# ENERGY AND CARBON BALANCES IN CHEATGRASS: AN ESSAY IN AUTECOLOGY[1]

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*Abstract.* Biotic and abiotic pathways of incident energy are rarely considered together in comparable detail, so little is known about whether energy or carbon relations remain constant in contrasting energy environments. An experiment to determine the fates of energy and carbon in cheatgrass (*Bromus tectorum* L.) was carried out on steep (40°) north- and south-facing slopes on a small earth mound, using many small lysimeters to emulate swards of cheatgrass. Meteorological conditions and energy fluxes that were measured included air and soil temperatures, relative humidity, wind speed, incoming and reflected shortwave radiation, net all-wave radiation, heat flux to the soil, and evaporation and transpiration separately. The fate of photosynthetically fixed carbon during spring growth (31 March to 31 May) was determined by separation of the plant tissues into mineral nutrients, ash, crude protein, crude fat, crude fiber, and nitrogen-free extract (NFE) (the proximate analysis scheme routinely used for feed analysis) for roots, shoots, and seeds separately.

Temperatures and humidities were not notably different betweeen slopes. However, all terms in the radiation balances were significantly larger on the south exposure, and the sensible heat flux to the atmosphere on the south exposure was much greater than on the north.

The energy-saturated south exposure was subjected to water stresses much earlier than the north exposure. Total transpired water, the fraction of energy used to transpire water, and soil water content simultaneously showed an abrupt decrease in slope at about 10% soil water content (−14 bars average water potential) in the 60-cm lysimeter soil profile, indicating a rather sudden decrease in water availability to the plants. This change occurred near day 30 on the south exposure, and near day 45 on the north exposure, implying that water was readily available to the north exposure for about 2 wk longer than on the south exposure.

Root and seed production were both about 30% greater on the north exposure than on the south, but shoot production was not different. Heats of combustion (caloric content) differed between roots, shoots, and seeds, but not between exposures. Total production and total energy fixation were not statistically different on the two exposures, because the greater biomass and variability of the shoots overwhelmed the statistically significant differences in roots and seeds. Incident shortwave radiation was very much greater on the south exposure than on the north, so the south exposure was much less efficient in converting solar energy into chemical energy stored in plant tissues.

The clearest difference in carbon pathways occurred for crude protein in shoot tissues at the end of the growing season (23 g m$^{-2}$ on the north compared to 30 g m$^{-2}$ on the south). Since both exposures began the growing season with 33 g m$^{-2}$, shoot protein was translocated to other tissues during the season, to a greater extent on the north exposure than on the south. The crude fiber and NFE (g m$^{-2}$) in seed tissues were both greater on the north exposure, reflecting only a greater total seed biomass; but for roots and shoots there were no appreciable differences between exposures other than crude protein.

The average individual seed weight was only about 10% heavier on the north exposure, although the north produced more than a third more total seed biomass. The composition of an average seed indicated that the difference in seed weight was caused primarily by about 8% more NFE in north exposure seeds, probably starches in the endosperm. By contrast, the crude protein in an average seed was almost identical between slopes—possibly a very important compensation for seedling size and vigor.

Homeostasis (self-regulation) was evident as a gradation decreasing in the order seed viability (very strongly homeostatic) > seed composition (strong) > shoot and root composition (moderately strong) > average seed weight = shoot production (moderate) > seed number = mineral content (weak) > total root and seed production (no detectable homeostasis).

*Key words:* Bromus tectorum; *carbon balance; cheatgrass; energy budgets, plants; homeostasis, plants; mineral uptake, plants; plant water relations; productivity, plants; seed production.*

## INTRODUCTION

*Bromus tectorum* L. is an annual grass introduced accidentally into the United States about a century ago on the eastern seaboard. It spread westward rapidly and was reported in Washington State in 1901. It is now very abundant in the Great Basin and Columbia Basin, and is dominant on millions of hectares in those regions. It has become an important

forage in places and has generated a substantial literature which is well reviewed by Stewart and Hull (1949) and Klemmedson and Smith (1964). A great deal of taxonomic and autecological information was reported by Hulbert (1955).

Much of the early literature was concerned with reducing stands of cheatgrass and encouraging regrowth of native perennial grasses (Leopold 1949). However, recent years have seen some of the communities invaded by an even more aggressive and obnoxious species, medusahead rye [Elymus caput-medusae L. in Hitchcock and Cronquist (1973); synonymously, Taeniatherum asperum (Sim.) Nevski] (cf. West 1968), and some recent work now is aimed at maintaining existing cheatgrass stands against this invader (Young and Evans 1970).

