and transpiration rate for each leaf was calculated.

Gravimetric soil moisture (%) was determined for 3 depths (0–20 cm, 20–40 cm, and 40–60 cm) at each sample date for each pair of

Table 1. Soil moisture (% by wt.) on shallow disturbance and deep disturbance in the Piceance Basin, Colorado 1985.

Treatment	Depth	Date: 6 June	27 June	9 July	27 July	15 August	6 September	3 October	Avg.
	(cm)	(% by weight)							
Shallow Disturbance	0–20	21	8	6	10	7	6	9	10
	20–40	32	11	7	9	7	8	7	12
	40–60	30	13	8	8	7	7	*	12
	Avg.	27	11	7	9	7	7	8	
Deep Disturbance	0–20	18	8	9	12	7	6	8	10
	20–40	22	10	12	10	7	6	7	11
	40–60	25	13	12	12	6	7	*	12
	Avg.	22	10	11	11	7	6	8	

*Data unavailable.

plants (6). This information was used to determine soil moisture depletion during the growing season for the 2 levels of soil disturbance.

Stem or leaf xylem potential for each plant species was measured (MPa) with a Scholander-type pressure chamber (Waring and Cleary 1967) on 9 July, 27 July, 15 August, 6 September, and 3 October. The pressure chamber was unavailable for making measurements on 7 and 27 June. Stem or leaf xylem potential was measured between 11:00 a.m. and 2:00 p.m. MST. One stem from each winterfat plant and 1 leaf from each wheatgrass plant was measured. Measurements were made on 6 plants for each species combination on each level of soil disturbance.

Leaf conductance, transpiration, and plant water potential data were subjected to a factorial analysis of variance procedure. Differences in all variables were tested for date effect, and then, within each date, differences were tested for significance according to species combination, soil disturbance level, and an interaction of the main effects. Differences among means were considered significant if F-tests were significant at $P \leq 0.05$. Significant differences among means were then tested using the Student-Newman-Keuls procedure at $P = .05$.

Results

Soil Moisture

Precipitation was above average (57 mm) during April and May, and soil moisture was near field capacity of all depths and on both sites on 6 June; 27 and 22%, respectively, for shallow and deep disturbance of soil (Table 1). Rapid depletion of this moisture occurred between 6 June and 27 June when plants were rapidly growing. Soil moisture on 27 June ranged from 6 to 12% at all 3 depths for the remainder of the growing season. Only small differences in soil moisture between the 2 types of disturbances were noted throughout the growing season. However, a lower soil moisture for all 3 depths on 6 June on the deep disturbance site may be related to a greater aboveground biomass production in winterfat as compared with winterfat on the shallow disturbance (Mack 1986, Bonham and Mack 1987).

Effect of Site Disturbance

Transpiration rates for all species for both shallow and deep disturbances were directly related to leaf conductance and xylem water potential. Both xylem water potential and leaf conductance generally declined during the growing season as did transpiration rates (Table 2). Early season transpiration rates were highest in western wheatgrass, and transpiration rates of all 3 species were very low after 15 August. Very little soil water (6 to 8%) remained at any rooting depth, and xylem water potential of all species declined throughout the remainder of the growing season (Tables 2 and 3).

Growth of winterfat was rapid early in the season when soil moisture was high (Mack and Bonham 1988). Leaf conductance in winterfat plants differed significantly between deep and shallow disturbances of soil on 27 June and 9 July (Table 2). Leaf conductance was greater early in the season in winterfat plants grown on the deep disturbance than on the shallow disturbance. Conductance was 77% and 31% greater on the deep disturbance than on the shallow disturbance site (26.0 mmol $\bullet$ m^{-2} $\bullet$ s^{-1} and 14.7 mmol $\bullet$ m^{-2} $\bullet$ s^{-1}, respectively) on 27 June and 9 July, respectively. However, by 3 October leaf conductance was 285% greater on the shallow disturbance than on the deep disturbance (Table 2). Soil moisture was depleted earlier in the deep disturbance compared to the shallow disturbance site (Table 1).

Transpiration rates for winterfat on the shallow disturbance were, on the average, 40% greater on 7 June than for plants on the

Table 2. Leaf conductance (mmol $\bullet$ m^{-2} $\bullet$ s^{-1}), transpiration (mmol $\bullet$ m^{-2} $\bullet$ s^{-1}), and xylem potential (MPa) of winterfat, beardless bluebunch wheatgrass, and western wheatgrass on shallow disturbance and deep disturbance in the Piceance Basin, Colorado, 1985.

