Comparison of water use by *Artemisia tridentata* spp. *wyomingensis* and *Chrysothamnus viscidiflorus* spp. *viscidiflorus*

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Abstract

With the reduction of fire frequency in the northern Great Basin, shrubs have increased in abundance at the expense of the herbaceous component. The ability of shrubs to acquire limited soil water resources is probably an important process in determining plant succession and composition. Water use by Wyoming big sagebrush *(Artemisia tridentata* subsp. *wyomingensis)* and green rabbitbrush *(Chrysothamnus viscidiflorus* subsp. *viscidiflorus)* was measured during the growing season. I tested the hypothesis that Wyoming big sagebrush utilizes soil water at a more rapid rate, early in the growing season than green rabbitbrush. Water use by these 2 shrubs was compared by determining total water potential (ψ), leaf conductance, transpiration per unit leaf area, and transpiration per unit of canopy throughout 2 growing seasons. Soil water depletion around isolated plants was also measured during both growing seasons. Both plants initiated spring growth at approximately the same time; however, Wyoming big sagebrush maintained a larger leaf area index within the canopy throughout the growing season. Leaf conductance and transpiration were significantly ($P \leq 0.05$) higher in green rabbitbrush, while transpiration per unit of canopy was higher in Wyoming big sagebrush. Soil water depletion was significantly ($P \leq 0.05$) more rapid at the canopy edge of isolated Wyoming big sagebrush than green rabbitbrush plants. Wyoming big sagebrush has a greater capacity to exploit early spring soil water than green rabbitbrush.

Key Words: leaf area index, conductance, transpiration, total water potential, soil water content, Wyoming big sagebrush, green rabbitbrush

With the reduction of fire frequency in the northern Great Basin, shrubs have increased in abundance, while herbaceous vegetation has decreased in abundance regardless of management (West 1978, Sneva et al. 1984). Plant competition for limited soil water resources can play an important role in determining plant composition and succession. When developing management plans, it is essential to understand the ability of plant species to capitalize on soil water. Two common shrubs frequently found growing on the same site, throughout this region, are Wyoming big sagebrush *(Artemisia tridentata* subsp. *wyomingensis)* and green rabbitbrush *(Chrysothamnus viscidiflorus* subsp. viscidiflorus). Frishknecht (1963) reported big sagebrush has a greater impact on crested wheatgrass production than does grey rabbitbrush *(C. nauseosus).* He suggested earlier active spring growth and a more strongly developed lateral root system in big sagebrush versus a taproot system in rabbitbrush as the primary reasons for the greater influence on herbage production by big sagebrush. Sturges (1977) found sagebrush roots compete directly with associated herbaceous vegetation for soil water. In the northeastern part of the Great Basin, however, spring growth of Wyoming big sagebrush and green rabbitbrush, have been observed to occur at approximately the same time. Both species, also, frequently grow in soils less than 60 cm deep where potential competition for soil water is intensified.

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The purpose of this study was to compare seasonal use of soil water by Wyoming big sagebrush and green rabbitbrush, and test the hypothesis that Wyoming big sagebrush utilizes soil water at a more rapid rate, early in the growing season, than green rabbitbrush. To test this hypothesis leaf conductance, transpiration per unit leaf area, transpiration per unit of canopy, and soil water depletion were compared between species throughout 2 growing seasons.

Methods

Study Area

The study was conducted on the Squaw Butte Experimental Range, in southeastern Oregon, 67 km west of Burns. The experimental range, located within the Great Basin, is representative of the sagebrush-steppe biome. The 40-year mean annual precipitation for this area is approximately 30 cm. The Squaw Butte Experimental Range typically receives the majority of moisture between September and June, mostly as snow, with little precipitation received in July and August. The study site is located in a Wyoming big sagebrush-Thurber's needlegrass *(Stipa thurberiana)* habitat type, at an elevation of 1,370 m. Soils are classified as Xerollic Durothids (Lentz and Simonson 1986). Soils vary in depth from 40 to 50 cm and are underlain by an indurated duripan 5 to 20 cm thick, which is underlain by unweathered bedrock.

