Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species

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Summary. Causes for the widespread abundance of the alien grass *Bromus tectorum* (cheatgrass) after fire in semiarid areas of western North America may include: (1) utilization of resources freed by the removal of fire-intolerant plants; and (2) successful competition between *B. tectorum* and individual plants that survive fire. On a site in northwestern Nevada (USA), measurements of soil water content, plant water potential, aboveground biomass production, water use efficiency, and *B. tectorum* tiller density were used to determine if *B. tectorum* competes with either of two native species (*Stipa comata* and *Chrysothamnus viscidiflorus*) or simply uses unclaimed resources. Soil water content around native species occurring with *B. tectorum* was significantly lower ($P < 0.05$) than around individuals without *B. tectorum* nearby. Native species had significantly more negative plant water potential when they occurred with *B. tectorum*. Aboveground biomass was significantly higher for native species without *B. tectorum*. However, the carbon isotope ratio of leaves for native species with *B. tectorum* was not significantly different from individuals without *B. tectorum*. Thus, *B. tectorum* competes with native species for soil water and negatively affects their water status and productivity, but the competition for water does not affect water use efficiency of the native species. These adverse effects of *B. tectorum* competition on the productivity and water status of native species are also evident at 12 years after a fire. This competitive ability of *B. tectorum* greatly enhances its capability to exploit soil resources after fire and to enhance its status in the community.

Key words: Soil water content – Water use efficiency – Carbon isotope ratio – *Stipa comata* – *Chrysothamnus viscidiflorus*

Fires can cause many changes in the composition and physical environment of plant communities. The ability

of a plant to survive fire is influenced by species-specific characteristics such as location of the shoot meristem (Conrad and Poulton 1966; Antos et al. 1983) and the ability of heat to reach meristematic tissues (Wright 1971; Young and Miller 1985) as well as plant age (Cable 1967) and phenology (Wright and Klemmedson 1965). Although differential plant mortality has an immediate effect on community composition, subsequent composition is also influenced by resprouting (Young and Evans 1978) and reproductive effort (Cable 1967; Old 1969; Uresk et al. 1976; Knapp 1984; Young and Miller 1985). Changes in the physical environment such as plant microclimate (Old 1969; Knapp 1984) or nutrient availability (Old 1969; Raison 1979; Wright and Bailey 1982; Hobbs and Schimel 1984; Rundel and Parsons 1984; Koviac et al. 1986) also affect post-fire vegetation dynamics.

These rapid shifts in community composition and growing conditions following fires undoubtedly alter the competitive interactions among species. Reduced competition is one mechanism that is postulated to cause some of the effects of fire on vegetation dynamics. For example, the increased productivity of grasses in semiarid shrub-grass communities is often attributed to competitive release because of the mortality of fire-intolerant shrubs (Cable 1967; Harniss and Murray 1973; Young and Evans 1978; Young 1983; Young and Miller 1985). Furthermore, increased availability of nutrients may reduce nutrient competition. However, soil moisture throughout the soil profile can be depleted more rapidly on burned sites than on unburned sites in semiarid areas (Daubenmire 1968; Redmann 1978). Thus, competition for water, which is the limiting factor for growth of plants in arid environments (Smith and Nowak 1990), may be important after fire. Unfortunately, few studies have specifically examined the competitive interactions among species after fire in semiarid ecosystems.

The semiarid, sagebrush steppe communities in western North America represent an ideal system to investigate competitive interactions after fires. Many of these communities have been invaded by the annual grass *Bromus tectorum* L. (cheatgrass) (Mack 1981). *B. tectorum* can quickly dominate sites disturbed by fires (Steward

and Hull 1949; Klemmedson and Smith 1964; Young and Evans 1973). Some perennial species, such as the dominant shrub *Artemisia tridentata* Nutt. (sagebrush), decline or fail to recover following fires, whereas other perennial species experience little or no mortality (Young and Evans 1978). Thus, the post-fire landscape is a matrix of resource availability. Resources are freely-available near dead plants, but resources in other areas are still dominated by perennial plants that survived the fire. Although *B. tectorum* is thought to be very competitive (Harris 1967), we do not know if its competitive ability contributes to its post-fire dominance.