Species and Date	Leaf Conductance Site Disturbance: Shallow	Deep	Transpiration Site Disturbance: Shallow	Deep	Xylem Potential Site Disturbance: Shallow	Deep
	-(mmol $\bullet$ m^{-2} $\bullet$ s^{-1})-		-(mmol $\bullet$ m^{-2} $\bullet$ s^{-1})-		(MPa)	
Winterfat						
7 June	69.9a[1]	64.3a	4.9a	3.6b	— —	— —[2]
27 June	14.7b	26.0a	1.5a	1.5a	— —	— —
9 July	20.1b	26.3a	2.0a	2.3a	-3.6a	-3.0b
27 July	25.9a	21.3a	1.2b	1.6a	-2.5a	-2.4a
15 Aug.	10.2a	11.5a	1.1a	1.2a	-3.9a	-3.7a
9 Sept.	11.6a	12.8a	0.7b	1.0a	-3.7a	-4.0a
3 Oct.	13.4a	4.7b	0.6a	0.5b	-4.5a	-4.8a
Beardless Bluebunch Wheatgrass						
7 June	48.1b	69.0a	3.7a	3.3a	— —	— —
27 June	13.9b	28.9a	1.3b	1.6a	— —	— —
9 July	15.7a	15.2a	1.9a	1.6a	-2.3b	-2.9a
27 July	24.6a	20.6a	1.5a	1.6a	-2.4a	-2.0b
15 Aug.	12.4a	12.3a	1.3b	1.5a	-5.2a	-4.4b
9 Sept.	17.7a	18.0a	0.8a	1.5a	-5.4b	-6.5a
3 Oct.	11.6a	8.5a	0.7a	0.7a	-4.5a	-4.6a
Western Wheatgrass						
7 June	133.2b	180.2a	6.0a	6.2a	— —	— —
27 June	30.8b	57.0a	2.1a	2.2a	— —	— —
9 July	32.6b	42.5a	2.0b	2.5a	-4.1a	-4.8b
27 July	43.3b	52.0a	1.3b	2.1a	-2.7b	-2.1a
15 Aug.	15.6b	21.3a	1.2b	1.5a	-4.1b	-3.4a
9 Sept.	22.1b	35.7a	0.7b	1.6a	-6.4b	-5.3a
3 Oct.	12.5b	14.4a	0.5b	0.7a	-3.9a	-4.8b

[1]For shallow and deep disturbance, leaf conductance, transpiration, and xylem potential values followed by the same letter on each date are not significantly different ($P \leq 0.05$).
[2]Equipment not available for measurements.

Table 3. Leaf conductance (mmol • m^{-2} • s^{-1}), transpiration (mmol • m^{-2} • s^{-1}), and stem xylem potential (MPa) of winterfat growing near another winterfat (EULA/EULA), a beardless bluebunch wheatgrass (PSIN), or a western wheatgrass (PASM) plant for site disturbance-x-species association interactions in 1985.

	Shallow Disturbance			Deep Disturbance		
Variable and Date	EULA/EULA	EULA/PSIN	EULA/PASM	EULA/EULA	EULA/PSIN	EULA/PASM
Leaf Conductance	mmol • m^{-2} • s^{-1}					
7 June	79.5a[1]	52.2a	78.1a	72.2a	57.2a	64.7a
27 June	14.2b	13.9b	16.1b	46.6a	14.9b	18.3b
9 July	22.2a	17.1a	20.3a	25.5a	27.9a	25.6a
27 July	29.0a	22.1a	25.5a	20.7a	20.0a	23.2a
15 Aug.	10.8a	11.4a	8.5a	10.4a	12.5a	11.7a
9 Sept.	12.5a	9.5a	13.3a	9.2a	12.4a	16.8a
3 Oct.	17.5a	13.0a	9.6b	4.7c	3.2c	6.1c
Transpiration	mmol • m^{-2} • s^{-1}					
7 June	6.5a	3.9a	5.2a	3.4a	3.2a	3.5a
27 June	1.3b	1.7a	1.5a	2.1a	1.2b	1.3b
9 July	2.1a	2.2a	1.8a	2.8a	1.9a	2.3a
27 July	1.2a	1.3a	1.1a	1.5a	1.6a	1.7a
15 Aug.	1.3a	1.3a	0.8b	1.0b	1.3a	1.3a
9 Sept.	0.9a	0.6b	0.6bc	1.0a	0.9a	1.2a
3 Oct.	0.8a	0.6a	0.5b	0.6b	0.3c	0.5b
Stem Xylem Potential	(MPa)					
9 July	−2.8b	−2.9b	−2.3c	−2.7b	−2.8b	−3.5a
27 July	−2.5a	−2.5a	−2.4a	−2.4a	−2.4a	−2.3a
15 Aug.	−3.9a	−4.0a	−3.7a	−3.7a	−3.7a	−3.8a
9 Sept.	−3.6a	−4.0a	−3.6a	−4.4a	−4.2a	−3.5a
3 Oct.	−4.0a	−4.2a	−5.3a	−4.6a	−4.3a	−4.7a