Climate and Soil Parameters

Precipitation was measured throughout the year with a standard U.S. Weather Bureau gauge located 3.5 km from the study site. All other climatic and plant water measurements were recorded concurrently during the growing season, from April through August in 1985 and 1986. Air temperature and relative humidity were measured on site with a steady state porometer. Vapor pressure deficit was calculated from air temperature and relative humidity measurements. Soil water samples were collected in the shrub interspaces adjacent to shrubs on which plant water measurements were recorded. Five samples were collected from 2 soil depths, 2–20 cm (A horizon = gravelly fine sandy loam) and 20 cm to the duripan (Bt to BCt = gravelly clay loam to a gravelly silty clay loam), on the same day plant water measurements were recorded. Soil water content was measured gravimetrically and soil water release curves developed for each depth to convert percent soil water to soil water potential.

Plant Water Measurements

Plant water measurements were recorded on 9 dates during the growing season of 1985 and 7 dates in 1986. Six mature plants of both Wyoming big sagebrush and green rabbitbrush of comparable aboveground size were selected randomly at the beginning of the 1985 growing season for plant water measurements. Total water potential (ψ_1) was measured on one branchlet on each shrub with a pressure chamber (Scholander et al. 1965) at 0400, 0800 and 1400 h. Samples were removed from the shrub and immediately measured in the pressure chamber. Leaf conductance was measured with a steady-state porometer fitted with a cylindrical chamber. Leaf conductance was measured on one branchlet on each plant following the completion of ψ_1 readings at 0800 and 1400 h. At the end of each sampling day, branchlets on which leaf conductance was measured were collected, sealed in ziploc plastic bags, and placed on ice for determination of leaf area with a leaf area meter accurate to 0.01 cm^2. Leaf area measurements were then used to correct leaf conductance data recorded in the field. All plant water measurements were recorded on vegetative branchlets in Wyoming big sagebrush and below the inflorescence in green rabbitbrush. Transpiration (J) was calculated from simultaneous measurements of leaf conductance (g) and vapor pressure deficit (VPD) using the equation J = (g)(VPD).

Phenology

Leaf development was observed and recorded during each visit to the site. Observations were made on 3 permanently marked branches on each of the 12 shrubs selected for plant water measurements. During each visit, all leaves at the terminus of each branch were marked with a dot of black indelible ink so newly developed leaves could be identified during the following visit.

Leaf Area Index

Five mature plants of both Wyoming big sagebrush and green rabbitbrush, ranging from 60 to 75 cm in height, were randomly selected and permanently marked for leaf area measurements in 1985. Plants with full, healthy canopies were used. Leaf area was estimated on 4 April, 1 May, 1 June, 28 June, and 1 August using a nondestructive point-quadrat technique (Knight 1973). Leaf area on green rabbitbrush was not measured on 4 April because only a