Cheatgrass is normally a winter annual, germinating after adequate rains in the autumn, growing slowly during the winter, and maturing as soil water disappears in the spring. The life history of the grass is fully discussed in the previously named reviews. Cheatgrass seeds germinate rapidly in laboratory tests; usually, all viable seeds have germinated within 3–4 days. However, in the field, germination is continuous rather than simultaneous, as the spectrum of "safe sites" is progressively brought to germination conditions (Young et al. 1969). Some cheatgrass populations show germination polymorphism, in that some individuals will cast seeds with germination behavior very different from the bulk of the population (Palmblad 1969). In most cheatgrass swards, the seeds germinate aerially, in the litter, rather than in soil. Young et al. (1971) showed that under these conditions, seed viability was very high at 10°C but low at 20°C; and seedling root growth rates were higher than competitors at 15°C (Harris and Wilson 1970). These germination and root growth characteristics have earned cheatgrass a reputation for being a very competitive cool season grass, but in fact it is competitive only if existing climax vegetation is disturbed—cheatgrass makes few inroads into perennial grasslands otherwise (Leopold 1949, Harris 1967).

The phenology and morphology of cheatgrass are both very plastic (Finnerty and Klingman 1962, Rickard et al. 1971). In poor conditions, cheatgrass can flower and set a single viable seed on plants no more than 2 cm tall; in salubrious conditions, each plant may have several tillers up to 40 cm tall with hundreds of seeds. Seed production is density dependent (Young et al. 1969) but total aboveground production tends to be constant over a wide range of densities (Hulbert 1955).

Cheatgrass is very responsive to fertilization, especially at relatively low levels (Eckert and Evans 1963); yields are much more sensitive to nutrition than to water relations (Cline and Rickard 1973). Fertilization of mixed cheatgrass-bunchgrass stands usually results in the death of the bunchgrass (Wilson 1966, Kay and Evans 1965).

Cheatgrass provides a good forage when immature (Cook and Harris 1952, 1968, National Academy of Sciences 1969) but matures rapidly into a mass of straw with sharp seeds that ". . . make hay with some mature cheatgrass in it miserable to handle" (Stewart and Hull 1949). Green cheatgrass is valuable to wildlife as well as domestic animals; it forms a major part of the diet of Chukars in the fall, (Weaver and Haskell 1967) and in both fall and spring for Sharptail Grouse (Jones 1966). Its seeds are consumed in quantity by several species of small animals, but seeds alone are not desirable for Chukars (Savage et al. 1969). Cheatgrass swards are definitely poor cover for ground-nesting birds; Jones and Hungerford (1972) found that 80% of simulated nests in cheatgrass were destroyed by magpies.

Cheatgrass has become a naturalized member of the ecosystems in western United States (Daubenmire 1970), even if its success in undisturbed communities is miniscule, because undisturbed communities are a vanishing resource. It has put its roots down in American soil for keeps.

## ENERGY FLUXES AND AUTECOLOGY

Energy has become somewhat a touchstone for ecologists in the past couple of decades, and with good reason: its gradients and transfers move all manner of things about—the muscle on an ecological skeleton. Energy need not be biotically fixed to be influential, although most ecological literature on energetics is devoted to tracing biochemically fixed energy through trophic transfers. Comprehensive measurements of the "fate and effects" of energy in an ecosystem are rare; energy relations are not yet typical concerns of autecological studies (cf. West 1968). This oversight will probably be corrected as ecological analyses penetrate organism/environment relationships.

Several methods have been used to alter energy relations in communities, including shade cloth (Campbell et al. 1969), latitude (Gibbon et al. 1970), elevation (Grable et al. 1966), and artificial lighting (Bjorkman and Holmgren 1963); but ecologically, the most meaningful alteration for a sward of cheatgrass is of slope exposure. South-facing slopes intercept solar radiation at steep angles, somewhat analogous to southern latitudes, and conversely for north-facing slopes. Because insolation is a potent energy flux, this approach guarantees contrasts if the slopes are steep enough.