The primary focus of this research project is how *B. tectorum* acquires soil resources after fire. Two strategies that this annual species could use are: exploit resources that are freed by the removal of fire-intolerant, perennial plants; or successfully compete for soil resources against plants that survive fire. Thus, the two primary objectives of this study were to: (1) determine patterns of soil water use after fire by plants in an arid environment; and (2) investigate if competition between native species and *B. tectorum* affects productivity and water status of the perennial plants. In order to determine a time frame for these two objectives, we compared results from a recently-burned area with those from an area that burned 12 years prior to the study.

Materials and methods

Study area

This research was conducted during 1987 and 1988 at Bedell Flats, 35km north of Reno, NV, USA, at 39° 51' N latitude and 119° 48' W longitude. The area lies at 1570 m elevation and is estimated to have an average annual precipitation of 250 mm (Evans and Young 1977). Soils are coarse-loamy, mixed, mesic Xerollic Haplargids, approximately 0.8 m deep. The vegetation type is a sagebrush-bunchgrass community. Major species present are *Artemisia tridentata, Chrysothamnus viscidiflorus* (Hook.) Nutt. (rabbitbrush), *Tetradymia canescens* DC. (horsebrush), *Stipa comata* Trin. and Rupr. (needle-and-thread grass), *Sitanion hystrix* (Nutt.) J.G. Smith (squirreltail), and the introduced species *B. tectorum.*

A 1 ha area that burned naturally during late-summer, 1986 was chosen for the burned site. An adjacent 0.7 ha area that has not burned for at least 12 years served as a long-term reference area. The purpose of this long-term reference area was to determine if results that occur in the years immediately after fire persist for extended periods of time. Both areas were fenced to exclude grazing by wildlife and livestock.

Target species

Two native species, *C. viscidiflorus and S. comata,* were selected to determine soil water exploitation after fire and to evaluate their competitive interactions with *B. tectorum* for soil water. These species were selected on the basis of abundance and because both species generally survive a late-summer fire (Wright 1971; Young 1983). *S. comata* is a perennial bunchgrass, and *C. vicidiflorus* is a perennial shrub. Basal cover of target individuals was measured at the beginning of the study of standardize plant size.

The study followed the same 48 individuals of each target species during two years (1987 and 1988). Thirty-two individuals of
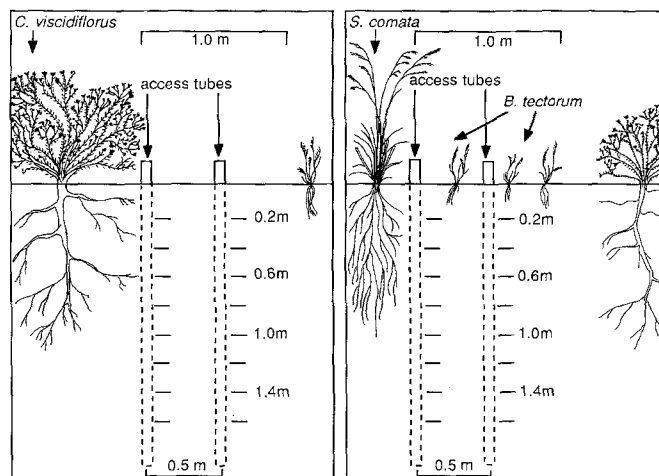

Fig. 1. *Left frame: Chrysothamnus viscidiflorus* target individual in the burned area without *Bromus tectorum.* Vegetation within 1.0 m radius around individuals was totally removed to preclude competition for soil water. *Right frame: Stipa comata* individual in the burned area with *B. tectorum.* Vegetation within 1.0 m radius around individuals was removed with the exception of *B. tectorum.* For all target plants, an aluminum neutron probe access tube for soil water measurements was located at both the edge of the plant canopy and 0.5 m away

each target species were used for measurements in the burned area, and 16 individuals of each target species were used in the long-term reference area. Target individuals were selected from a stratified random sample of the population on the basis of initial basal cover that was measured in the fall, 1986. To eliminate competition, vegetation around one half of the individuals in the burned area was totally removed within a 1 m radius of the target individuals (target individuals without *B. tectorum,* Fig. 1). Vegetation was also removed around the other half of the individuals in the burned area, with the exception of *B. tectorum* (target individuals with *B. tectorum,* Fig. 1). Vegetation was removed with a hoe during fall, 1986 and as needed during the next two years. This allowed comparison between native species with and without *B. tectorum* competition. Vegetation in the long-term reference area was not altered and provided reference measurements for what may occur among the species 12 years after fire.