[1]Values on each sampling date followed by the same letter are not significantly different ($P \leq 0.05$).

deep disturbance (Table 2). However, leaf conductances for plants on the shallow disturbance were not significantly different during the same time period. Transpiration rates for winterfat were significantly greater on the deep disturbance for both July dates. Transpiration rates were 15, 35, and 45% greater for winterfat from the deep disturbance than from the shallow disturbance on 9 July, 27 July, and 9 September, respectively.

Winterfat was physiologically more active in October on the shallow disturbance compared to the deep disturbance site. Transpiration was 40% greater for plants from the shallow disturbance than from the deep disturbance (Table 2). However, transpiration rates were at a minimum for the growing season at this time for both soil disturbances.

Stem xylem potential was significantly lower for winterfat on the shallow disturbance on 9 July as compared to the deep disturbance (Table 2). Stem xylem potentials reached a minimum on 3 October. Stem xylem potentials did not differ between soil disturbances during most of the growing season.

Species Combination-Site Disturbance Interactions

Leaf conductance and transpiration in winterfat had a significant disturbance-x-species combination interaction by 27 June (Table 3). Leaf conductance on 27 June was greater on the deep disturbance in the winterfat-winterfat combination than in the winterfat-beardless bluebunch wheatgrass and winterfat-western wheatgrass combinations. This resulted in a greater transpiration rate for winterfat in the winterfat-winterfat combination. Only small differences in either leaf conductance or transpiration were noted between 27 June and 15 August.

Winterfat exhibited very low rates of transpiration for plants grown in combination with western wheatgrass on the shallow disturbance site on both 15 August and 9 September. Soil moisture had declined to 7% by this time (Table 1) and stem xylem potential was −3.7 MPa.

On 3 October, leaf conductance had a significant site disturbance-x-species combination interaction. No differences in species combinations were noted for the deep disturbance. The highest leaf conductance (17.5 mmol • m^{-2} • s^{-1}) was observed on this date for winterfat grown in combination with another winterfat plant on the shallow disturbance (Table 3). This rate was 5-fold greater than the lowest rate of conductance in winterfat grown in combination with beardless bluebunch wheatgrass on the deep disturbance site. Leaf conductances did not differ significantly in pure-stand pairs of winterfat on the shallow disturbance and winterfat associated with beardless bluebunch wheatgrass from the same site. However, conductances were lower for the winterfat-western wheatgrass combination on this site.

Transpiration rates for winterfat declined markedly by 3 October (Table 3). The highest transpiration rates for this day were observed for winterfat growing in pure-stand pairs on either the deep or shallow disturbances. The lowest transpiration rates on this date (0.3 mmol • m^{-2} • s^{-1}) were observed in winterfat growing in combination with beardless bluebunch wheatgrass on the deep disturbance site.

Stem xylem potential of winterfat declined throughout the growing season as soil water became less available (Table 3). The highest stem xylem potential of winterfat was observed on 9 July in winterfat growing in combination with western wheatgrass on the shallow disturbance (−2.3 MPa). In contrast, the lowest xylem potential was found for this same species combination on 3 October (−5.3 MPa).

Effect of Intra- and Interspecific Competition

Leaf conductance in winterfat was 40% and 100% greater on 7 June and 27 June, respectively, for the winterfat-winterfat combination (pure-stand pair) compared to the winterfat-beardless bluebunch wheatgrass combination (Table 4). Species combination did not affect leaf conductance in winterfat from 9 July until 9 September. However, on 9 September, when winterfat was associated with western wheatgrass, significantly greater conductance in winterfat was observed. That is, winterfat associated with western wheatgrass had a leaf conductance of 15.1 mmol • m^{-2} • s^{-1}; where-

Table 4. Leaf conductance (mmol • m^{-2} • s^{-1}), transpiration (mmol • m^{-2} • s^{-1}), and stem xylem potential (MPa) of winterfat grown in combination with another winterfat (EULA), beardless bluebunch wheatgrass (PSIN), or western wheatgrass (PASM) plant in the Piceance Basin, Colorado in 1985.

