

MOUNT ST. HELENS ASH: RECREATING ITS EFFECTS ON THE STEPPE ENVIRONMENT AND ECOPHYSIOLOGY¹

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Abstract. The 18 May 1980 ash fall from Mount St. Helens was experimentally reproduced in May 1982 by applying silt-sized ash to a stand of the *Artemisia tridentata*/*Agropyron spicatum* association in south-central Washington. Compared to the adjacent control site, ash caused an immediate increase in albedo from 13% to 28%, while other parameters of the energy budget were simultaneously lowered: net radiation by $\approx 20\%$, soil surface temperatures by as much as 10°C , and soil heat flux by as much as 50%. The ash's mulching action initially increased water availability and delayed leaf abscission in *Artemisia tridentata* (Big sagebrush) by 2 wk in summer 1982. But after summer 1982 water availability declined, while water use increased, illustrating the diverse effects of the ash. Increased reflection from the ash-covered surface increased the radiation load on plant canopies. In turn, air temperature at 0.5 m increased, latent heat flux often doubled in summer, and xylem pressure potentials decreased. Available water at the -1 m soil depth eventually decreased as much as 40%. This decrease was the result of the increase in latent heat flux and the decline in infiltration through the stratified layer created by the ash cap. The sudden alteration of the soil surface by an ash layer revealed the close coupling of the water use of *A. tridentata* with available soil water. In summer in both 1982 and 1983, predawn xylem pressure potentials declined as soil water potentials approached -4.5 MPa on both sites. Total shrub leaf area index routinely decreased 75% as large (> 2 cm long) spring-emergent leaves were shed. Highest leaf conductance (0.3 to 0.5 s/cm) and highest transpiration occurred among the remaining smaller (< 2 cm long) leaves after leaf abscission in spring. Water conservation through leaf area reduction followed by high transpiration rates apparently allows the development of inflorescences during the dry, hot summer, culminating in autumn flowering and seed maturation. *Lupinus sulphureus* on the ash-covered surface exhibited no difference from conspecifics on the control site in xylem pressure potentials, but did have higher leaf conductances during the 1st yr following the ash fall; no differences were observed in the 2nd yr. *Lupinus sulphureus* aestivated ≈ 2 wk earlier on control sites the 1st yr following ash deposition. The responses to ash that we measured were probably the maximum expressed by Big sagebrush; the thin layer of ash to the east and the coarse-textured ash to the west did not significantly alter the movement of water. Short-term increases in *A. tridentata* in the Pacific Northwest ≈ 6700 yr BP may have been caused by similar decreases in soil temperature and increases in aridity with the deposition of Mazama ash. In addition to allowing assessment of the effects of the 18 May 1980 ash fall on arid steppe, application of ash provided an unexpected level of precision in detecting the often subtle effects that occur when some microenvironmental parameters change while the overall macroclimate remains the same.

Key words: albedo; *Artemisia tridentata*; ecophysiology; energy budgets; *Lupinus sulphureus*; Mount St. Helens; mulch; phenology; steppe; volcanic ash; xylem pressure potentials.

INTRODUCTION

Any alteration in the environment that affects water use, such as a change in the radiant energy budget, may be rapidly expressed in plant growth and survival (Geiger 1965, Hinds 1975). Such interactions between radiant energy and plant water use can be modified by the soil's reflectivity. For example, the lowering of surface albedo following fire raises soil temperatures (Rouse and Kershaw 1971) and often alters seedling establishment (Black and Bliss 1980). In contrast, when the albedo of soil is raised (as with application of kaolin), the soil temperature declines, while the temperature of

the overlying canopy may rise through reflectance (Fuchs et al. 1976).

Water availability, as the other component of water balance, can be altered independently of the energy environment. Covering the soil surface, by applying a mulch, for example, may radically alter infiltration or evaporation, but once water has entered the soil profile the surface layer may be an important barrier to evaporation (Geiger 1965, Miller 1981). Any alteration of water availability becomes especially important in arid environments.

Much of the arid Columbia Basin of central and eastern Washington was covered by silt-sized or finer ash from the 18 May 1980 eruption of Mount St. Helens in Skamania County, Washington (Sarna-Wojcicki et al. 1981). Compared to the soil surfaces it covered,

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the ash has a higher albedo and a roughly equivalent textural class (Mack 1986). The bulk density of the uncompacted ash in the central part of the Columbia Basin was $\approx 0.6 \text{ g/cm}^3$, but it approximately doubled within 2 mo after deposition due to compaction (Sarna-Wojcicki et al. 1981).

With the ash falling along a northeasterly axis (Sarna-Wojcicki et al. 1981), unaffected areas were both north and south of the fallout area. This distribution was viewed initially as an opportunity to monitor plant response at potential "treatment" and "control" sites on equivalent habitats in the steppe of Washington (Mack 1981). But such direct comparisons were hampered by the variation in weather between sites that were often $> 100 \text{ km}$ apart. Consequently, in our experiment we duplicated the conditions of the 18 May ash fall so that a site's microenvironment was altered by ash while continuing to share the macroenvironment with an adjacent control site.

We asked questions at several levels about the effect of this ash. First, we asked simply whether the ash had affected the ecophysiology of perennial plants. Since *Artemisia tridentata* dominates much of this steppe and *Lupinus sulphureus* is a common perennial forb, the ecophysiology of these species became the focus of our study. Given the aridity of the steppe environment, this initial question led us to focus also on whether the ash had altered either water use or water availability beyond the annual variations caused by weather. Because water use depends upon a site's energy budget, we investigated potential alteration in water use by simultaneously measuring plant water relations and the energy budget. Typologically these questions have been addressed elsewhere for arid land perennials (Cunningham and Strain 1969, Moore et al. 1972, Oechel et al. 1972), but, in contrast to many other ecophysiological investigations at field sites, in our study the ability to detect plant response was not dependent on the change in weather between consecutive growing seasons, such as "wet" and "dry" years (e.g., Campbell and Harris 1977), or on the manipulation of soil moisture, such as with rain-out shelters (Federer and Gee 1976).

Finally, we recognized the opportunity provided by this event to examine heretofore untestable hypotheses regarding the direct effects of Quaternary ash falls on regional vegetation (Mehring et al. 1977, Mack et al. 1978) and on the physical environment. The accompanying alteration of surface reflectivity with ash deposition has even been predicted as a prelude to climatic change, including the initiation of glaciation (Bray 1979).

MATERIALS AND METHODS

The study area (elevation 446 m) was on the Arid Lands Ecology (ALE) Reserve (southeast quarter, S.34 T11N R26E, Iowa Flats Quadrangle, 46°23'30" N, 119°32'08" W) of the United States Department of

Energy's Hanford Reservation in Benton County, Washington. The area is within the *Artemisia tridentata*/*Agropyron spicatum* habitat type (sensu Daubenmire 1970). The ALE Reserve was subject to livestock grazing earlier in this century, but public access has been prohibited since 1943. Although fires have occurred locally, the area throughout our study supported a mature community with adult *A. tridentata* (Big sagebrush) and *A. spicatum*.

The ALE Reserve received an inconsequential amount of ash ($< 1 \text{ mm}$) directly from the Mount St. Helens ash fall on 18 May 1980 (day 138 of year); in 1982, at the time of our study, it was environmentally equivalent to other locations in the Columbia Basin as they had been prior to the deposition of substantial amounts of ash in May 1980. We experimentally covered a site on the Reserve with ash on 18 May 1982 by applying 21 Mg of tephra from the May 1980 ash fall of Mount St. Helens. The ash, with a textural class of silt loam, had been collected from a landfill near Ritzville, Washington (Adams County), where it had lain unaltered by soil mixing since shortly after May 1980. This tephra was applied aerially from above the plant canopy and spread with hand tools to form a 27 m diameter disc of ash; the depth of ash (up to 70 mm) approximated the thickest accumulation that had occurred in the steppe (also near Ritzville) on 18 May 1980 (Sarna-Wojcicki et al. 1981).