Soil water content

Circular study plots allowed soil water content to be sampled in concentric circles around the study plants. Two concentric circles were chosen: the edge of the plant canopy and 0.5 m away from the canopy edge (Fig. 1). The volume of soil below the canopy of the plant was chosen because it represents soil that is probably dominated by that plant (Caldwell and Richards 1986). The volume of soil 0.5 m from the edge of the plant represents a soil resource that was probably dominated by another plant but became available after removal of that other plant by fire.

An aluminum access tube was installed along the perimeter of each of the two concentric circles at a random compass angle, and soil moisture was measured with a neutron probe (Model 503 Hydroprobe Moisture Depth Gauge, Campbell Pacific Nuclear Corp., Martinez, CA, USA). The neutron probe technique allowed direct, repeatable and non-destructive measurements of soil water content (van Bavel et al. 1963; Hauser 1984) to a 1.6 m soil depth at 0.2 m increments. Gravimetric measurements were used to calibrate the neutron probe ($R = 0.87$; $n = 21$). The probe was calibrat-

ed in September 1987 using a method similar to that described by Reginato and Nakayama (1988). Our calibration differed from theirs in that we irrigated only two of the three calibration plots, used a 22 mm diameter gravimetric core sampler, and assumed the 0.2 m probe reading was representative of the 0.1–0.3 m soil layer. Gravimetric measurements were converted to volumetric by multiplying mass water content by bulk density of the soil. Bulk density of soil was measured with the compliant cavity method (Bradford and Grossman 1982). Because of time and expense to purchase, install, and read the neutron probe access tubes, only 16 individuals of each species in the burned area (8 plots with *B. tectorum* and 8 plots without *B. tectorum*) and 8 individuals of each species in the long-term reference area were used for soil moisture measurements.

Between April and August of 1987 and March and July of 1988, soil moisture measurements were taken twice per month. During the rest of the year, measurements were taken at approximately one-month intervals. Neutron probe measurements in the long-term reference area were consistently greater than those in the burned area. In order to compare results from both areas, results for volumetric soil water from the 1987 and 1988 growing seasons are expressed as a percentage of the initial water content measured in December 1986.

Plant water potential

Water potential of target individuals and *B. tectorum* was measured with a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR, USA) (Turner and Long 1980). Water potential measurements were taken at predawn and midday from April to July of 1988 for target individuals and during late April and early May of 1988 for *B. tectorum*. Water potential measurements from each of the target individuals used for soil water measurements were taken twice a month on the same dates that soil water measurements were taken.

Aboveground biomass

Standing aboveground biomass of target individuals was measured for all plots at the end of the 1988 growing season by removing total aboveground biomass. In addition, aboveground biomass of *B. tectorum* and other species within 1 m around target individuals was harvested in the appropriate plots. Aboveground biomass of *S. comata* and *B. tectorum* in the burned area was also measured at the end of the 1987 growing season after the majority of *B. tectorum* seed had disarticulated. After harvest, total aboveground biomass was oven-dried and weighed.

B. tectorum tiller density

For plots of target individuals in the burned area with *B. tectorum* interaction and in the long-term reference area, *B. tectorum* tiller density was measured at the end of both the 1987 and 1988 growing seasons.

Water use efficiency

Carbon isotope ratios ($\delta^{13}C$) were used to estimate water use efficiency of the native species (Farquhar et al. 1982). A 5.0 g leaf sample was collected from 4 randomly selected target individuals at the end of the 1988 growing season. Each sample was oven-dried,

ground with a cyclonic sample mill, and analyzed in J. Ehleringer's laboratory (University of Utah, Salt Lake City, UT, USA).