Therein lies a prickle; the ecological literature on slope effects is almost entirely devoted to species

presence and abundance. From Potzger (1939), concealing atmometers from transient hunters, to Ayyad and Dix (1964), scoring stands on prairie slopes, the emphasis is on taxonomy (although all agree it is more or less warmer and drier on the south slopes).

The following text aims to weld climatological and biological literatures and ideas into a meaningful autecological description of a cheatgrass community. In both the literature survey and experimental results, energy is analyzed as a cascade, from radiant energy fluxes to storage in mature plant tissues, touching upon (1) microclimates and energy fluxes; (2) ecological interpretations of abiotic energy balances; (3) community water relations; (4) photosynthetic efficiency; (5) carbon pathways in roots, shoots, and seeds; (6) homeostasis; and (7) environmental influences on production and reproduction in *Bromus tectorum* L.

### Abiotic fluxes and storages

In the broadest sense, energy enters a community as radiation (shortwave, from the sun) and leaves the community (earth) as radiation (longwave, to space). Figure 1 is a diagram of the major biotic and abiotic pathways for energy transfers and transformations, and the next several paragraphs provide a perspective for the abiotic fluxes and storages noted there. The fate of radiant energy captured by plants via photosynthesis is examined in succeeding sections.

The general energy balance equation relating fluxes in the environment can be written in two ways, providing different insights:

$$S - rS + I_d - I_u = S_n + I_n = R_n$$
$$= LE + LT + G + H + P_n \quad (1)$$

$$S + I_d = rS + I_u + LE + LT + G + H + P_n \quad (2)$$

where $S$ = insolation (0.2–3.2 $\mu$m wavelengths),
　$r$ = reflectivity,
　$I_d$ = atmospheric (downward) longwave radiation (6–25 $\mu$m wavelengths),
　$I_u$ = longwave radiation (upward) from terrestrial surfaces,
　$S_n$ = net insolation,
　$I_n$ = net longwave radiation,
　$R_n$ = net all-wave radiation,
　$LE$ = latent heat flux due to evaporation,
　$LT$ = latent heat flux due to transpiration,
　$G$ = sensible heat flux to the soil,
　$H$ = sensible heat flux to the atmosphere, and
　$P_n$ = net photosynthesis.

Equation (1) shows that net all-wave radiation ($R_n$) is the energy that undergoes transformation to stored forms at or in the community. Equation (2) shows that the energy flux incident upon the plant community
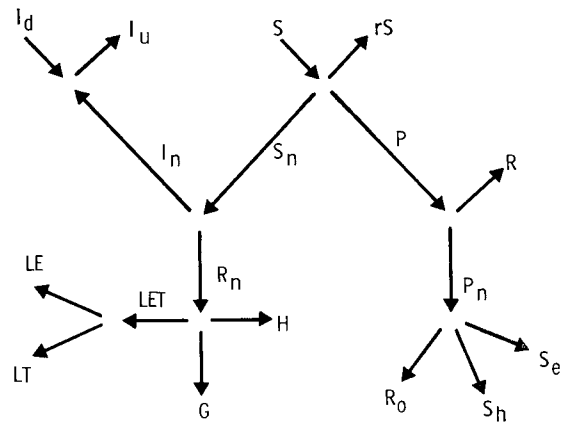


| | |
|---|---|
| G | HEAT FLUX TO THE SOIL |
| H | HEAT FLUX TO THE ATMOSPHERE |
| $I_d$ | LONGWAVE RADIATION FROM THE ATMOSPHERE |
| $I_n$ | NET LONGWAVE RADIATION |
| $I_u$ | LONGWAVE RADIATION FROM PLANT AND SOIL SURFACES |
| LE | EVAPORATION FROM SOIL SURFACE |
| LET | TOTAL OF EVAPORATION AND TRANSPIRATION |
| LT | TRANSPIRATION FROM LEAVES |
| P | GROSS PHOTOSYNTHESIS |
| $P_n$ | NET PHOTOSYNTHESIS |
| rS | REFLECTED SHORTWAVE RADIATION |
| R | RESPIRATION |
| $R_n$ | NET ALL-WAVE RADIATION |
| $R_o$ | ROOT BIOMASS |
| S | SHORTWAVE RADIATION |
| $S_e$ | SEED BIOMASS |
| $S_h$ | SHOOT BIOMASS |
| $S_n$ | NET SHORTWAVE RADIATION |

FIG. 1. Energy flows in a plant community and its environment.

is a function of large-scale processes—cloudiness, air temperature, season—whereas the fate of the incident energy is determined by the local character of the environment and the community—reflectivity, surface character, soil type, soil water availability, and characteristics of the plant species extant.

