

RESPONSE OF SAGEBRUSH STEPPE SPECIES TO ELEVATED CO₂ AND SOIL TEMPERATURE

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ABSTRACT.—Elevated atmospheric CO₂ may cause long-term changes in the productivity and species composition of the sagebrush steppe. Few studies, however, have evaluated the effects of increased CO₂ on growth and physiology of species important to this ecosystem. Since the response of plants to elevated CO₂ may be limited by environmental factors, soil temperature was also examined to determine if low soil temperatures limit CO₂ response. To determine how CO₂ and soil temperature affect the growth of species native to the sagebrush steppe, bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], Thurber needlegrass (*Stipa thurberiana* Piper), and Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle) were grown in ambient (374 mL L⁻¹) or high (567 mL L⁻¹) CO₂ and low (13°C) or high (18°C) soil temperature for approximately 4 months. Although soil temperature affected the growth of squirreltail and needlegrass, temperature did not modify their response to elevated CO₂. Total biomass of sagebrush was consistent across soil temperature and CO₂ treatments, reflecting its slow-growing strategy. All 3 species had higher leaf water-use efficiency at elevated CO₂ due to higher net photosynthesis and lower transpiration rates. We conclude that elevated CO₂ and soil warming may increase the growth of grasses more than shrubs. Field studies in the sagebrush steppe are necessary to determine if differences in biomass, resulting from changes in CO₂ and soil temperature, are exhibited in the field.

Key words: elevated CO₂, soil temperature, *Artemisia tridentata*, *Stipa thurberiana*, Sitanion hystrix.

Sagebrush steppe, a major vegetation type occupying approximately 45 × 10⁶ ha in the western United States, has undergone long-term changes in species composition due to overgrazing and introduction of exotic plants (West 1983). Increasing atmospheric CO₂ may also cause long-term changes in species composition and productivity of rangelands (Mooney et al. 1991, Polley 1997, Campbell et al. 2000, Smith et al. 2000, Morgan et al. 2001).

Only a few studies to date have quantified how elevated CO₂ affects the growth and physiology of grasses and shrubs common to semi-arid systems. In one study CO₂ enrichment increased leaf weights of 3 grasses; water-use efficiency was higher at elevated CO₂ due to reduced stomatal conductance and higher net photosynthesis (Smith et al. 1987). Elevated CO₂ increased shoot biomass of *Artemisia tridentata* (Nutt.), but effects on leaf area and root:shoot ratios were inconclusive (Johnson and Lincoln 1990, 1991). In another study elevated CO₂ increased root but not shoot biomass of *Artemisia tridentata* (Klironomos et al.

1996). In the field elevated CO₂ increased net photosynthesis (Morgan et al. 1994) and growth (Morgan et al. 2001) in plants native to the short-grass steppe. Elevated CO₂ increased shoot production by 50% in a desert shrub community in a high-rainfall year (Smith et al. 2000).

Predicting how elevated CO₂ will affect the sagebrush steppe may be complicated by the 2°–5°C global increase in air and soil temperature expected by 2300 (IPCC 2001). In one study in California annual grassland, the effect of CO₂ on growth was higher in ambient than elevated temperature plots (Shaw et al. 2002), whereas in the short-grass steppe the CO₂ response was higher at elevated temperatures (Coughenour and Chen 1997). Most studies of global warming test the simultaneous effects of increased soil and air temperature, but few have independently tested the effects of elevated soil temperature and CO₂ on plant growth. In tomato (*Lycopersicon esculentum* Mill.), there were interactive effects of CO₂ and root temperature on root but not shoot biomass (Yelle et al. 1987). No interactive effects

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were found in root or shoot growth of tussock sedge (*Eriophorum vaginatum* L.; BassiriRad et al. 1996).

The effects of soil temperature on growth may differ between grasses and shrubs. Soil temperature may alter growth and competition by favoring the shoot growth of grasses, since their apical meristems are located at the soil surface (Engels 1994). Although the effects of soil temperature on plant growth may depend on growth form, the effects of elevated CO₂ are also dependent on growth rates, with higher growth stimulation in fast- than slow-growing species (Poorter 1993). This could be particularly detrimental to degraded rangelands if fast-growing invasive species such as cheatgrass are stimulated by elevated CO₂ (Smith et al. 1987, 2000).