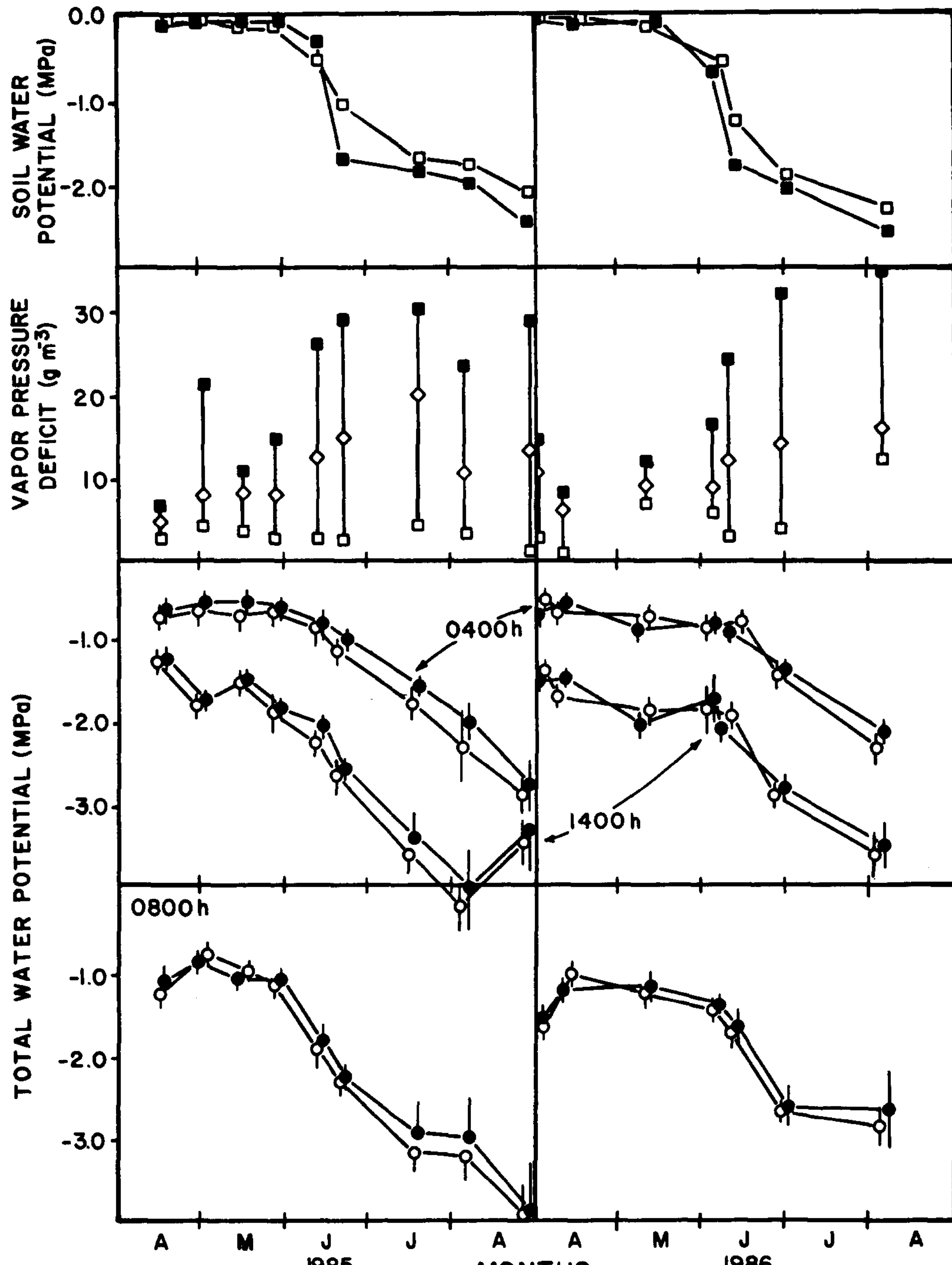

Fig. 1. *Soil water potential at 2–20 cm (■) and 20–40+ cm (□), vapor pressure deficit at 0400 h (□), 0800 h (◇), and 1400 h (■), and total water potential for Wyoming big sagebrush (●) and green rabbitbrush (○). Vertical bars drawn through the means of total water potential are 95% confidence limits.*

trace was present. Steel stakes were driven into the ground adjacent to each shrub so the point frame could be placed in the same position over the plant on all 5 dates. Pin angle selected was 30°. All green leaves contacted by the sharpened tip of the pin, as it was lowered through the canopy, were recorded as a hit. Measurements were initiated and terminated at the canopy edge during each sampling period. During each sampling date 215 to 367 pins were observed for each canopy. Leaf area index within the canopies of Wyoming big sagebrush and green rabbitbrush was determined from the average number of contacts per pin multiplied by 0.866 to correct for the angle.