Statistical analyses

Data were analyzed using factorial ANOVA techniques. Each species was treated separately. Effects of year (1 d.f.), level of competition (2 d.f.), lateral distance from the study plant (1 d.f.), depth (7 d.f.), and time of the year (at least 6 d.f.) were evaluated. Comparison of means were done with L.S.D. techniques. Comparisons between burned and long-term reference areas also evaluated. $P < 0.05$ was the level of significance used.

Results

Soil water content

For both the 1987 and 1988 growing seasons, relative soil water content around target individuals of both species in the burned area without *B. tectorum* was significantly greater than that around individuals in either the burned area with *B. tectorum* or the long-term reference area (Figs. 2 and 3). Soil water depletion in the upper
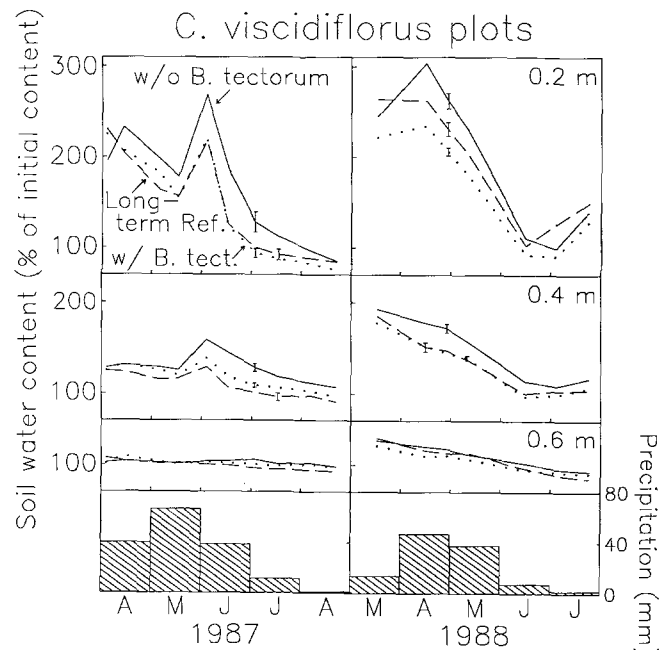

Fig. 2. Relative volumetric soil water content for *Chrysothamnus viscidiflorus* plots at three selected depths during the 1987 and 1988 growing seasons. Results are shown for *C. viscidiflorus* in the burned area without *Bromus tectorum* (*solid line*) and with *B. tectorum* (*dotted line*) as well as in the long-term reference area (*dashed line*). Soil water content for both 1987 and 1988 is expressed as a percentage of the water content measured in December 1986. Error bars for each set of plots are averages of the standard errors of the mean from each date. For clarity, error bars are not shown for the 0.6 m depth but they were similar in size to those at the 0.4 m depth. Precipitation for each month during the 1987 and 1988 growing seasons are also shown
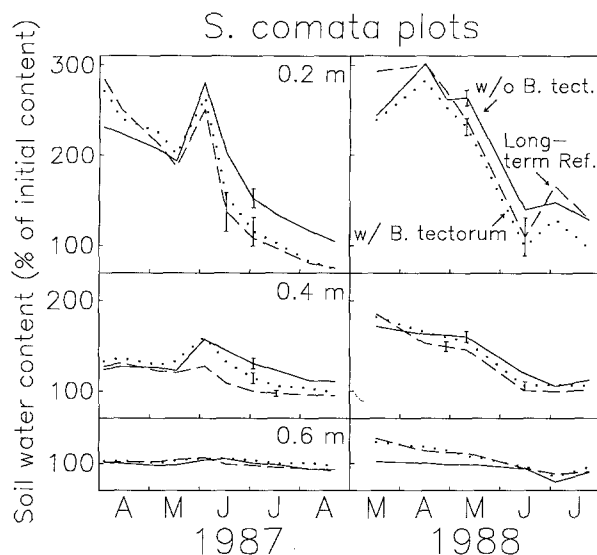
S. comata plots

Fig. 3. Relative volumetric soil water content for *Stipa comata* plots at three selected depths during the 1987 and 1988 growing seasons. Results for *S. comata* in the burned area without *Bromus tectorum* (*solid line*) and with *B. tectorum* (*dotted line*) as well as in the long-term reference area (*dashed line*) are shown. Soil water content for both years is expressed as a percentage of the soil water measured in December 1986. Error bars are as described in Fig. 2