Incident shortwave radiation (insolation) usually includes both direct beam and diffuse components. The spectral character of these two components differ somewhat (Kondratyev 1969), but only detailed work in photosynthesis requires separate spectra (Anderson 1964), because the principal difference is that diffuse radiation shows a maximum at shorter wavelengths than direct radiation. No significant

loss of information will result herein from lumping both fluxes into the general term, "shortwave radiation," because the energy transfers considered here involve gross energetics rather than absorption spectra.

Several factors are important in determining the amount of shortwave radiation available for the plant community: latitude, altitude, slope, exposure (or aspect), season, and climate. The effect of each of these factors on shortwave radiation is well understood and discussed in references and textbooks (List 1957, Geiger 1965, Sellers 1965, Kondratyev 1969, Monteith 1973).

Sensible heat flux to the atmosphere arises by convection from surfaces of the earth or plant communities warmed by absorption of solar radiation. This flux can be a very significant proportion of the incident energy, especially in arid regions where the competitive process of evaporation may be small. Evaporation typically occurs at two different surfaces: bare mineral soil, and dead plant material (mulch or litter). A few centimeters of mulch suppresses evaporation and was shown by Jones et al. (1969) to retain more water in the upper profile (to depths of 30 cm) than does a bare surface. Soil texture alone (e.g., sands compared to clays) strongly affects the amount of water stored but has little effect on the depth to which soil water can be lost (Alizai and Hulbert 1970).

Transpiration affects water deep in the soil that otherwise would remain unmoved; where plants and soil water are both abundant, transpiration greatly exceeds evaporation. In some circumstances, the separation of evaporation from transpiration is either unnecessary or difficult, and the two are subsumed into a single flux, evapotranspiration. However, because of their contrasting influence on soil water, the two fluxes ought to be separated where possible.

Water relations of plants probably can be correlated with everything in the environment. For example, Prasad (1967) found correlations exceeding 0.85 between leaf water status and (1) net radiation, (2) vapor pressure deficit, (3) wind speed, and (4) air and (5) soil temperatures, primarily because these environmental parameters are physically related, but partly because the water relations of plants are in fact governed by more than one gradient. The transpiration flux from a single leaf has been thoroughly analyzed (Gates and Papian 1971), with incident radiant flux, relative humidity, and wind speed the independent environmental variables, and stomatal diffusion resistance and leaf size the plant factors.

Root growth is important to efficient absorption of water from the soil, because new root structures absorb water faster than do older ones (Kramer 1969). However, water must be readily available to maintain that root growth. For example, Lawlor (1973) reported that wheat roots grew progressively slower as water stress increased, ceasing at a water potential of −10 bars. Water stresses can produce a variety of other problems for plants (Crafts 1968) but not necessarily for their seeds. Wardlaw (1967) found that translocation to newly formed wheat seeds was not affected even by water stress to the point of leaf wilting. The high priority of seed formation (Harper et al. 1970) has far-reaching consequences for stressed plants, and is a recurring theme in later sections.

### Abiotic fluxes and productivity

Total production in a plant community is closely related to the total amount of water available for its use, perhaps a log–log relation between climax communities (Rosenzweig 1968) but linear within species (Chang 1968:123–128). The productivity of many grass species depends upon both the amount and timing of precipitation during the growing season (Smoliak 1956). However, in contrast to plant water relations, the total productivity of a community is not well correlated with specific environmental factors. For example, Scott and Billings (1964) found the productivity of an alpine community to be uncorrelated with 53 different environmental factors; the only important variable was "potential for soil movement," which they considered to be some measure of the water status of the various sites.

Light relations rank with water relations as fundamental for plant production in communities; the vast literature was well reviewed by Anderson (1964). One generalization used to compare communities is the efficiency with which a community captures insolation as reduced carbon compounds in plants. Efficiency is here defined as the energy content stored in plant tissues (net photosynthesis) per unit incoming energy (total insolation during the growing season), but other definitions are possible (Botkin and Malone 1968). Typically, plant communities are inefficient, for a variety of reasons, with leaf display, radiation intensities, and action spectra for photosynthesis being among the most important (Bonner 1962). Botkin and Malone (1968) summarized many estimates of efficiency for several contrasting communities, mostly about 1% or less for aboveground productivity.