The objective of this study was to determine how atmospheric CO₂ concentration and soil temperature affect the growth and physiology of 3 species native to the sagebrush steppe. To isolate the effects of soil warming, we exposed seedlings to different soil temperature treatments while keeping the air temperature constant. We hypothesized that (1) elevated CO₂ and elevated soil temperature would increase root, shoot, and total biomass, (2) low soil temperatures would limit growth responses to CO₂, and (3) elevated CO₂ would increase water-use efficiency of all 3 species. We also hypothesized that the fast-growing grass, bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], would be the most responsive to CO₂; Thurber needlegrass (*Stipa thurberiana* Piper), a slow-growing grass, would be intermediate in its response; and the slow-growing shrub, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle), would be the least responsive. We also expected soil temperatures to have a greater effect on grasses than shrubs.

METHODS

Seed Collection and Propagation

Seeds from Wyoming big sagebrush, bottlebrush squirreltail, and Thurber needlegrass were collected from the Northern Great Basin Experimental Range (199°43'W, 43°29'N) in Harney County, Oregon, in November 1993. In March 1994 we initially planted seeds in flats. Soil medium was a 3:1 mixture of steril-

ized coarse river sand and soil obtained from the experimental range (coarse to fine sandy loam Holte-Milican complex; Lentz and Simonson 1986). Flats were placed in continuously stirred tank reactors (CSTR) with a 16-hour photoperiod and constant day (24°C) and night (15°C) temperatures. In April we transplanted 2 seedlings of each species into pots (10 × 10 × 25 cm) containing the soil mixture. The pots were thinned to 1 seedling. After soil analysis in April revealed that percentage nitrogen in pots was lower than N at the Northern Great Basin Experimental Range, we subsequently fertilized the plants each week with 57 mM nitrogen, 10 mM phosphorus, and 17 mM potassium.

Experimental Design

This experiment was a split-plot design in which the CSTR was designated as the whole plot. At the whole-plot level, 6 CSTR chambers were randomly allocated to ambient (374 ppm) and 6 chambers to high CO₂ (567 ppm) treatment. These conditions reflected the local concentration of atmospheric CO₂ and the predicted CO₂ concentration in the year 2050 (IPCC 2001). Within each CO₂ treatment, 3 chambers were randomly assigned high (18°C) and 3 were assigned low (13°C) soil temperatures. The low soil temperature treatment reflects average soil temperature in March at a sagebrush site in south central Washington (Black and Mack 1986), while the high soil treatment represents a 5°C increase in temperature predicted by 2300 (IPCC 2001). This design allowed for 3 replicates of each CO₂ and soil temperature treatment combination. At the subplot level, each chamber contained 36 pots (12 pots per species per chamber).

Treatment Conditions

During the experiment, the 12 CSTR chambers were maintained at a relative humidity of 48% (Humicap, HMD 20, Vaisala Sensor Systems, Woburn, MA) using a steam generator (EHU-500, Armstrong Machine Works, Three Rivers, MI). Chambers were illuminated by 1000-W metal halide lamps that subjected seedlings to photon flux of 600 μmol m⁻² s⁻¹ (SB-190 Quantum Sensors, LI-COR, Inc., Lincoln, NE) and a 16/8 hour light/dark period. Air temperatures were maintained at 15°C during the dark period and at 24°C during the light period.

Soil temperature was regulated independently of air temperature by using a root chiller located at the base of each chamber. In addition, a foam septum within each chamber limited the mixing of air between the roots and shoots. Soil temperature was measured hourly at a depth of 10 cm. Chambers allocated to the low soil temperature treatment were maintained at $13 \pm 1^\circ\text{C}$ ($s_{\bar{x}}$), while the high temperature chambers had an average root temperature of $18 \pm 2^\circ\text{C}$.

Low CO_2 chambers were maintained at CO_2 concentrations of 374 ± 24 ppm, while high CO_2 chambers averaged 567 ± 5 ppm. To ensure adequate water supply for each species, we watered seedlings every other day to field capacity. Two pots of each species were randomly selected and watered until water was observed at the base. The volume of water added to each pot was averaged between the 2 plants, and the average volume of water was added to all plants of that species.

Gas Exchange Analysis

To compare physiological responses with CO_2 and soil temperature between species, gas exchange measurements were taken before harvest. Photosynthesis, transpiration, and water-use efficiency were measured using a LI-COR 6200 Portable Photosynthesis System (LI-COR, Inc., Lincoln, NE) on the most recently emerged, fully expanded leaf of 9 randomly selected plants from each treatment. Measurements were taken 3 times daily on 20, 26, and 30 June. A small window in the chamber door allowed for gas exchange measurements within the CSTR.