Soil Water around Individual Plants

Five mature plants of both Wyoming big sagebrush and green rabbitbrush, of comparable aboveground size, were randomly selected in 1984 and a second set in 1985 to monitor soil water depletion by individual plants. In the fall of 1984, all surface vegetation within 4.6 m of each plant to be studied in 1985 was removed by cutting all shrubs to ground level, removing vegetation beneath the canopy by hand, and spraying the remaining vegetation with Roundup®. In the following growing season, new vegetation beneath the canopy was periodically removed by hand, while the area around isolated plants was maintained free of vegetation with several applications of Roundup®. Roundup® was applied with a backpack sprayer during wind-free periods. This procedure was repeated in the fall of 1985 and spring of 1986 for the second set of plants studied. Sturges (1977) and Sturges and Trlica (1978) reported maximum lateral root extension for big sagebrush ranges from 92 to 152 cm from the plant base, thus 4.6 m should have been adequate to isolate plants from surrounding vegetation. Two soil water samples were collected at the canopy edge for each plant, at each of the 2 depths (2–20 cm and 20 cm to duripan) concurrently with other plant and soil water measurements recorded in the undisturbed community. Soil samples were analyzed as previously described.

Data analysis

Differences between Wyoming big sagebrush and green rabbitbrush within dates in ψ_1, leaf conductance, transpiration, and soil water content were evaluated with the Student's t-test.