Given the scale of the experiment, use of one disc of ash was the only feasible option in our experimental design. This obvious lack of replicates limited our use of inferential statistics to site comparisons only; for treatment effects we indicate only trends. Separate regression analyses of environmental data were used to compare the two sites both before and after the application of ash (cf. Hurlbert 1984).

Meteorologic instrumentation was installed on both the experimental and a control site 7 mo before our experiment; these sites were 50 m apart. Air temperature (above the soil surface, at +1.5, +0.5, and +0.05 m), soil temperature (below the surface, at -0.1 and -1.0 m), soil heat flux (at -2 cm), net radiation (at +2.0 m, $\approx 1 \text{ m}$ above the canopy of *A. tridentata*), and total solar radiation were recorded hourly. Air temperatures were measured with shielded thermistors (Fenwal, Model UUT 51J1), while soil temperatures were measured with unshielded thermistors. Soil heat flux (G) measurements were made with plates fabricated from thermopiles (Melcor, Model CP 1.4-71-10L) (G. S. Campbell, *personal communication*). Net radiation (R_n) was measured with a Fritschen-style net radiometer (Micromet Instruments); total solar radiation (S) was measured with a pyranometer (LI-COR LI-200S). Each site's sensible heat flux (H) was calculated from its temperature profile while using the same estimate of resistance to heat flux for both sites. Latent heat flux (λE) was estimated by difference using the equation: $0 = R_n + H + \lambda E + G$. Potential evapo-

transpiration (E_p) was calculated using a modified Penman equation (Campbell 1977). Precipitation was recorded continuously with a tipping-bucket rain gauge (Edmund Scientific). Data from all sensors were stored in the field on magnetic tapes with Campbell Scientific CR21 Microloggers. Surface temperatures were measured periodically using a Barnes infrared thermometer. Soil water potential and water content were determined by psychrometric (Campbell 1979) and gravimetric techniques, respectively, about every 4 wk during summer at -0.2 and -1 m. Albedo was calculated as the ratio of reflected to incoming shortwave radiation and was measured with the LI-COR pyranometer.

Ecophysiological measurements were made approximately every 4 wk on *A. tridentata* and *Lupinus sulphureus* (lupine) beginning in April and continuing through September in 1982 and 1983. Measurements on two *A. tridentata* shrubs (three samples per plant) and on six lupines (one sample per plant) were taken on each site at predawn and at solar 0900, 1200, 1500 and 1800. Only xylem pressure potential was measured during the predawn sampling; xylem pressure potential (ψ), leaf conductance (g_{wn}), photosynthetic photon flux density (PPFD), air temperature (T_a), leaf temperature (T_l), and vapor density of air were measured during all other sampling periods.

Leaf conductance was measured with a steady-state porometer (Campbell 1975). Conductances for *A. tridentata* were measured repeatedly at each sample period on the same 5–10 cm long branches; each branch supported 20–50 leaves. Only branches from the upper canopy (south side) were used. These branches were harvested at the end of the day, and one-sided leaf area was determined with a leaf area meter (LI-COR 3100). Conductances for *L. sulphureus* were measured on single leaves selected from plants that were uniformly distributed over the site and that had received full exposure to solar radiation; each plant was sampled only once on a sampling date. After each measurement leaves were harvested and leaf areas determined.

Xylem pressure potentials of *A. tridentata* were measured with a pressure chamber (PMS) (Ritchie and Hinckley 1975) on 5–10 cm long branches (20–50 leaves each) that had been excised near the branches used for conductance measurements. Xylem pressure potentials of *L. sulphureus* were measured on the same leaves used for conductance measurements. Leaf and air temperatures and PPFD were measured with fine-wire (0.025 mm, Omega) thermocouples and with a quantum sensor (LI-COR LI-190SB), respectively, connected to a microvoltmeter (Wescor, MJ-55). Vapor density of air was measured with a sling psychrometer.

RESULTS

Addition of the ash brought about immediate changes in the energy balance of the experimental site and caused decreases in water availability through increased run-

off. However, these decreases were masked in the 1st yr after application of ash by the ash's apparent mulching action on a recharged soil profile. This mulching increased soil water retention through lowered soil temperatures and apparent decreases in direct evaporation from the soil. The ecophysiology and phenology of *Artemisia tridentata* and *Lupinus sulphureus* changed synchronously with these environmental reversals.

Environmental measurements

Energy balance.—Monthly totals of shortwave radiation received on the sites ranged from 40 to 732 MJ·m⁻²·mo⁻¹ in 1982 and from 91 to 797 MJ·m⁻²·mo⁻¹ in 1983 (Table 1). The maximum intensities observed in 1982 and 1983 were 1062 and 1281 W/m², respectively. Before ash deposition, net radiation had been significantly ($P < .001$) higher on the experimental site than on the nearby control site (Fig. 1a). Immediately following ash deposition, however, net radiation on the experimental site decreased 20% during daylight hours (Fig. 1b); little difference was apparent at night. In addition, monthly totals of net radiation were at least 20% lower on the ash-covered site than on the control (Table 1). These differences in energy flux were most apparent during summer and became negligible during winter. Albedo doubled following ash deposition ($\bar{X} \pm \text{SD}$: $28.8 \pm 1.2\%$, ash-covered site; $13.5 \pm 1.9\%$, control site; $n = 340$).

The daytime soil heat flux on the experimental site, which at first was significantly ($P < .001$) higher than on the control site, was halved by the addition of ash (Fig. 1b); little difference between the sites was apparent at night. During summer, monthly totals of soil heat flux on the ash-covered site were also $\approx 50\%$ of the totals from the control site (Table 1). Addition of ash also extended the duration of negative soil heat flux for 1 mo in both spring and autumn versus the control site. These changes in the magnitude and direction of net radiation, soil heat flux, and albedo persisted throughout the study.

As with soil heat flux, sensible heat flux on the experimental site was slightly higher than on the control site for 2 wk before 18 May 1982 but was as much as one order of magnitude lower following ash deposition (Table 1). Estimates of latent heat flux (Table 1) were similar on the experimental and control sites for 2 wk before deposition of ash and during spring 1983. Latent heat flux became lower on the control than on the experimental site in June in 1982 and 1983 and remained low throughout the rest of each year. Compared to the control site, latent heat flux on the ash-covered site was nearly twice as high throughout June and July in 1982 and 1983. Throughout both years Bowen ratios for the ash-covered site changed less and did not exhibit the marked increase in summer seen on the control site. Bowen ratios increased on the control site in June and July, indicating increased sensible versus latent heat flux.

TABLE 1. Monthly summaries of energy exchange* for the control and the experimentally ash-covered sites in Benton County, Washington. Ash was experimentally added on 18 May 1982 (day 138 of year).

Month	<i>S</i>	<i>R_n</i>		<i>G</i>		<i>H</i>		λE		Bowen ratio†		<i>E_p</i>
	Con- trol	Ash- cov- ered	Con- trol	Ash- cov- ered	Con- trol	Ash- cov- ered	Con- trol	Ash- cov- ered	Con- trol	Ash- cov- ered		
Energy flux (MJ·m ⁻² ·mo ⁻¹)												
1982												
January	...‡	19	27	...	47
February
March	221	...	-20	...	76	...	166	...	0.5	...
April	...	363	325	...	-22	86	127	...	220	...	0.6	...
May (before 18 May)	...	188	208	5	-7	74	98	109	117	0.7	0.8	...
May (after 18 May)	323	148	115	9	-3	98	40	41	77	2.4	0.5	160
June	709	346	316	23	23	176	16	147	277	1.2	0.1	482
July	732	379	285	64	18	200	35	116	232	1.7	0.1	489
August	...	336	...	35	...	223	...	79	...	2.9
September	373	158	163	5	-6	47	...	105	...	0.4	...	128
October	236	110	99	-4	-7	23	-19	91	125	0.3	-0.2	...
November	...	75	74	-7	-13	41	19	41	68	1.0	0.3	67
December	40	29	34	-15	-6	16	-24	28	63	0.6	0.4	3
1983												
March	...	226	180	4	34	36	-18	186	164	0.2	-0.1	...
April	596	323	252	24	13	86	0	213	238	0.4	0	204
May	797	457	322	64	34	104	65	289	224	0.4	0.3	462
June	753	426	313	38	5	263	84	126	224	2.1	0.4	420
July	721	418	250	40	13	213	30	166	208	1.3	0.1	442
August	529	355	183	30	16	155	18	171	149	0.9	0.1	375
September	514	268	...	5	-8	96	31	167	...	0.6	...	248
October	388	194	101	-6	-4	40	22	159	...	0.3	...	145
November	154	67	60	-11	-6	-21	34	99	32	-0.2	1	46
December	91

* *S* = shortwave radiation, *R_n* = net radiation, *G* = soil heat flux, *H* = sensible heat flux, λE = latent heat flux, and *E_p* = potential evapotranspiration.