	Leaf Conductance			Transpiration			Stem Xylem Potential		
Date	EULA/ EULA	EULA/ PSIN	EULA/ PASM	EULA/ EULA	EULA/ PSIN	EULA/ PASM	EULA/ EULA	EULA/ PSIN	EULA/ PASM
	mmol • m^{-2} • s^{-1}						(MPa)		
7 June	75.8a[1]	54.9b	71.4a	4.4a	3.5b	4.4a	— —	— —	— —[2]
27 June	30.4a	14.4b	17.2b	1.7a	1.4b	1.4b	— —	— —	— —
9 July	23.9a	23.0a	22.9a	2.4a	2.0a	2.1a	-2.8a	-2.9a	-2.9a
27 July	25.1a	21.0a	24.4a	1.4a	1.5a	1.4a	-2.4a	-2.4a	-2.4a
15 Aug.	10.6a	11.9a	10.1a	1.1a	1.3a	1.1a	-3.8a	-3.9a	-3.7a
9 Sept.	11.0b	11.2b	15.1a	0.9a	0.8a	0.9a	-4.0a	-4.1a	-3.5b
3 Oct.	11.1a	8.1a	7.9a	0.7a	0.5b	0.5b	-4.3b	-4.3b	-5.0a

[1]Leaf conductance, transpiration, or stem xylem potential values within the same date followed by the same letter are not significantly different ($P \leq 0.05$).
[2]Equipment not available for measurements.

as, winterfat associated with beardless bluebunch wheatgrass had a leaf conductance of 11.2 mmol • m^{-2} • s^{-1}.

Transpiration rates of winterfat were significantly different for species combinations on 7 June and 27 June and followed a trend similar to that of leaf conductance (Table 4). Transpiration rates were greatest in winterfat for all combinations of species on 7 June as compared with transpiration rates on other dates. Transpiration rates, however, were 25% greater in winterfat grown in pure stands compared to when winterfat was growing in combination with beardless bluebunch wheatgrass. On 27 June transpiration rates were 20% greater in winterfat in pure stands than in the winterfat beardless bluebunch wheatgrass or western wheatgrass combinations. Transpiration rates for winterfat were then not affected by species combination until 3 October. On this date transpiration rates of winterfat were again greater in pure stands than when winterfat was associated with either beardless bluebunch wheatgrass or western wheatgrass.

Stem xylem potential for winterfat was not significantly affected by species combination until 9 September (Table 4). At this time, stem xylem potential was 15 to 20% greater when winterfat was growing in combination with western wheatgrass (-3.5 MPa) than when it was growing in combination with beardless bluebunch wheatgrass (-4.1 MPa) or in pure stands (-4.0 MPa). However, soil water was depleted rapidly so that by 3 October winterfat in combination with western wheatgrass had a stem xylem potential that was 15% lower (-5.0 MPa) than when it was growing in combination with another winterfat plant (-4.3 MPa) or beardless bluebunch wheatgrass (-4.3 MPa).

Discussion

Seasonal growth, phenological development, and soil moisture depletion had major influences on leaf conductance and transpiration in all 3 species. That is, leaf conductance in winterfat was nearly 7 times greater in June than in October, and leaf conductance of western wheatgrass was nearly 16 times greater in June than in October. This change was probably related to soil moisture depletion and ambient temperature changes throughout the growing season. Soil water content is known to influence stomatal conductance (Schulze et al. 1987). Because high stomatal conductance generally indicates high rates of photosynthesis, data from the current study suggest that photosynthetic rates were probably highest in the spring when soil moisture was greatest.

White (1976) determined that the optimum temperature for photosynthesis in winterfat was between 10 and 20° C. He also found that photosynthetic rates declined rapidly at temperatures above 20° C, and no shift in optimum temperature for photosynthesis occurred with changes in phenological status. Average, midday ambient air temperature in July and August in our study was above 20° C, which should account for reduced leaf conductance and photosynthetic rates. White (1976) also found that plant phenological status, plant moisture stress, and vapor pressure deficit significantly affected photosynthetic rates in winterfat. These factors were probably also important in the overall decline in physiological activity of plants through the growing season in our study.