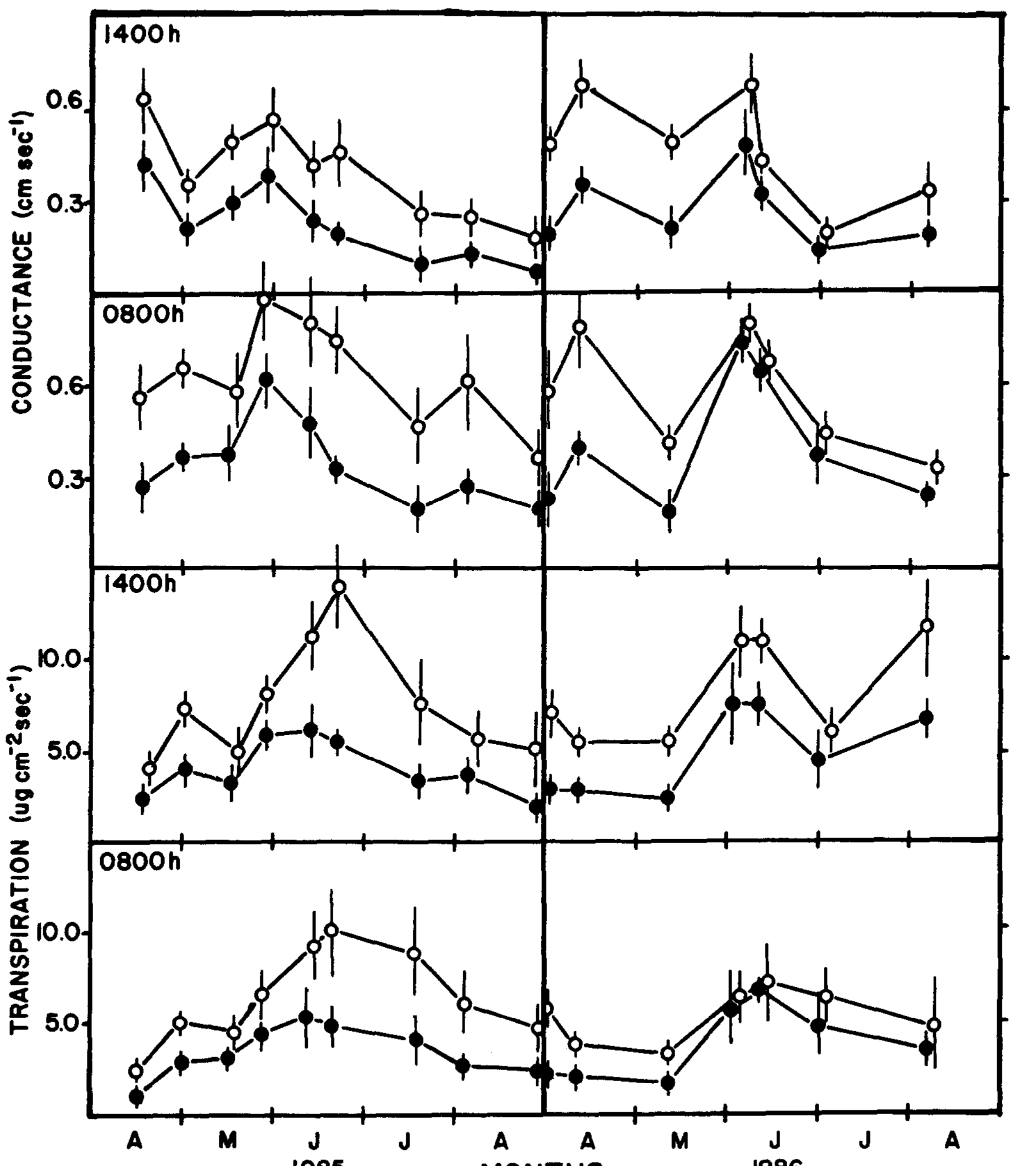

Fig. 2. *Leaf conductance and transpiration for Wyoming big sagebrush (●) and green rabbitbrush (○). Vertical bars are 95% confidence limits for each mean.*

Results

Climate

Precipitation for the 1985 and 1986 growing seasons was 20.5 and 30.1 cm, respectively. In both years the soil profile was near field capacity at both depths at the beginning of the growing season (Fig. 1). June precipitation was 23 and 11.5% of normal in 1985 and 1986, respectively, allowing rapid soil water depletion due to limited soil water replenishment.

Phenology

Both Wyoming big sagebrush and green rabbitbrush initiated early spring growth during the second week of April in 1985 and 1986. Leaf expansion continued for both species until early July, followed by senescence of the previous season's perennial and current year's large ephemeral leaves in big sagebrush, and the early spring leaves in green rabbitbrush during late July and early August. Wyoming big sagebrush maintained a significantly ($P \leq 0.05$) larger leaf area index within its canopy than green rabbitbrush throughout the growing season (Table 1). Leaf area index of Wyoming big sagebrush was 4.8 times larger than green rabbitbrush in early spring to 2.75 times larger in August. Green leaves present on Wyoming big sagebrush on 4 April were winter persistent leaves.

Plant Water

Seasonal patterns of predawn, morning, and midday ψ_l between the 2 shrubs were similar in both growing seasons (Fig. 1). Total water potentials were usually not significantly ($P > 0.05$) different between species. Although seasonal patterns in leaf conductance were similar in both species, morning and midday leaf conductance were usually significantly ($P \leq 0.05$) higher in green rabbitbrush than Wyoming big sagebrush (Fig. 2). Transpiration per unit leaf area was also usually significantly ($P \leq 0.05$) greater in green rabbitbrush than Wyoming big sagebrush throughout the 2 growing seasons (Fig. 2). Wyoming big sagebrush, however, would still potentially transpire more water per unit of canopy than rabbitbrush due to its higher leaf area index. If we assume the relative differences in transpiration between the 2 shrubs is maintained throughout the canopies during the 0800 h measurements and multiply transpiration per unit leaf area by leaf area index within the canopy of each shrub species, then Wyoming big sagebrush potentially would transpire 2.5, 2.2, 1.2, and 1.5 times more water per unit of canopy, on 1 May, 1 June, 28 June, and 1 August, respectively, than green rabbitbrush. Midday transpiration on these dates would also potentially be greater per unit of canopy in Wyoming big sagebrush

Table 1. Mean leaf area index (LAI) within the canopy and standard deviation for Wyoming big sagebrush and green rabbitbrush in 1985.

Date	Sagebrush	Rabbitbrush
	LAI	
April 4	0.7 (0.097)	trace
May 1	1.2 (0.311)*[1]	0.25 (0.032)
June 1	1.7 (0.384)*	0.6 (0.066)
June 28	2.2 (0.390)*	0.7 (0.114)
August 1	1.1 (0.249)*	0.4 (0.050)

[1]LAI, followed by * is significantly ($P \leq 0.05$) different between species within dates; comparison not made for April 4. Differences between means were tested with a Student's-t test.