† The Bowen ratio $\beta = H/\lambda E$, where *H* = sensible heat loss, λ = latent heat of vaporization, and *E* = evaporation.

‡ ... indicates missing data.

Trends in temperature.—Temperatures ranged widely at 1.5 m above the surface (Fig. 2a). Highest monthly average temperatures occurred in August in 1982 and 1983 (24.6° and 25.4°C, respectively); lowest occurred in December (-0.2° and -2.3°, respectively). During the 29 mo study, the largest diurnal ranges between maximum and minimum temperature at 1.5 m were 22.5° and 22.8° in July of 1982 and 1983, respectively; little difference was found in the diurnal ranges between summer and winter on the control site.

Air temperatures at 0.5 m above the soil surface were significantly lower ($P < .001$) on the experimental site than on the control site before deposition of the ash, but increased following deposition of the ash. Air temperatures at 0.5 m on the ash-covered site averaged 1° higher than on the control site. Air temperatures at 0.05 m did not change after the ash fall. Diurnal ranges in temperature at 0.05 m (Fig. 2b) therefore exceeded 35° on both sites.

Major differences in soil temperature also occurred between the sites. Soil surface temperature often exceeded 55° on the control site during summer (61.8° on 8 June 1983, day 159 of year), as measured in isolated readings; no temperature above 55° was ever measured on the ash-covered surface. During summer

(e.g., 8 June 1983; Fig. 3) surface temperatures on the ash were typically 10° lower than those on the control site. Differences between the sites in surface temperatures diminished in winter, although we measured soil freezing to 15 cm on the ash-covered site compared to only 9 cm on the control site in January 1983. Soils at -0.1 and -1.0 m on the experimental site were cooler after the 18 May 1982 (day 138 of year) ash deposition (Fig. 4). Annual maximum soil temperatures at -0.1 m on the ash-covered site were 4°–5° lower than on the control site: 25.8° and 35.8° in 1982, 29.5° and 34.4° in 1983, respectively (Fig. 4a). But minimum temperatures at -0.1 m on the ash-covered site were only 1°–3° lower than on the control site: -1.7° and -0.9° in 1982, -6.2° and -3.3° in 1983, respectively (Fig. 4a). Differences between the soil temperatures of the sites lessened with increasing depth; maximum soil temperatures at -1 m on the ash-covered site were <4° cooler than on the control site: 20.0° and 23.8° in 1982, 21.7° and 23.6° in 1983, respectively (Fig. 4b). Minimum temperatures at -1 m on the ash-covered site were only ≈1° lower than on the control site: 3.2° and 4.6° in 1982, 4.0° and 5.2° in 1983, respectively (Fig. 4b).

Thus, for some parameters of the energy budget and

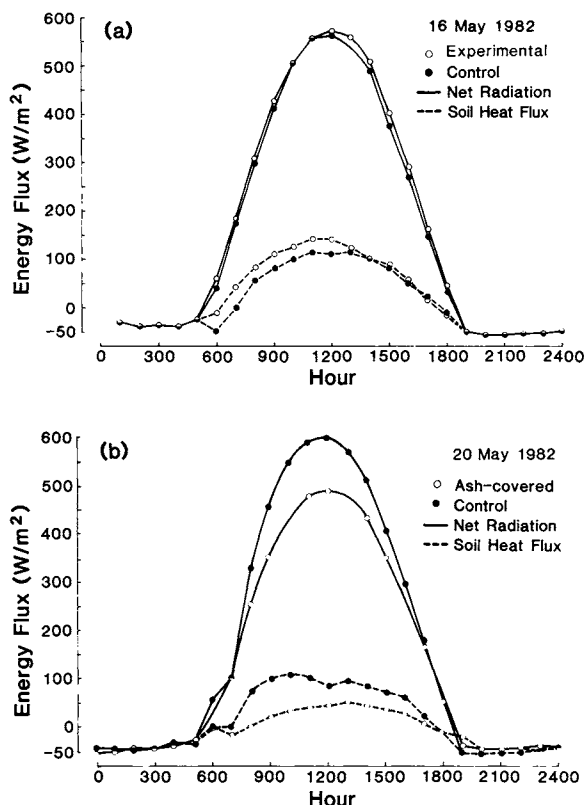


FIG. 1. Diurnal trends in net radiation and soil heat flux for experimental and control sites (a) 2 d before and (b) 2 d after the experimental deposition of ash on 18 May 1982. Data points are integrated records from dataloggers.

for temperature, significant differences were found between the two sites prior to deposition of ash. We believe that these differences are largely attributable to undetected variation in the placement of sensors. While the "similarity" between sites before treatment or through time after treatment is neither likely nor obviates replication (Hurlbert 1984), the relative changes between sites in these environmental parameters and the magnitude of the changes after the ash fall are nonetheless striking.

Precipitation and soil water.—Daily precipitation records from our sites are incomplete. Consequently we relied on records from the Hanford Meteorological Tower (20 km northeast of our site) to supplement our data for $\approx 5\%$ of the days on which rain occurred. The Tower records are highly correlated ($r^2 = 0.85$) with our data but underestimate precipitation by 20%. Annual precipitation at our sites for 1982 and 1983 was 199 and 281 mm, respectively. Rain fell primarily in winter, although infrequent yet often intense showers occurred in summer (Fig. 5). Summer showers (e.g., 5 mm on 11 July 1982, day 192 of year) contributed to detectable soil water recharge (a 2% increase in soil moisture) only in the upper 0.2 m of the profile. Soil water recharge to -1 m through winter precipitation

was evident by mid-February on both sites (Fig. 5). Water was generally more available on the ash-covered site in summer 1982, as reflected by both psychrometric and gravimetric measurements of soil water.

Deep recharge (-1 m) on the ash-covered site was reduced compared to recharge on the control site in 1983 (Fig. 5). Despite 40% more precipitation in 1983 than in 1982, recharge still was lower on the ash-covered site. Soil water content in the upper profile was above 10% by 15 November (day 319 of year) in both 1982 and 1983. Soil water potential at -0.2 m decreased to -1.5 MPa after 10 July (day 191 of year) in 1982 and 1983. Gravimetric measurements of soil water indicated an earlier decrease in water content (20 April, day 110 of year) compared to psychrometric measurements, although these changes in soil water content were not reflected in changes in plant water potential (Fig. 6). Soil water potential exceeded the limits of psychrometric detection (-4.5 MPa) at -0.2

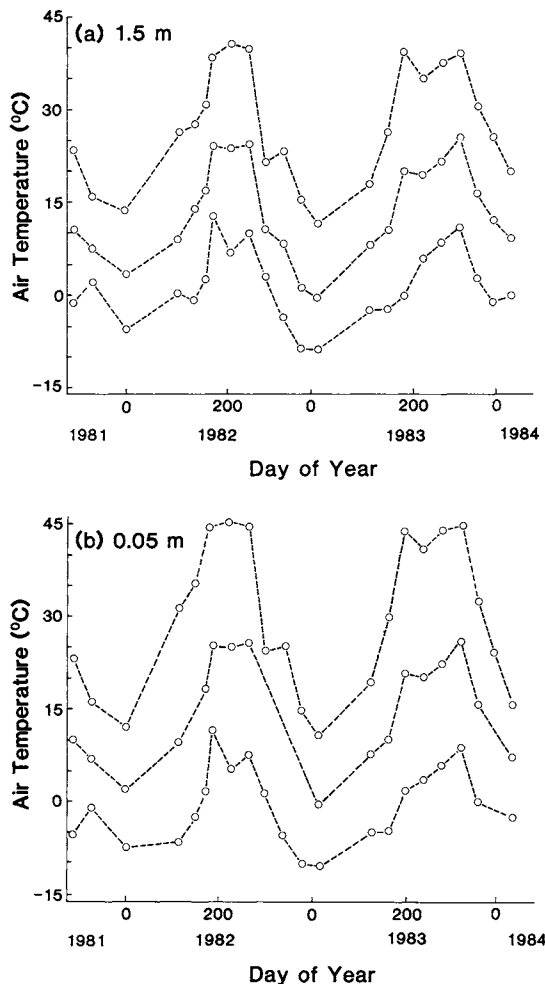


FIG. 2. Air temperatures (monthly average maximum, average minimum, and average) at (a) 1.5 m and (b) 0.05 m above the soil surface for the control site from January 1982 to January 1984.