Fig. 4. Plant water potentials of *Chrysothamnus viscidiflorus* (*left frames*) and *Stipa comata* (*right frames*) individuals in the burned area without *Bromus tectorum* (*solid line*) and with *B. tectorum* (*dotted line*) as well as the long-term reference area (*dashed line*) were made during 1988. Error bars for each plot are averages of the standard errors of the mean from each date

Fig. 5. Predawn and midday water potentials of *Bromus tectorum* growing in *Chrysothamnus viscidiflorus* plots (*left frames*) and *Stipa comata* plots (*right frames*) during April and May, 1988. Diagonal bars are from plants in the burned area and crosshatch bars are from plants in the long-term reference area. Means denoted by different letters were significantly different at $P < 0.05$

soil profile was more rapid around target individuals in the burned area with *B. tectorum* than around individuals in the burned area without *B. tectorum*. Overall, soil water content of plots in the long-term reference area was more similar to that in the burned area with *B. tectorum*. For *C. viscidiflorus* plots, differences in the soil water content for individuals in the burned area with and without *B. tectorum* and the long-term reference area were significant up to 0.6 m depth (Fig. 2). *S. comata* plots in the burned area without *B. tectorum* had significantly higher soil water content than plots in the burned area with *B. tectorum* and the long-term reference area to a depth of 0.4 m (Fig. 3).

No significant differences among plots of target individuals were found for soil water content during periods of plant dormancy (September to February). No significant differences in soil water content were found due to lateral distance from target individuals (edge of the plant and 0.5 m away). Also, no significant differences were found for depths between 0.8 and 1.6 m, regardless of season.

Similar patterns of soil water depletion occurred for both target species during each growing season. Changes in soil water content through time were related to precipitation and the use of water by plants. Values for soil water content increased with precipitation and decreased during the growing season.

Plant water potential

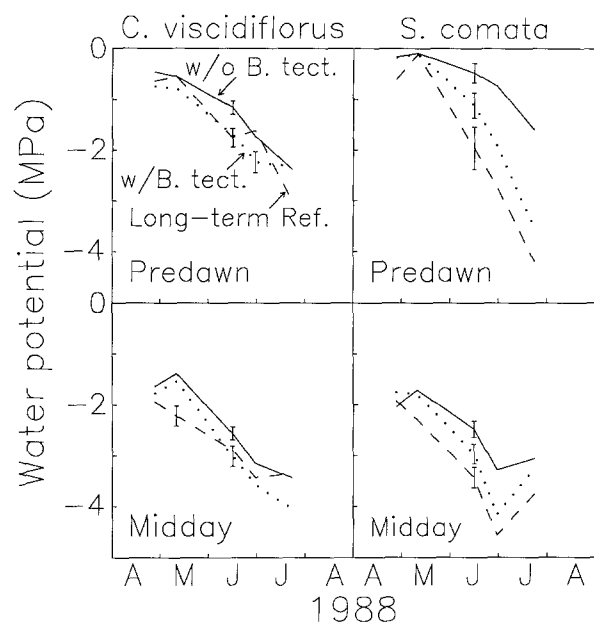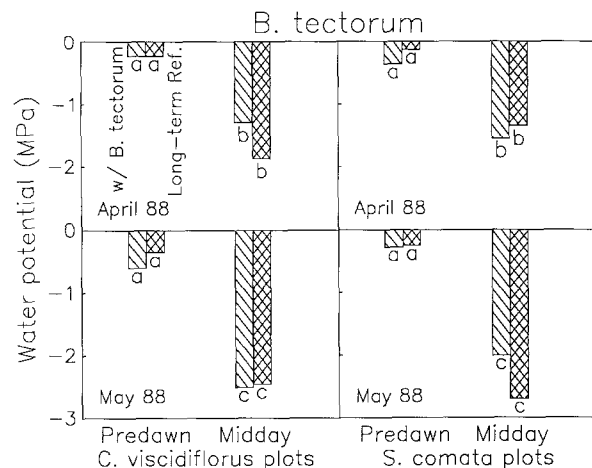Target individuals in the burned area without *B. tectorum* had significantly greater water potentials during 1988

than individuals in either the burned area with *B. tectorum* or the long-term reference area (Fig. 4). *C. viscidiflorus* individuals without *B. tectorum* were generally 0.3 MPa greater than those with *B. tectorum* and in the long-term reference area. Differences among *S. comata* treatment means were larger but had a similar pattern. Generally, target individuals in the long-term reference area had the most negative values at predawn and midday.