Soil Water around Individual Plants

Soil water content at 2–20 cm depth within dates was significantly lower ($P \leq 0.05$) around Wyoming big sagebrush than green

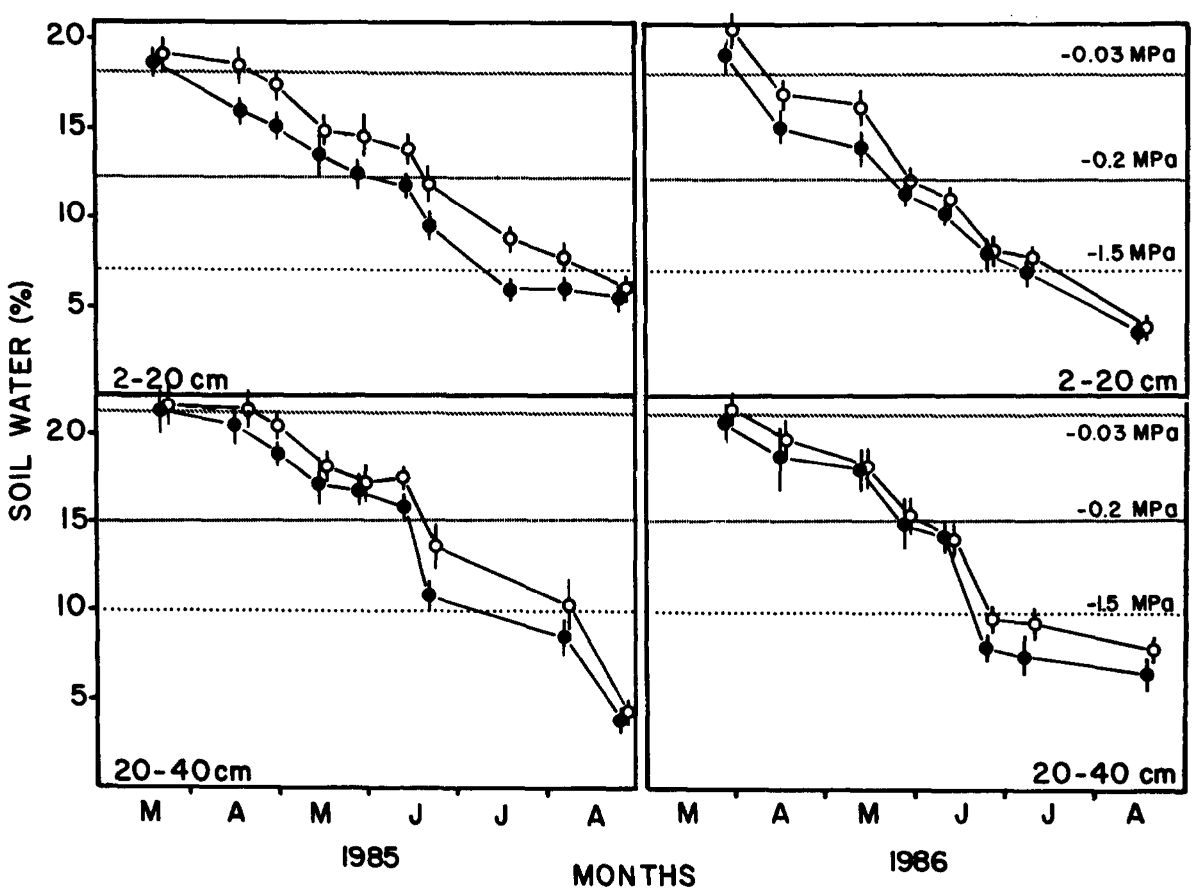

Fig. 3. *Soil water content for 2 depths at the canopy edge of isolated Wyoming big sagebrush (●) and green rabbitbrush (○) plants. Vertical bars are 95% confidence limits for each mean. Data are presented as percent soil water content to more easily observe differences between species during wet soil conditions.*

rabbitbrush from April through early August in 1985 (with the exception of 15 May), and April through early May in 1986 (Fig. 3). Soil water content below 20 cm was only occasionally significantly different ($P \leq 0.05$) between the 2 species, although a similar trend in soil water depletion occurred.