Several biochemical pathways exist for photosynthesis (cf. Zelitch 1971:Chap. 4), but dogmatic separation of species into groups according to carbon reduction pathways seems inappropriate, because most plants exhibit at least a little activity in more than one cycle (Black 1973) and species can exhibit characteristics typical of two or more cycles (Williams and Markley 1973). *Bromus tectorum* is known

to possess the high $CO_2$ compensation concentration typical of a "$C_3$ pathway" species (Downton and Tregunna 1968), so it certainly lacks the high efficiency and potential productivity typical of "$C_4$ pathway" species.

Photosynthesis via the $C_3$ pathway exhibits a typical enzyme saturation response curve as incident radiant flux density increases from zero (Bonner 1962). Consequently, single-leaf photosynthesis typically levels off at flux densities of about one-fifth of full sunlight. Photosynthesis by a canopy of leaves, however, is very different, because higher flux densities at the top of the canopy imply higher flux densities lower down, where leaves are not light saturated. Consequently, productivity within a stand increases with increasing energy availability (cf. Hesketh and Baker 1967).

Verhagen et al. (1963) presented a perceptive analysis of some theoretical types of foliage distributions. They concluded that in an ideal foliage (maximally productive, i.e., with absorbed flux density on the leaves constant with depth in the canopy), the extinction coefficient must be quite small at the top of the canopy and very large indeed at the bottom, implying upright foliage at the top and prostrate foliage near the bottom. This is a realistic description of the growth habits of some plants, including mature *Bromus tectorum*. However, they showed that the light emerging from the base of an ideal foliage exceeded the light emerging from a foliage with the bottom leaves at compensation point. That is, maximum productivity is not associated with maximum productive absorption; it is the distribution of absorption that is critical.

Experimental alteration of insolation to study productivity in field conditions has been exploited recently. Gibbon et al. (1970) grew corn, kale, and sugar-beet in two contrasting insolation climates (Britain and Italy), noting generally increased yields and decreased efficiencies in the higher insolation intensities of Italy. Campbell et al. (1969) shaded wheat in field conditions in Canada, noting that the biomass of grain and straw decreased with increased water stress, and that shading tended to increase yield in relatively dry years, but again, the increased yields were accompanied by decreased efficiency as insolation increased.

### Carbon balances

A suitable generalization of carbon pathways within plants is a carbon balance diagram suggested by Mooney (1972), which is presented in a very simplified form in Fig. 2. Four endpoints appear in this diagram: saccharides for storage and construction; aromatic and phenolic compounds for function and control purposes; proteins; and fatty acids. The num-
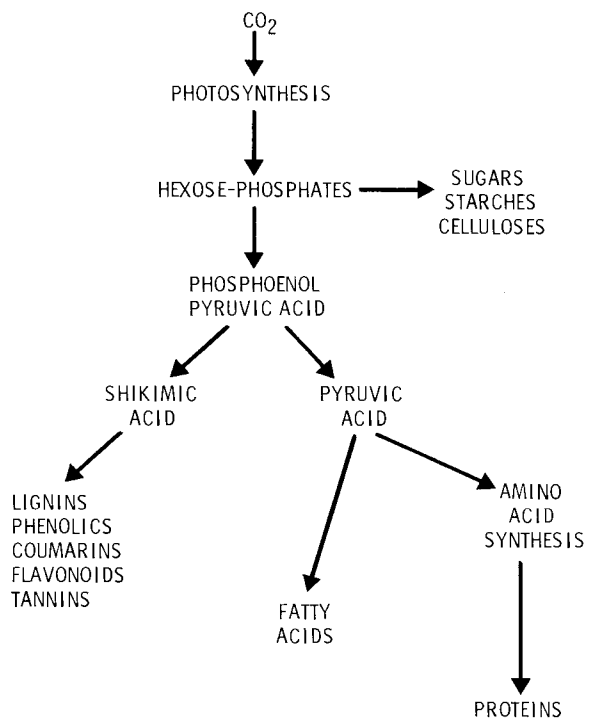


FIG. 2. Carbon pathways in typical green plants (after Mooney 1972).

ber of compounds associated with the function and control (shikimic acid) group is very large, but the mass associated with each of them is often small because the concentrations required are miniscule. The other end points in the diagram can be roughly thought of as containing relatively smaller numbers of compounds in relatively higher concentrations.