Growth Analysis

Plants were harvested in July, approximately 127 days after planting. Squirreltail and needlegrass were separated into shoots and roots, and sagebrush was separated into stems, leaves, and roots. We then oven-dried this material at 60°C for 72 hours. Root:shoot (R:S) ratios were calculated for each plant, and leaf area was measured on a random sample of the population (9 plants per species per treatment) using a LI-3000 Portable Area Meter (LI-COR, Inc., Lincoln, NE).

Statistical Analysis

To determine the effects of CO_2 and soil temperature on total plant weight, shoot weight,

root weight, and leaf area, we analyzed data using the generalized linear models (GLM) procedure in SAS with error terms dictated by the split plot design. When species interactions were significant at the $P < 0.05$ level, we analyzed the effects of CO_2 and temperature separately by species. Gas exchange measurements were averaged over the 3 days (24, 26, and 30 June) and analyzed using GLM.

RESULTS

Effects of Elevated CO_2

Total biomass of both grasses, squirreltail and needlegrass, was higher at elevated CO_2 , whereas biomass was similar between CO_2 treatments for the slow-growing shrub, sagebrush (Fig. 1). Since squirreltail has a higher growth rate than needlegrass, we expected CO_2 enrichment would stimulate the growth of squirreltail more than needlegrass. Contrary to our hypothesis, elevated CO_2 had similar effects on squirreltail and needlegrass; CO_2 enrichment increased their total growth by 14% and 11%, respectively.

Elevated CO_2 significantly increased root growth of needlegrass but not squirreltail or sagebrush (Fig. 1). Elevated CO_2 did not significantly affect shoot growth. Needlegrass was the only species in which CO_2 significantly affected R:S ratios. At ambient CO_2 , R:S ratios averaged 0.39 but were 0.55 at elevated CO_2 . Carbon dioxide concentrations had no impact on leaf area or leaf thickness (data not shown).

As expected, leaf water-use efficiency was significantly higher at elevated CO_2 in all species (Fig. 2). This increased efficiency resulted from higher photosynthetic rates and lower transpiration rates in response to high CO_2 , although these effects taken separately were not statistically significant.

Effects of Soil Temperature

Higher soil temperature significantly increased the root and total plant weights of squirreltail and needlegrass and the shoot weights of needlegrass (Fig. 3). Surprisingly, soil temperature stimulated total growth of slow-growing needlegrass by 48% while increasing growth of slow-growing squirreltail by only 18%. Sagebrush was not significantly affected by soil temperature. Soil temperature

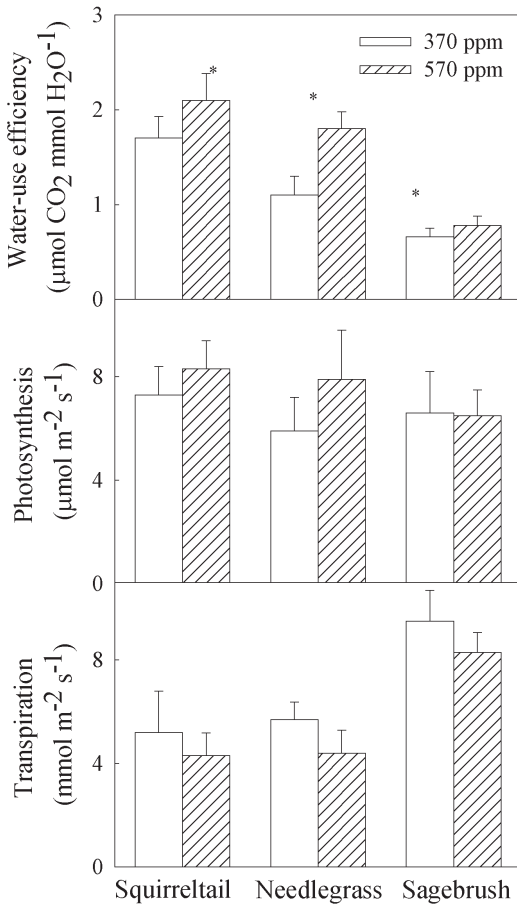


Fig. 1. Mean total plant, shoot, and root weights of squirreltail, needlegrass, and sagebrush exposed to ambient (370 ppm) or high (570 ppm) CO₂. Error bars indicate standard errors. *N* = 69–72 plants.

had no effect on photosynthesis, transpiration rates, or water-use efficiency (data not shown) and did not significantly modify the response to CO₂ in any of the species. However, trends indicate that growth stimulation of roots and shoots may be higher at low soil temperatures.