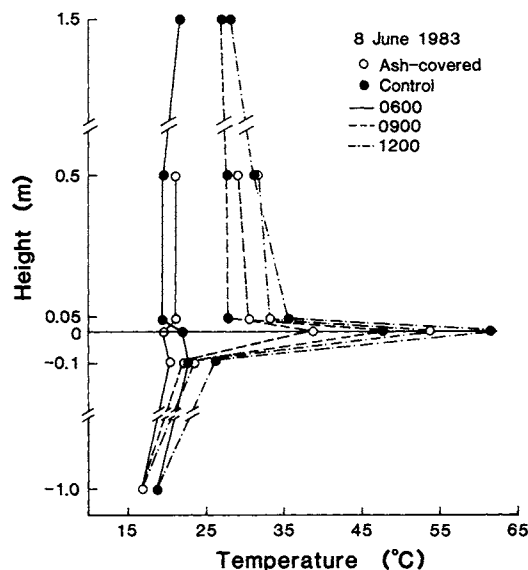


FIG. 3. Temperature profiles from 1.5 m above to 1 m below the soil surface at —600, --- 900, and ···· 1200 for the ash-covered and control sites on 8 June 1983. Surface temperatures are averages of 10 observations taken with an infrared thermometer. All other data are integrated observations from temperature recorders.

m and decreased to -3.0 MPa at -1 m in midsummer in 1982.

Responses of Artemisia tridentata to the ash deposition

A. tridentata shrubs on the experimental vs. control sites did not differ in predawn and midday xylem pressure potentials prior to the ash deposition in May 1982 (Fig. 6). During the rest of 1982 plants on the ash-covered site generally maintained predawn and midday xylem pressure potentials 0.8 MPa higher than control plants. However, only shrubs on the control site responded to summer showers. For example, on 16 July 1982 (day 197 of year), 5 d after a 5-mm shower, plants on the control site displayed higher xylem pressure potentials than plants measured 1 mo earlier (see arrows, Figs. 5 and 6).

In early 1983 there was no difference in xylem pressure potential between plants on the two sites. After 1 August 1983 (day 213 of year), however, the plants on the ash-covered site consistently displayed lower predawn and midday xylem pressure potentials than plants on the control site (e.g., the difference was 1.5 MPa on 13 September, day 225 of year). This decline in the status of water in the plants on the ash-covered site was apparently in response to a decrease in available water in the lower soil profile.

Before ash deposition, leaf conductance on the experimental site was equal to or less than conductance on the control site (Fig. 6). After ash deposition, leaf conductances were higher than for controls in 1982, except for measurements taken soon after a summer

shower (16 July 1982, day 197 of year) (see arrows, Figs. 5 and 6). No consistent between-site differences were detected in leaf conductance in 1983. In 1982 and 1983 leaf conductance on both sites increased in August following senescence and abscission of the large (> 2 cm long) spring-emergent leaves. The highest leaf conductance values measured in the study occurred in August 1983: 0.53 cm/s at midday on the control site (Fig. 6) and 0.60 cm/s at 1500 on the ash-covered site. These high values occurred when xylem pressure potentials were relatively low (-3.0 and -3.3 MPa, respectively).

In 1982 transpiration rates declined on both sites before June in association with decreasing predawn xylem pressure potentials (Fig. 7). In June plants on the ash-covered site had transpiration rates twice as high as plants on the control site, whereas by July transpiration on both sites was restricted. Restricted transpiration rates in July coincided with the initiation

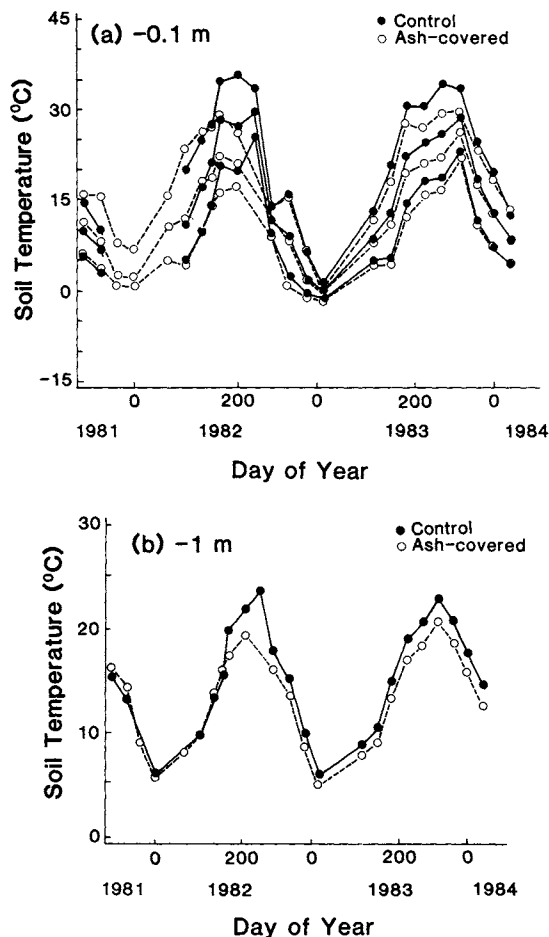


FIG. 4. Monthly average soil temperatures at (a) -0.1 m and (b) -1 m (distance below the soil surface) on \circ ash-covered and \bullet control sites from January 1982 to January 1984. Monthly average maximum and minimum temperatures are also shown for -0.1 m. The experimental ash deposition occurred on 18 May 1982 (day 138 of year).