Table 1. Average (±standard error) standing aboveground biomass production of *Chrysothamnus viscidiflorus, Stipa comata, Bromus tectorum*, and Total (*B. tectorum* plus other species) at the end of the 1987 and 1988 growing seasons in the burned and reference areas ($N=16$ for each level of competition). Biomass for target individuals is expressed in g; *B. tectorum* and total biomass as g m^{-2}. For each target species, means within columns followed by different letters were significantly different ($P<0.05$)

Target species	Level of competition	1987		1988		
		Target spp.	*B. tectorum*	*Target spp.*	*B. tectorum*	Total
C. viscidiflorus	w/o *B. tectorum*	–	–	310±23a	–	–
	w/ *B. tectorum*	–	72±6	219±23b	27±3a	27±3a
	long-term reference	–	–	284±29ab	18±2b	34±6a
S. comata	w/o *B. tectorum*	8±1a	–	21±3a	–	–
	w/ *B. tectorum*	5±1a	67±9	10±1b	31±3a	31±3a
	long-term reference	–	–	11±2b	15±2b	26±4a

During 1988, water potentials of *B. tectorum* growing in plots in the burned and long-term reference areas were not significantly different (Fig. 5). *B. tectorum* water potential in plots around *C. viscidiflorus* was also not significantly different from that in plots around *S. comata*. For all species, changes in water potential were related to available water present in the soil. When values for soil water content declined, the values for plant water potential also decreased.

Aboveground biomass

C. viscidiflorus and *S. comata* individuals in the burned area without *B. tectorum*, which were sampled at the end of the 1988 growing season, had significantly greater biomass than individuals in the burned area with *B. tectorum* (Table 1). Aboveground biomass of *S. comata* individuals in the burned area without *B. tectorum* was not significantly different than that of individuals with *B. tectorum* in 1987, but the trend was similar to that in 1988.

During 1988, productivity of *B. tectorum* growing around target individuals in the burned area was significantly higher than *B. tectorum* productivity in the long-term reference area (Table 1). Between 1987 and 1988, there was a significant decrease in biomass production of *B. tectorum* growing around target individuals in the burned area, probably the result of extremely low precipitation during 1988 (Table 1). Biomass of other plants growing in plots around target individuals in the long-term reference area averaged 16.3 g m^{-2} for *C. viscidiflorus* plots and 11.3 for *S. comata* plots. These other plants included additonal plants of the two target species as well as plants of *A. tridentata, T. canescens, S. hystrix*, and *Oryzopsis hymenoides* (R. & S.) Ricker.

B. tectorum tiller density

Densities of *B. tectorum* in plots around target individuals were significantly higher in 1988 than in 1987. However, no differences were found between the burned and the long-term reference areas in either growing season (Fig. 6).
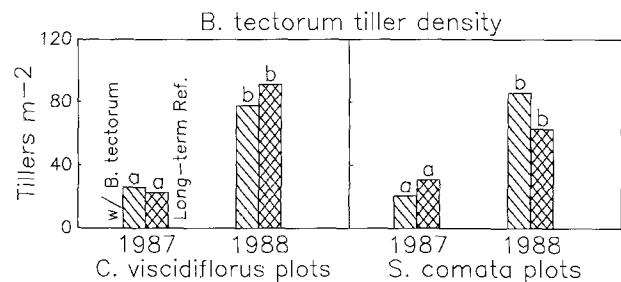

Fig. 6. *Bromus tectorum* tiller density during 1987 and 1988 around *Chrysothamnus viscidiflorus* plots (*left frame*) and *Stipa comata* plots (*right frame*). Diagonal bars are individuals in the burned area and crosshatch bars are individuals in the long-term reference area. Means denoted by a different letter were significantly different at $P<0.05$

Water use efficiency

$\delta^{13}C$ ratios were not significantly different among target individuals in the burned areas and the long-term reference area. $\delta^{13}C$ ratios of *C. viscidiflorus* individuals in the burned area without *B. tectorum* averaged −25.7; in the burned area with, −25.9; and in the reference area, −26.0. $\delta^{13}C$ ratios for *S. comata* in both the long-term reference area and in the burned area without *B. tectorum* averaged −24.5 whereas those with *B. tectorum* were −24.9.