DISCUSSION

The effects of elevated CO₂ on growth are often dependent on potential growth rates, with higher stimulatory effects of CO₂ in fast- than slow-growing species (Poorter 1993). As predicted, elevated CO₂ increased biomass of squirreltail and needlegrass more than that of sagebrush. Unexpectedly, the growth of fast-

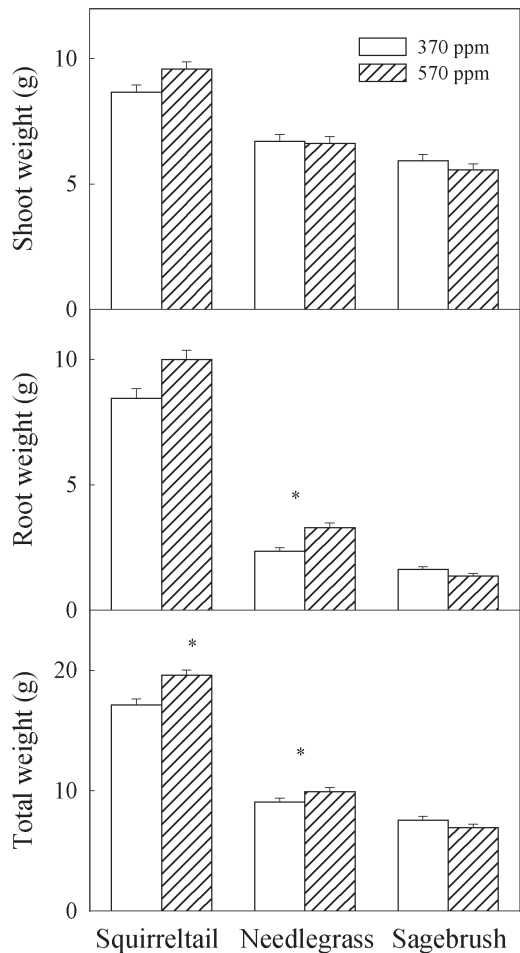


Fig. 2. Mean water-use efficiency, photosynthetic rate, and transpiration rate of squirreltail, needlegrass, and sagebrush exposed to ambient (370 ppm) or high (570 ppm) CO₂. Error bars indicate standard errors. *N* = 6 plants.

growing squirreltail at elevated CO₂ was statistically indistinguishable from that of slow-growing needlegrass. Since CO₂ stimulated the growth of grasses more than shrubs, increased CO₂ may lead to changes in seedling competition between these 2 growth forms.

Higher overall biomass of squirreltail and needlegrass at elevated CO₂ was primarily due to root growth, although CO₂ increased root biomass significantly only in needlegrass. Sagebrush root biomass was similar between CO₂ treatments, which agrees with a previous study (Johnson and Lincoln 1991). These results, however, disagree with another study that found sagebrush root biomass was higher at elevated

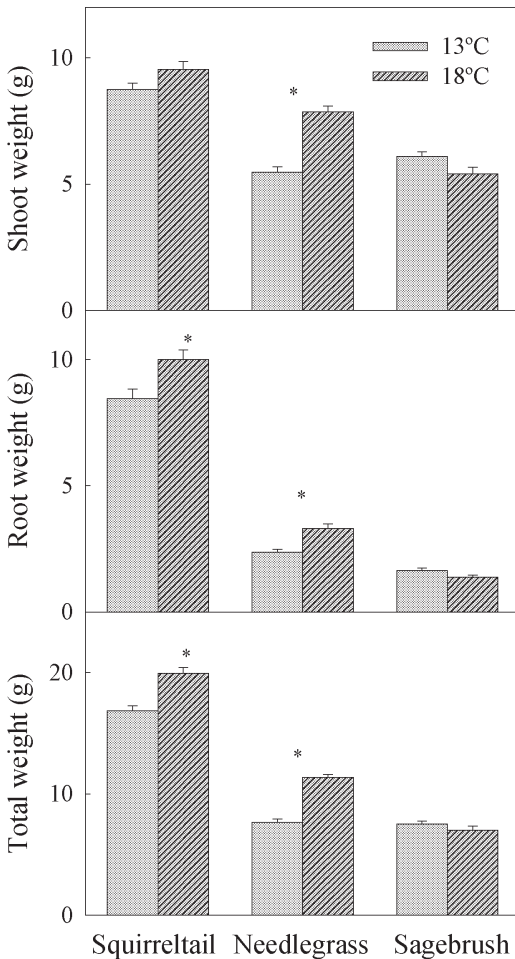


Fig. 3. Mean total plant, shoot, and root weights of squirreltail, needlegrass, and sagebrush exposed to low (13°C) or high (18°C) soil temperature. Error bars indicate standard errors. $N = 69$ –72 plants.