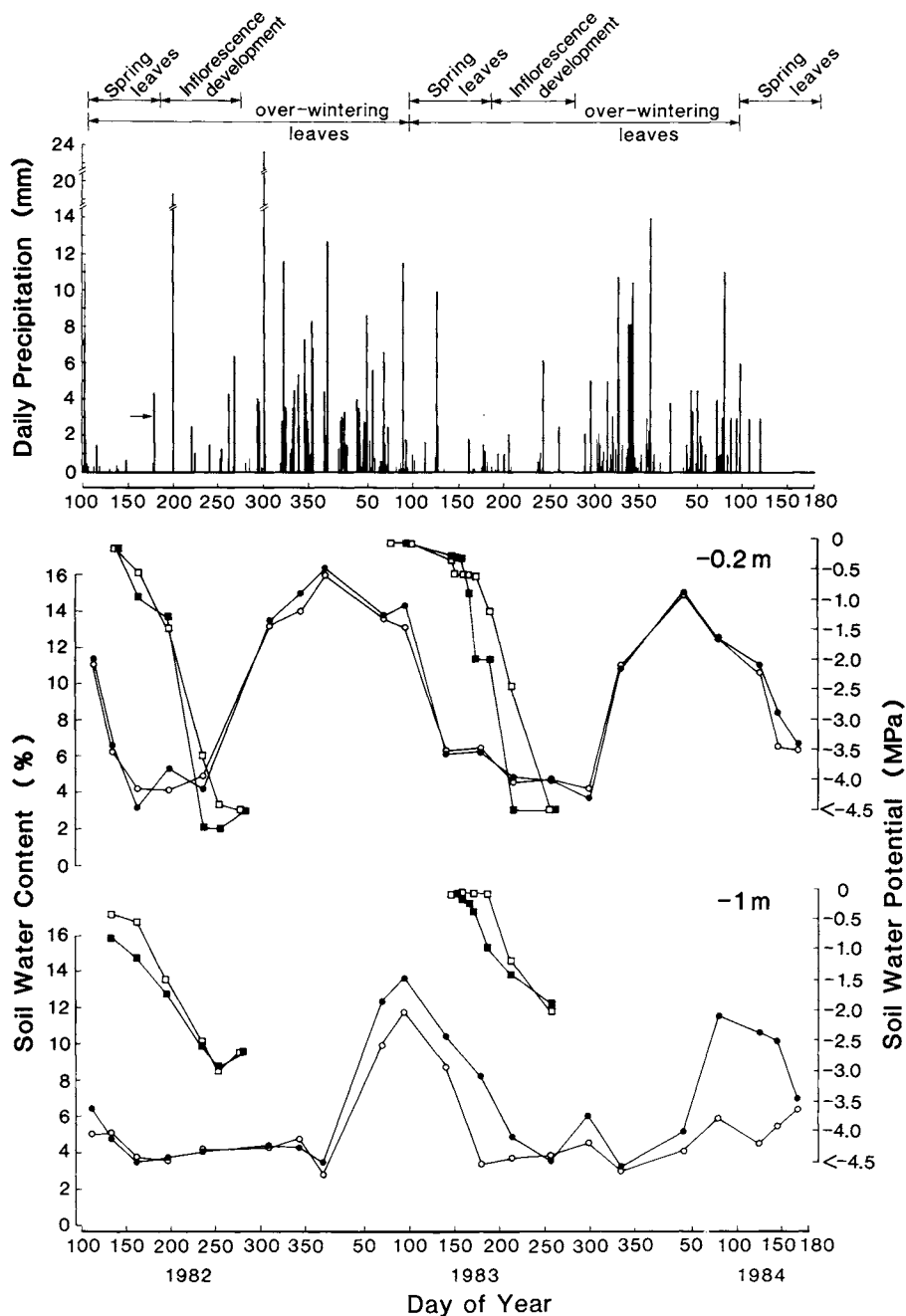


FIG. 5. Daily precipitation and periodic measurements of \circ , \bullet gravimetric and \square , \blacksquare psychrometric soil moisture at -0.2 and -1 m (distance below the soil surface), from 10 April 1982 (day 100 of year) until 1 July 1984 (day 183 of year) on the ash-covered (\circ , \square) and control (\bullet , \blacksquare) sites. The arrow indicates 5 mm of rain on 11 July 1982 (day 193 of year).

of abscission among spring leaves. Plants on the ash-covered site retained the spring-emergent leaves for ≈ 2 wk longer in June than the control plants. Following abscission of spring leaves, transpiration rates increased in August to the highest rates observed in 1982 (Fig. 7). These high rates of transpiration were associated with declining xylem pressure potentials and high vapor pressure deficits on both sites, a pattern that was repeated in 1983. Transpiration decreased

after August and was associated with declining leaf conductance and xylem pressure potentials. The slope of a line relating xylem pressure potential to transpiration rate did not change over a wide range of xylem pressure potentials. No differences in the slopes of these lines were detected between the ash-covered and control sites through the growing season (Fig. 7), indicating the plants extracted water without increases in resistance to flow.

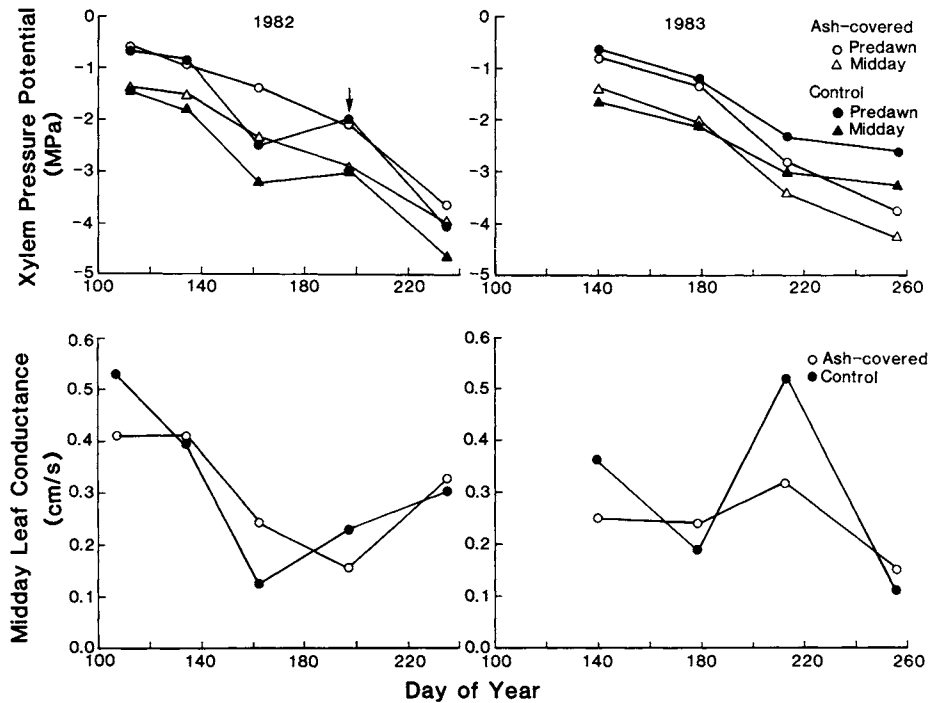


FIG. 6. Seasonal trends in midday stomatal conductances and predawn and midday xylem pressure potentials for *Artemisia tridentata* on ash-covered and control sites in 1982 and 1983. Each data point is the average of three measurements for each of two shrubs on the indicated date. The arrow indicates sampling on 16 July 1982 (day 198 of year), 5 d after a 5-mm shower.

The diurnal pattern of xylem pressure potential did not change with the addition of ash over a wide range of seasonal measurements. Xylem pressure potential decreased through the day to a constant minimum val-

ue between 0900 and 1500, followed by a late-afternoon increase (Fig. 8). The diurnal range between predawn and midday xylem pressure potentials was ≈ 1.0 MPa throughout 1982 and 1983 for plants on both

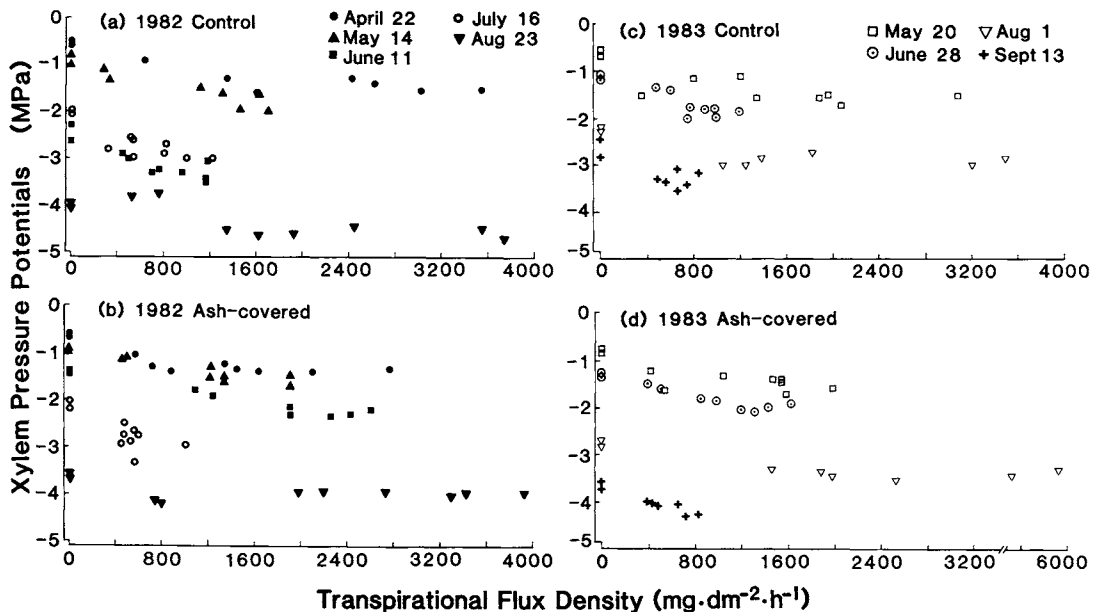


FIG. 7. Predawn xylem pressure potentials of *Artemisia tridentata* as a function of transpirational flux density for (a), (c) control and (b), (d) ash-covered sites in 1982 and 1983. Each data point is the average of three measurements for each of two shrubs on the indicated date.