Other workers have documented the importance of water stress and air temperature in other species. For example, DePuit and Caldwell (1973) found that when water stress was minimal, daily variation in the rate of photosynthesis of big sagebrush could be attributed to irradiance and air temperature. The effects of water stress and temperature on the physiological activity of winterfat are also important. White (1976) observed that photosynthetic rates of winterfat decreased at plant water potentials below -3 MPa. Stem xylem potential of winterfat in our study did not go below -3 MPa until August. Therefore, the decrease in leaf conductance in June may have been caused largely by increased air temperatures.

Love and West (1972) observed that the highest water stress in winterfat occurred in July and early August, and the lowest in May and late August. Maximum water stress, in their study, was observed about noon, but was not significantly different from 9:00 a.m. to 2:00 p.m. Water stress of winterfat increased throughout the growing season in our study and had not diminished by early October. The greatest water stress for winterfat (-5.0 MPa) occurred on 3 October when associated with western wheatgrass on the shallow disturbance site.

Winterfat also changes leaf morphology through the growing season; and this, in turn, affects leaf conductance. Winterfat leaves are smaller and covered with more lanate pubescence later in the season (Moore et al. 1972). The overall effect of this increase in pubescence should be a reduction in water loss from the leaves. Lower transpiration rates and leaf conductance during the latter part of the growing season were observed; however, other environmental factors also contributed to decreased rates of conductance and transpiration.

Transpiration rates in our study generally declined for all 3 species as the season progressed. Moore et al. (1972) observed that transpiration rates of winterfat decreased markedly in the latter part of summer and suggested that such a decrease was largely caused by an increase in plant water stress. Plant water stress of winterfat and the wheatgrasses also played a significant role in reduced transpiration rates in our study.

Leaf conductance in winterfat was not greatly different throughout the growing season on the deep disturbance as compared with plants on the shallow disturbance. In addition, transpiration rates were often not significantly different among plants from the 2 sites. Plant water stress did not differ for winterfat on either of the 2 soil disturbances. Welden and Slauson (1986) pointed out that the intensity of competition is not necessarily correlated with the intensity of disturbance. However, others have observed greater physiological activity in winterfat on disturbed sites. In fact, Love and West (1972) observed increased potential photosynthetic rates on winterfat on disturbed soils and suggested that the present-day distribution of winterfat was largely a reflection of disturbance. In our study, type of disturbance was not a major determinant of physiological activity in winterfat. However, western wheatgrass was more active throughout the growing season on the shallow disturbance site.

Leaf conductance was greater early and late in the season in winterfat associated with western wheatgrass than winterfat associated with beardless bluebunch wheatgrass or in monospecific stands. Mack and Bonham (1988) found a reduction in biomass of winterfat when grown in combination with beardless bluebunch wheatgrass that had an extensive root system. This latter species, in fact, had a greater rooting density at shallow depths and produced more root biomass than did winterfat (Bonham and Mack 1987). Beardless bluebunch wheatgrass probably depleted soil water resources more rapidly than winterfat and was, thus, an effective competitor with neighboring winterfat plants (Caldwell and Richards 1986). Love and West (1972) proposed that more variation (stress) was observed in monospecific stands of winterfat than in mixed stands. However, in our study, winterfat had higher transpiration rates in monospecific pairs of winterfat compared to pairs where winterfat was growing in association with the wheatgrasses.

Summary and Conclusions

Physiological activity, as indicated by leaf conductance and transpiration rates, declined in winterfat as the growing season progressed. This reduction was associated with higher ambient air temperatures and increased plant water stress. Soil disturbance also had an interactive effect on the physiological activity of winterfat. Soil water on the deep disturbance site was utilized by plants earlier in the spring as compared with water depletion on the shallow disturbance. Winterfat had greater root mass in the 0–40 cm depth in the deep disturbance (8.8 g/individual) as compared with root mass in the shallow disturbance (5.2/g individual) (Mack and Bonham 1987). This was probably why water use by winterfat was greater in late June and early July on the deep disturbance site.