CO₂ (Klironomos et al. 1996). Elevated CO₂ affected R:S ratios of needlegrass but not squirreltail or sagebrush. Among rangeland species, there is no consistent pattern of carbon allocation in response to elevated CO₂ since some species increase (Smith et al. 1987, Larigauderie et al. 1988), decrease (Johnson and Lincoln 1991), or have no change (Johnson and Lincoln 1990) in their R:S ratios.

Although previous studies indicate that CO₂ stimulates shoot growth by 10%–150% in species native to the sagebrush steppe (Smith et al. 1987, Johnson and Lincoln 1990), we found no significant effects of CO₂ on shoot biomass or leaf area. In particular, we expected

shoot weights of sagebrush to increase with elevated CO₂ as found in a previous study with *Artemisia tridentata* ssp. *tridentata* (Johnson and Lincoln 1990) grown at 650 $\mu\text{L L}^{-1}$ for 3 months. *Artemisia tridentata* ssp. *wyomingensis*, used in this study, has slower growth rates (Bonham et al. 1991) and therefore may be less responsive to CO₂ than *Artemisia tridentata* ssp. *tridentata*. Although not significant, photosynthesis was higher at elevated CO₂ as previously found in many studies with range plants (e.g., Larigauderie et al. 1988).

We found that elevated CO₂ increased water-use efficiency of all 3 species, confirming previous studies with crop and rangeland plants (Kimball and Idso 1983, Dahlman et al. 1985, Larigauderie et al. 1988, Jackson et al. 1994). Needlegrass exhibited a 40% greater increase in water-use efficiency than sagebrush or squirreltail at elevated CO₂. Since water is often limiting in rangelands, small increases in water-use efficiency of seedlings may cause relatively large changes in seedling survival and competition between species. Therefore, alterations in water-use efficiency in response to CO₂ enrichment may cause relatively large changes in the structure of rangelands (Polley 1997).

Soil temperature plays an important role in determining community composition of the sagebrush steppe (West 1983) and tallgrass prairie (DeLucia et al. 1992). High soil temperature increases growth rates (Benzioni and Dunstone 1988) and photosynthetic (Bassiri-Rad et al. 1993) rates of rangeland plants. As predicted, soil temperature increased total growth of both grasses, needlegrass and squirreltail. Sagebrush had consistent total and root growth across soil temperature treatments, confirming germination trials that indicate its ability to tolerate a broad range of soil temperatures ranging from 10° to 30°C (McDonough and Harniss 1974).

We expected high soil temperatures to affect shoot growth of both grasses (Larigauderie et al. 1991, Engels 1994), but soil warming significantly increased shoot biomass only of needlegrass. Although higher soil temperatures have been reported to increase net photosynthesis (Duke et al. 1979, Day and Heckathorn 1991, Vapaavuori et al. 1992) and decrease transpiration rates (Benzioni and Dunstone 1988), we found no significant changes in physiology in response to soil temperature. This could be due to the small sample size in our study or the

small difference (5°C) between soil temperature treatments.

These results suggest that elevated CO₂ will stimulate the growth of squirreltail and needlegrass seedlings more than sagebrush, under conditions where water and nutrients are not limiting. Since soil temperatures did not affect growth responses to CO₂, diurnal and seasonal changes in nutrient and water availability may play a more important role in regulating responses to CO₂. Since the plants in this study were harvested after 4 months to prevent root restriction in the pots, additional studies are needed to assess how elevated CO₂ will affect mature individuals in the field.

CONCLUSIONS

This study suggests that elevated CO₂ and soil temperature have the potential to alter growth and carbon partitioning of seedlings in the sagebrush steppe. In addition, elevated CO₂ and soil warming may affect grasses more than shrubs. These controlled environment studies should pave the way for field studies in the sagebrush steppe to determine whether differences in carbon allocation, resulting from changes in CO₂ and soil temperature, are exhibited in the field. Alterations in growth and carbon allocation in response to elevated CO₂ may potentially alter the competitive relationships between species and influence successional processes in the sagebrush steppe.

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