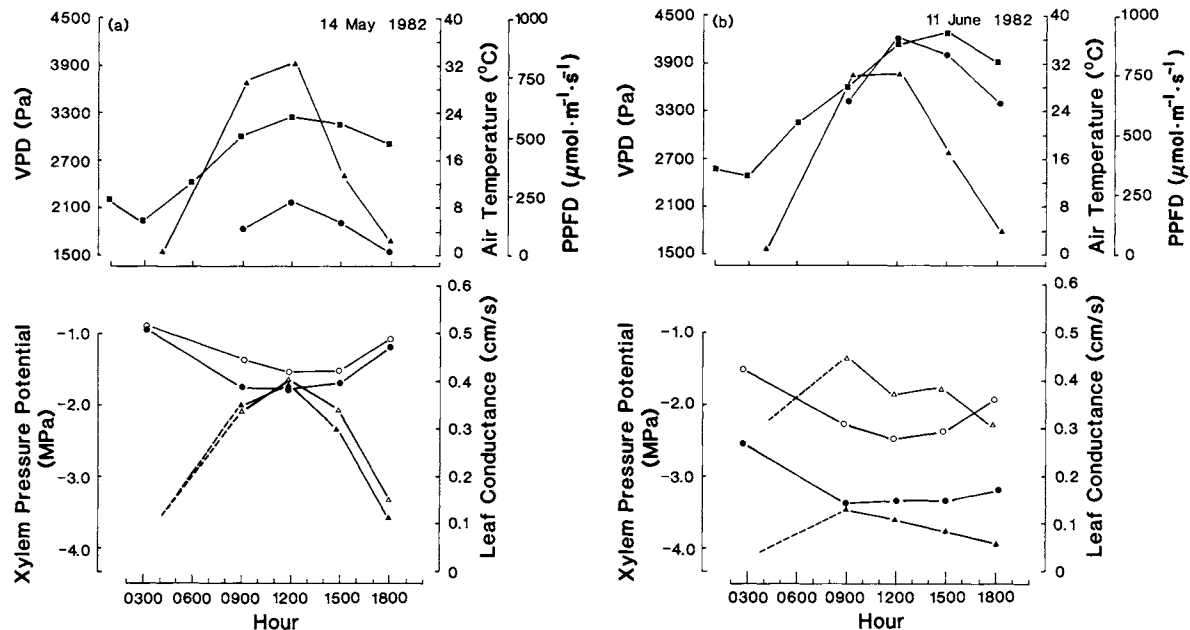


FIG. 8. Diurnal trends in (upper graphs) ● vapor pressure deficit (VPD), ■ average air temperature, and ▲ photosynthetic photon flux density (PPFD), and in (lower graphs) ○, ● xylem pressure potentials and △, ▲ leaf conductance of *Artemisia tridentata* for ○, △ ash-covered and ●, ▲ control sites: (a) 4 d before deposition of ash (14 May 1982, day 134 of year and (b) 24 d after the deposition of ash (11 June 1982, day 193 of year). Predawn conductance values that were below the level of detection are connected to the other values with dashed lines. Each data point is the average of three measurements for each of two shrubs at the indicated time.

sites. In addition, this diurnal range occurred over a seasonal range of predawn xylem pressure potentials from -0.6 to -4.0 MPa (Fig. 7).

On both sites throughout 1982 and 1983, leaf conductances were almost always highest during the 0900 and 1200 measurements (Fig. 8). Leaf conductance decreased after the late morning maxima; apparently water loss was stabilized at xylem pressure potentials within a 1.0-MPa diurnal range. The only exception to this pattern of leaf conductances was for plants on the ash-covered site during the afternoon of 1 August 1982 (day 213 of year), a date after spring leaves had abscised. Leaf conductances at sundown and before sunrise were always lower than the detection limits of the porometer, suggesting nighttime stomatal closure.

From comparisons with the control site, we conclude that the ash increased the availability of soil water to plants at -1 m in summer 1982, but decreased the availability in 1983; this change in turn induced a reversal in predawn xylem pressure potentials. On both sites plants apparently equilibrated to the soil environment each night and were responsive to soil water depletion through summer by the same physical and physiological controls. Psychrometric measurements of soil water potential at -1 m on both sites was the best predictor of predawn xylem pressure potential (Fig. 9). Psychrometric measurements at -0.2 m, although correlated to predawn xylem pressure potentials, included soil measurements that were more negative than the pre-

dawn plant potentials. Consequently, water probably was more available deeper in the soil profile. Soil water potentials estimated from gravimetric measurements apparently lack the accuracy necessary for comparison to plant water relations. But these measurements do indicate a continued restriction of soil water recharge through 1983 and into 1984 in ranges undetected by

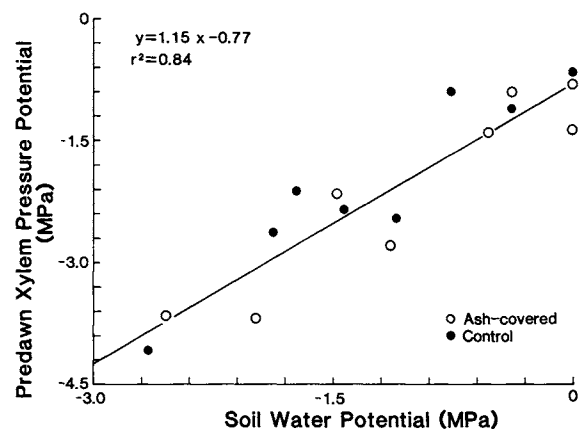


FIG. 9. Predawn xylem pressure potential of *Artemisia tridentata* as a function of soil water potential at 1 m depth for the ○ ash-covered and ● control sites in 1982 and 1983. Each xylem pressure potential is the average of three measurements; each soil water potential value is the average of two measurements.

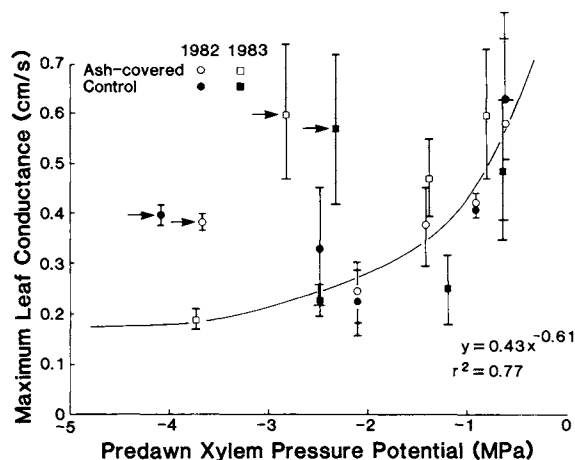


FIG. 10. Maximum leaf conductance as a function of predawn xylem pressure potential in *Artemisia tridentata* for ash-covered and control sites in 1982 and 1983. Each datum is the mean of six observations from two shrubs for each sample date. Vertical bars represent 95% confidence interval estimates. Arrows indicate the data for August 1982 and 1983 that are not included in the regression analysis.

psychrometry. Furthermore, the delay in the abscission of spring leaves that had occurred in 1982 on the ash-covered site was not observed in 1983.