Discussion

Competition between *B. tectorum* and adult perennial plants occurred during the first two years after fire. Plots around native individuals in the burned area with *B. tectorum* had a faster depletion of soil water during the periods of active growth of *B. tectorum* (April and May) than plots around individuals without *B. tectorum*. Further evidence that *B. tectorum* used soil water that could have been used by the native species comes from an interaction term in the ANOVA's: the treatment X lateral distance from the edge of the native species. For each native species, this interaction term was *not* significant. Thus, soil water located at both the edge and 0.5 m from

the edge of the target individual was utilized regardless of whether *B. tectorum* was present or absent. Finally, competition with *B. tectorum* negatively affected the productivity and water status of native perennial species.

The presence of *B. tectorum* also has important long-term implication for its neighbors. Effects of *B. tectorum* competition were evident during the first two growing seasons following the burn. Furthermore, results from the long-term reference area were more similar to the burned area with *B. tectorum* than the burned area without *B. tectorum*. Thus, effects on biomass production and water status of native species were linked to competition with *B. tectorum* rather than to the length of time after fire. Once established in the open spaces around native species, *B. tectorum* is thus able to suppress the water status and productivity of native species for an extended period of time. Dominance of *B. tectorum* is also enhanced by its greater grazing tolerance (Mack 1981; Pyke 1987).

Water use efficiency of the native species was not affected by *B. tectorum* competiton. Modifications in water use efficiency of native species may help counteract the competition from *B. tectorum* for soil water: if increased water use efficiency is accompanied by decreased transpiration rates, then soil moisture would be conserved. However, modification of these physiological traits has a potential disadvantage: if the native species use less water by being more efficient, more soil water may then be available to the competitor *B. tectorum*.

Post-fire vegetation dynamics may also be influenced by competition for soil nutrients. For example, the application of fertilizers greatly enhances the productivity of *B. tectorum* (Eckert and Evans 1963), even when co-occurring perennial species are inhibited (Kay and Evans 1965; Wilson et al. 1966). Burning converts plant biomass into ash, which releases nutrients, especially P, Mg, K and Ca, into plant-available forms (Raison 1979; Wright and Bailey 1982). Nitrogen availability may also increase in the upper soil profile, but this increase in inorganic nitrogen is very transitory in sagebrush steppe communities (Hobbs and Schimel 1984). Although mechanisms that enhance water uptake can also enhance nutrient uptake (Caldwell and Richards 1986), further research would need to be conducted to determine the relative importance of competition for soil nutrients released by fire.

B. tectorum is well adapted to fire and often dominates plant communities after fire (Wright and Klemmedson 1965; Young et al. 1969). Its annual life-form coupled with the abilities to germinate readily over a wide range of moisture and temperature conditions, to quickly establish an extensive root system, and to grow early in the spring, contribute to its successful colonization (Harris 1967; Bookman 1982; Mack and Pyke 1983). Thus, the success of *B. tectorum* after fire is partially due to its ability to rapidly occupy the open spaces created by the removal of fire-intolerant plants. Although some native species also exhibit this trait, previous studies in the greenhouse and the field indicate that *B. tectorum* effectively competes with seedlings of

perennial species (Hull 1963; Harris 1967; Evans et al. 1970; Harris and Wilson 1970). In addition, we show that *B. tectorum* successfully competes with the native species that survive fire, despite these plants being well-established adult individuals able to reach deeper levels in the soil. Adverse effects on the productivity and water status of adult perennial plants were evident during the growing season of a year with 95% of normal precipitation (1987) as well as one with 50% of normal precipitation (1988). This competitive ability of *B. tectorum* also contributes towards its post-fire dominance.

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