Discussion

The different growth habits of big sagebrush (semideciduous) and green rabbitbrush (deciduous) may help explain some of the measured differences in leaf area development and water use. Within the canopy of Wyoming big sagebrush, leaf area index of leaves persisting through the 1985 winter was 0.7', approximately one-third of the maximum leaf area index occurring on 28 June. Miller and Shultz (1987) reported the previous season's overwintering leaves on Wyoming big sagebrush made up 32% of the total leaf biomass at peak leaf development. In 1985 and 1986, leaf growth was initiated at approximately the same time for both shrubs in April, with rapid leaf development occurring in May and June. Under more mesic conditions, rapid growth of Wyoming big sagebrush on this site was reported to continue until mid July in 1982 (Miller et al. 1986), approximately 2 weeks longer than in 1985 or 1986. Although timing of leaf development was similar for both species, Wyoming big sagebrush maintained a higher leaf area index than green rabbitbrush. During summer drought both species reduced their leaf surface areas through senescing a portion of their leaves.

Green rabbitbrush maintained a higher level of leaf conductance and transpiration per unit leaf area throughout both growing seasons. DePuit and Caldwell (1975) reported *Gutierrezia sarothrae* also maintained a higher level of leaf conductance than big sagebrush, but big sagebrush maintained a greater quantity of leaves. Ritchie (1974) reported it is important for a plant to maximize its leaf area as early as possible during the growing season to make the most beneficial use of water. The presence of a relatively large leaf area early in the spring may be extremely important for taking full advantage of favorable growing conditions (Slayter 1970, Caldwell 1978). In years of limited spring moisture, plants capable of using early spring soil water would appear to be at a competitive advantage for this resource. This may explain greater reductions in plant growth reported for green rabbitbrush when competing with mature big sagebrush than stands composed of green rabbitbrush and young sagebrush (Young and Evans 1974a), and reduced populations of rabbitbrush where big sagebrush plants are 40 to 50 years old (Young and Evans 1974b).

Total water potentials in both shrubs responded similarly to seasonal changes in environmental conditions. Predawn ψ_l is a good measure of water availability in the soil immediately around the roots (Ritchie and Hinckley 1975). Similar predawn ψ_l between Wyoming big sagebrush and green rabbitbrush suggests that zones of soil water occupied by roots of these 2 species are similar on this site.

Soil water content around isolated Wyoming big sagebrush and green rabbitbrush plants was not significantly different in late March of both years, in spite of the presence of overwintering leaves on sagebrush (Fig. 3). This was probably due to maximum daily winter temperatures remaining below 0° C and soil temperatures remaining near or below 0° C. Tabler (1968) found no evidence of winter soil water use by big sagebrush where temperatures were below 0° C and snow covered the ground. In warmer climates, however, big sagebrush does appear to use soil water during the winter (Rickard 1967).

The more rapid depletion of soil water early in the growing season by Wyoming big sagebrush than by green rabbitbrush, suggests the plant will have a greater impact on soil water content in the spring, thus potentially limiting herbaceous production to a greater degree. Presence of overwintering leaves and a relatively larger leaf area index within the canopy of Wyoming big sagebrush may be important mechanisms allowing the plant to capitalize on soil moisture early in the growing season when vapor pressure deficits are low and soil water content usually near field capacity. Although soil water withdrawal by big sagebrush roots may occur simultaneously with herbaceous vegetation (Sturges 1977) and green rabbitbrush, soil water depletion occurs at a faster rate in big sagebrush due to a larger evaporative surface displayed within its canopy, particularly early in the spring.

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