The control of water loss by *Artemisia tridentata* through leaf conductance was also correlated to water availability. For pooled data from both sites, the daily maximum of leaf conductance decreased exponentially with decreasing predawn xylem pressure potential in 1982 and 1983 (Fig. 10). Only for maximum leaf conductances in August 1982 and 1983 was there no correlation with predawn xylem pressure potentials (see arrows, Fig. 10). Maximum leaf conductances on both sites decreased again in September 1983.

No between-site difference was found in the plants' stomatal response to *PPFD*. Rather, stomatal response through summer was apparently influenced by changes in maximum leaf conductance. No predictable stomatal response to vapor pressure deficit was found throughout the study; correlations were apparently artifacts of the changing environment. Often the highest leaf conductances were associated with the highest vapor pressure deficits (e.g., 1 August 1983, day 213 of year).

Responses of Lupinus sulphureus to the ash deposition

Lupinus sulphureus persists in the steppe through aestivation rather than through the conservation of available water (control of leaf conductance, reductions in leaf area, etc.). Predawn xylem pressure potentials were not significantly different between the sites before the ash fall (-0.55 and -0.37 MPa, ash-covered and control sites, respectively) or after the ash fall (-1.95 and -1.97 MPa). Predawn xylem pressure potentials were not correlated to soil water potentials over the

relatively narrow range of measurements taken before plants became senescent. The lowest midday xylem pressure potentials were measured on the control site (-3.1 MPa, 11 June 1982).

Plants on the two sites showed no significant differences in leaf conductances prior to 18 May 1982, but leaf conductances remained high on the experimental site after ash was applied. The highest leaf conductances (1.05 and 1.26 cm/s from ash-covered and control plants, respectively) were measured early in the growing season (22 April 1982, day 112 of year), then values decreased to minima (0.22 and 0.11 cm/s from ash-covered and control plants, respectively, on 11 June 1982, day 162 of year). Maximum leaf conductance in *L. sulphureus* was correlated to predawn xylem pressure potential ($g_{wv}^{max} = 0.63 \psi_{predawn}^{-0.59}$, $r^2 = 0.86$, $n = 36$). No between-site difference was found in transpiration rate before the ash fall. On 16 June 1982 (day 197 of year) plants on the ash-covered site displayed transpiration rates and midday xylem pressure potentials higher than control plants. Plants on the ash-covered site were senescent ≈ 2 wk later than controls in 1982, but no difference in the time of senescence was observed in 1983.

DISCUSSION

Environmental alterations

The overall effects of ash on the environment changed radically over the course of our observations. Ash initially acted as a mulch by retarding evaporation from the soil surface, because the water conductivity of soil or ash is directly proportional to its moisture content (Kramer 1983). Only when the ash was thoroughly wetted by rain did water move through it. The above-average autumn wheat production in 1980 within eastern Washington has also been attributed in part to this mulching action of the ash (Cook et al. 1980).

For vascular plants a much more important physical change caused by the ash became apparent with resumption of rain in autumn: the annual recharge of the soil (Daubenmire 1970) was interrupted. While the ash became water saturated in autumn, the underlying litter and the cryptogamic crust persisted as the major barrier to infiltration. Similar in effect to a buried straw layer, these materials impede infiltration (Miller and Gardner 1962, Gardner 1979). With the wetting front impeded, water accumulated on the ash surface and was lost either through runoff, which we observed, or through evaporation. An increase in runoff in this steppe becomes significant to the water budget because infiltration rates in the region's loamy soils minimize sheet wash (Rasmussen 1971). Even a delay in infiltration for a few days in autumn allowed development of conspicuous ephemeral colonies of green algae on the ash (Rayburn et al. 1982). No response by higher plants to this perched (and thus unavailable) water was evident even in the first summer after ash deposition. For these

plants summer showers caused no change in the seasonal limitation of water, in contrast to the situation for plants on the control site. Measurements of infiltration were nevertheless variable because the litter and the cryptogamic crust vary greatly in thickness and composition.

Surface albedo for both sites before addition of ash ($\bar{X} \pm \text{SD}$) was $13.5 \pm 1.9\%$, in remarkably close agreement with the $13.4 \pm 0.6\%$ measured by Dirmhirn and Belt (1971/1972) for a similar site in southeastern Idaho. When undisturbed, stands in the *A. tridentata*/*A. spicatum* habitat type are completely covered by vegetation (Daubenmire 1970), and surface reflectance is determined almost solely by plants. Given the low overall density of shrubs in these communities (Daubenmire 1970), the reflectivity of the prominent ($> 50\%$ coverage) cryptogamic crust (Poulton 1955) substantially influences the energy budget of the shrubs (Geiger 1965, Fuchs et al. 1976, Miller 1981). Assuming the rough surface formed by this cryptogamic crust along with litter is comparable to a soil surface with small clods, the albedo could be reduced a further 20% (Konratyev 1969).

Covering the dark litter and cryptogamic surface with a relatively smooth veneer of light-colored ash (10YR 7/1 to 7/2; Munsell Soil Color Charts 1971) doubled the albedo. Increasing albedo decreased net radiation and soil heat flux while increasing the radiation load on the shrubs, an effect similar to that of adding kaolin to crop fields (Fuchs et al. 1976). Furthermore, the Bowen ratio for the ash-covered site reveals a 2-mo delay in summer in the decrease in latent heat flux, an additional source of water loss. Advection could have decreased sensible heat flux, making our estimates of latent heat flux an artifact, because the fetch requirements for the ash-covered site probably were not met (Campbell 1977). But these increases in latent heat flux were independently confirmed by the increase in the transpiration rates for *A. tridentata* and *L. sulphureus*. While estimates of potential evapotranspiration for these sites using the methods of Campbell (1977) are much higher, values derived by any of the above-mentioned procedures indicate the extreme limitations available water imposes on the energy budgets in this habitat. Our estimates of the energy budget for both sites are in general agreement with the estimates of Hinds (1975) for a nearby location.

Changes in the energy environment caused by ash occurred in 1982 and 1983, although the mulching effect of the ash caused more water to be available for transpiration in 1982. Between 1982 and 1983 xylem pressure potentials in the perennials decreased with high canopy radiation, high latent heat flux, and decreasing availability of soil water; this effect would be expected to have continued until the barrier to water infiltration was removed and albedo decreased. Moreover, these changes were the exclusive result of ash addition to the soil surface, because the ash is soon

shed from plants (Mack 1981). Thus, the increased aridity of the ash-covered site (and subsequent plant response) was an integrated response to the decreased infiltration and the increased radiation load on the canopy.

The ecophysiology of perennials

By imposing limitations on available water, our experiment revealed the contrasting features of *A. tridentata* and *L. sulphureus* for persistence in an arid environment. Annual production by *A. tridentata* is highly dependent on available water (Daubenmire 1975). In addition the shrub readily responds through leaf abscission to annual variation in precipitation; we calculated that maximum leaf area index of Big sagebrush on both sites decreased annually from 1.9 to 0.5 m^2/m^2 with summer leaf abscission. Our results suggest that abscission will occur earlier and total stand leaf area will be reduced on the ash-covered site in response to reduced soil moisture, until litter deposition and soil mixing reestablish the original moisture and energy exchange. Such seasonal limitations in soil water not only affect leaf loss for *A. tridentata*, but also influence flowering phenology (Sauer and Uresk 1976) as well as the maximum leaf area that a shrub produces (cf. Grier and Running 1977, Gholz 1982).

The mechanisms for controlling water loss displayed by *Artemisia tridentata* represent variations on a recurring pattern among evergreen nonsclerophyllous shrubs (e.g., *Larrea divaricata*, *Atriplex confertifolia*, and *Eurotia lanata*) in arid lands. With the onset of soil drought, all these shrubs generally reduce leaf osmotic potentials, reduce leaf conductance, and abscise leaves (Moore et al. 1972, Oechel et al. 1972, Monson and Smith 1982, Nilsen et al. 1984). The rate of leaf loss, however, appears to be most pronounced in *A. tridentata*, where the large leaves that emerge in early spring may all abscise in early summer (Diettert 1938, Mack 1977). In contrast, leaves are lost more gradually from these other shrub species as drought develops. All these shrubs, including *A. tridentata*, retain metabolically active leaves during periods of persistent soil drought (Diettert 1938, DePuit and Caldwell 1973, Dina and Klickoff 1973).