Species combination also had some influence on stomatal activity in all 3 species. This was related to different biomass allocation patterns of the different growth forms represented by winterfat versus the 2 grasses. The more shallowly rooted western wheatgrass produced more roots in the surface soil (0–20 cm) than at deeper depths (Bonham and Mack 1987) and had very high rates of transpiration during the early part of the growing season. Western wheatgrass also produced greater root mass at the 0–20 cm depth when growing adjacent to winterfat than when growing adjacent to another western wheatgrass plant.

Leaf conductance and transpiration of winterfat was often lower when winterfat was associated with the 2 wheatgrasses than when growing adjacent to another winterfat plant. Beardless bluebunch wheatgrass may be a greater competitor with winterfat than is western wheatgrass because of its large root mass in the 0–20 cm depth of the soil (Bonham and Mack 1987) and effective use of soil water. Lowest transpiration rates of winterfat were often found when winterfat was growing adjacent to beardless bluebunch wheatgrass. Thus, the intensity of competition (Welden and Slausen 1986) for soil water resources may be greater for winterfat when associated with wheatgrasses than when associated with another winterfat plant.

Literature Cited

Bonham, C.D., and S.E. Mack. 1987. Biomass responses of two *Agropyron* spp. in the presence of winter fat [*Ceratoides lanata* (Pursh.) J.T. Howell] on disturbed sites. Reclam. and Reveg. Res. 6:13-24.

Bureau of Land Management (BLM). 1984. Piceance Basin: Resource Management Plan and Environmental Impact Statement. Vol. I. U.S. Dep. Interior. INT DEIS 84-12.

Caldwell, M.M., and J.H. Richards. 1986. Competing root systems: morphology and models of absorption. pp. 251-273. *In:* T.J. Givnish (Ed.) On the economy of plant form and function. Cambridge Univ. Press, Cambridge, UK.

DePuit, E.J., and M.M. Caldwell. 1973. Seasonal pattern of net photosynthesis of *Artemisia tridentata.* Amer. J. Bot. 60:426-435.

Doerr, T.B., and E.F. Redente. 1983. Seeded plant community changes on deep disturbance soils as affected by cultural practices. Reclam. and Reveg. Res. 2:13-24.

Eissenstat, D.M., and M.M. Caldwell. 1988. Competitive ability is linked to rates of water extraction: field study of two arid land tussock grasses. Oecologia 25:1-7.

El-Sharkawy, M.A., and J.D. Hesketh. 1964. Effects of temperature and water deficit on leaf photosynthetic rates of different species. Crop Sci. 4:514-518.

Larcher, W. 1980. Physiological plant ecology, 2nd ed. Springer Verlag, New York.

Love, L.L., and N.E. West. 1972. Plant moisture stress patterns in *Eurotia lanata* and *Atriplex confertifolia.* Northwest Sci. 46:44-51.

Mack, S.E. 1986. Responses of *Eurotia lanata in association with two species of Agropyron* on disturbed soils. Ph.D. Diss., Colo. State Univ., Fort Collins.

Mack, S.E., and C.D. Bonham. 1988. Phytomass of *Eurotia lanata* [(Pursh) Moq.] in association with two species of *Agropyron* on disturbed soils. Reclam. and Reveg. Res. 6:285-298.

Moore, R.T., R.S. White, and M.M. Caldwell. 1972. Transpiration of *Atriplex confertifolia* and *Eurotia lanata* in relation to soil, plant, and atmospheric moisture stresses. Can. J. Bot. 50:2411-2418.

Redente, E.F., T.B. Doerr, C.E. Grygiel, and M.E. Biondini. 1984. Vegetation establishment and succession on disturbed soils in northwest Colorado. Reclam. and Reveg. Res. 3:153-165.

Schulze, E.-D., R.H. Robichaux, J. Grace, P.W. Rundel, and J.R. Ehleringer. 1987. Plant water balance. Bioscience 37:30-37.

Trlica, M.J., and M.E. Biondini. 1990. Soil water dynamics, transpiration, and water losses in a crested wheatgrass and native shortgrass ecosystem. Plant and Soil 126:187-201.

Van den Driessche, R., D.J. Connor, and B.R. Tunstall. 1971. Photosynthetic response of brigalow to irradiance, temperature, and water potential. Photosynthetica 5:210-217.

Waring, R.H., and B.D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248-1254.

Welden, C.W., and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Q. Rev. Biol. 61:23-44.

White, R.S. 1976. Seasonal patterns of photosynthesis and respiration in *Atriplex confertifolia* and *Ceratoides lanata.* Ph.D. Diss., Utah State Univ., Logan.