During summer drought the minimum xylem pressure potentials exhibited by *A. tridentata* are between -4.0 and -6.2 MPa (Fig. 6; Dina and Klickoff 1973, Campbell and Harris 1977), whereas *A. confertifolia*, *E. lanata*, and *L. divaricata* can tolerate conditions below the limits of detection (< -6.5 MPa) (Moore et al. 1972, Oechel et al. 1972, Nilsen et al. 1984). Maximum leaf conductance for these shrubs ranges between 0.3 and 0.6 cm^2/s (Fig. 6; Moore et al. 1972, Oechel et al. 1972, Campbell and Harris 1977). Once large leaves have been shed, xylem pressure potentials remain low (-3.5 to -4.5 MPa) in *A. tridentata*. As shown in Fig. 7, the shrub displays an extraordinary increase in leaf conductance and transpiration per unit leaf area (cf.

Cunningham and Strain 1969, DePuit and Caldwell 1973) coincident with the abscission of spring leaves. So high is the transpiration rate from the remaining small leaves that sap velocities remain constant (Gifford 1968) as shrub leaf area is reduced by 75%.

Even though soil water extraction apparently declines in the upper horizons (Fig. 5; Sturges 1977), the seasonal decrease in xylem pressure potentials in *A. tridentata* is dependent on soil water potential (Fig. 9; Branson and Shown 1975, Campbell and Harris 1977) as the shrub equilibrates to the wettest soil horizons. Soil water potential apparently controls the decrease in conductance and the phenology of leaf abscission. In summer *A. tridentata* probably extracts soil water at depth through root growth (Fernandez and Caldwell 1975); such growth is one mechanism of avoiding increases in soil-plant-atmosphere resistance even at high rates of water loss and low xylem pressure potentials. In contrast, leaf conductance in *A. tridentata* is not sensitive to evaporative demand and does not exhibit the midday closure seen in other shrubs (DePuit and Caldwell 1973, Mooney and Chu 1983). To our knowledge no other arid land shrub displays a similar increase in transpirational rate following abscission while soil water is still limiting. Furthermore, this increase in water loss occurs without change in the soil-plant-atmosphere resistance.

These seasonal adjustments of leaf morphology and physiology in *A. tridentata*, assuming photosynthesis is correlated to leaf conductance (DePuit and Caldwell 1975), permit Big sagebrush to display autumnal flowering, an unusual phenology among evergreen shrubs in arid western North America. The floral buds expand in late spring, and the inflorescences develop largely before the onset of autumnal rains (Daubenmire 1975). Such late-summer or autumnal flowering is characteristic of *Artemisia* throughout its range (Beetle 1960, Shishkin and Bobrov 1961). Flowering during late summer, when soil water potential is very low, is energetically expensive because shoot elongation, floral development, and seed-set are all accomplished through the production of soluble sugars that are also in demand for osmoregulation (Morgan 1984). Such flowering phenology seems more consistent with prior selection in climates with pronounced summer precipitation rather than with the summer drought that occurs in the Intermountain West. Perhaps the energetic cost of this flowering phenology is outweighed by the increase in germination after stratification (Daubenmire 1975) or possibly by a reduction in seed foraging by insects in autumn.

Implications for vegetation and climate: past and future

More than 50% of the *Artemisia tridentata*-*Agropyron spicatum* zone (sensu Daubenmire 1970) in Washington, the most extensive steppe on the Columbia Plateau, was covered by the ash fall on 18 May

1980. By reproducing the thickest accumulation of fine-textured ash in the steppe (near Ritzville), we probably measured the maximum responses within xerophytic vegetation. Water movement will continue to be impeded as long as the buried litter and the overlying ash remain intact. But we predict these effects of the ash are not permanent. Leaves of *A. tridentata* lose $\approx 30\%$ of their dry mass within 1 yr of abscission (Mack 1977); buried litter may decay even faster. As with earlier ash falls in the Columbia Basin, the ash will eventually be incorporated into the soil (cf. Okazaki et al. 1972). Both the development of prominent cracks (Mack 1981) and the creation of burrows (Andersen 1982) in the ash may aid incorporation of ash into the soil and the establishment of vascular plants.

The effect of the ash on rangeland in the *Artemisia tridentata*-*Agropyron spicatum* zone would have been less than on our undisturbed site. With livestock activity the cryptogamic crust is destroyed, the shrub canopy is reduced, and surface roughness is generally decreased; all these actions cause an increase in albedo (e.g., an increase to 0.18–0.27; Dirmhirn and Belt 1971/1972, Hinds 1975). Although annual primary productivity may increase threefold with disturbance (Rickard et al. 1977), this biomass is routinely removed by livestock. Consequently, the litter barrier to water would have been correspondingly less in disturbed versus undisturbed stands.

Also, the impact of the ash was probably less for xerophytic vegetation outside the ash fall area that we duplicated. Further east the ash declines in both textural class and depth (Sarna-Wojcicki et al. 1981). On eastern mesic sites the vascular plant canopy cover may be severalfold greater than in the *Artemisia tridentata*-*Agropyron spicatum* zone (Daubenmire 1970), and with annual production exceeding 250 g/m² (Daubenmire 1970), the thin ash layer soon became covered and then was incorporated into the litter. The resumption of growth by many of the vascular plants in these communities in the first summer after the ash fall (Mack 1981) would also have lowered albedo. At the western boundary of the Columbia Basin the ash has a sandy texture (Sarna-Wojcicki et al. 1981); such coarse ash would little alter water movement.

The coincidence between vulcanism and subsequent glaciation has been repeatedly identified (Kennett and Thunell 1975, Porter 1981), but we doubt Bray's (1979) contention that very large terrestrial ash falls ($>0.38 \times 10^6$ km²) contribute significantly to the initiation of glaciation. His estimates of albedo ($>50\%$) apparently fail to account for the reduction in reflectivity caused by absorption of radiation by plants, wetting of the ash (Munn 1966), and surface roughness. Similar high estimates have been reported for the albedo of ash from Mount St. Helens (Cook et al. 1980) but they have not been realized in field measurements (Seymour et al. 1983).

The overall decrease in surface temperatures and

increase in aridity that we measured does, however, clarify the possible role of Holocene ash falls in affecting vegetation in the Pacific Northwest. Repeatedly, *Artemisia* increased at the expense of conifers in the pollen records bracketing Mazama ash, which fell throughout the region ≈ 6700 yr BP (Mack et al. 1978 and references therein). Mehringer et al. (1977) attributed such short-term increases in steppe taxa, including *Artemisia*, to the mulching effect of fine-textured Mazama ash. But as is shown in our data, such ash is an effective mulch only when water already resides in the underlying soil. Ashes such as from Mt. Mazama probably increased aridity, thereby causing a temporary increase in the abundance of *Artemisia*.

At all levels of biological organization (e.g., an individual, a population, a community), a disturbance can reveal important information that might not be otherwise detected (Harper 1977). The 18 May 1980 ash fall from Mount St. Helens appears to have been such an informative event, because our investigation yielded results beyond identifying the effects of this one ash fall. In determining the role of ash in altering water availability and use in arid steppe, we were also able to quantify the mechanisms of water conservation in *A. tridentata* and to identify adjustments in this shrub that permit autumnal flowering. Furthermore, knowledge of the barrier to water movement created by the ash and of the changes in the energy budget caused by the ash's albedo clarifies the possible role of volcanic ash in inducing past changes in climate and vegetation. The location and certainly the occurrence of short-term natural disturbances such as floods, hurricanes, and ash falls cannot be predicted with accuracy; exploiting these opportunities when they do arise can, however, pay substantial dividends in information (e.g., Veblen and Ashton 1978, Woodley et al. 1981).

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