To separate carbon pathways into only these few categories is to oversimplify matters drastically, but the processes involved in the growth, development, and maintenance of plants are so complex that anything less than a textbook must simplify matters. A useful lumping procedure is to differentiate between carbohydrates, lipids, and proteins, three categories that coincide roughly with three of the four endpoints in Fig. 2. A traditional scheme of plant tissue analysis that approximates this subdivision is the Proximate Analysis Technique developed by workers at the Weende Experimental Station in Germany in 1865 (Crampton and Lloyd 1969). Proximate analysis differentiates between nitrogen-bearing compounds (called crude protein), ether-soluble compounds (called crude fat), the remaining soluble compounds (called nitrogen-free extract, NFE), insoluble substances (called crude fiber), and mineral constituents (called ash) (Fig. 3). Unfortunately, small but variable portions of cellulose and lignin end up in the NFE fraction instead of crude fiber, so structural materials (cell walls) cannot be completely separated
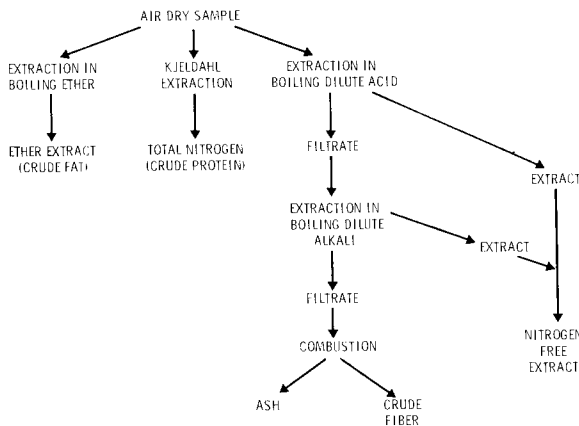
FIG. 3. Flow sheet for the Weende proximate analysis scheme (after Crampton and Lloyd 1969).

from functional materials (cell contents). This represents a serious shortcoming of proximate analysis, and better analyses are being promoted (Van Soest 1967).

Proximate analyses of forage grasses are an important part of range management, and an extensive compilation of average, or typical, composition has been published by the National Academy of Sciences (1969). However, general reviews of plant composition as a function of environment are apparently nonexistent.

## OBJECTIVES

The specific objectives of this study were

1) To measure aboveground and belowground productivity of cheatgrass on contrasting slope exposures.

2) To measure abiotic energy and water balances on contrasting slope exposures.

3) To relate the distribution of carbon in plant tissues to energy and water balances and micro-climatic conditions.

4) To examine the concept of homeostasis in autecological studies of energy, water, and biomass.

## METHODS AND MATERIALS

### Site description

The experimental site was on the United States Atomic Energy Commission's Arid Lands Ecology Reserve on the Hanford Reservation in south-central Washington. The site selected was at 360 m elevation near the southeastern end of the Rattlesnake Hills, at 119° 32' W, 46° 26' N. The climate in this region is semi-arid and the natural vegetation is best described as shrub-steppe (Daubenmire 1970). The lower elevations are dominated by big sagebrush

(*Artemisia tridentata* Nutt.), Sandberg bluegrass (*Poa sandbergii* Vasey), and cheatgrass (*Bromus tectorum* L.); the higher elevations, with somewhat more precipitation, support bluebunch wheatgrass (*Agropyron spicatum* [Pursh.] Scribn. and Smith) as the dominant grass rather than the smaller *Poa* and *Bromus*. Precipitation is scant, averaging about 16 cm annually, about a third of which occurs during the summer, and another third as snow between November and February. Precipitation stored as soil water during the winter supports a spring flush of growth between March and May. Evapotranspiration rapidly removes all the stored water; soils are dry between June and September. Average maximum temperatures in the spring growing season range from about 10°C in early March to about 30°C in late May.

The experiment was performed on a small earth mound, constructed from in situ materials, about 2 m high and 100 m long. The slopes, facing north and south at an angle of 40° ± 1° with the horizontal, were seeded with *Bromus tectorum* shortly after the mound was constructed in autumn 1971. A full tabulation of experimental details and data is available (Hinds 1974).

### Abiotic fluxes

Air temperatures and humidities were measured with hygrothermographs with sensors 10 cm above the surface on each slope. Soil temperatures were measured with copper-constantan thermocouples placed at 10, 20, and 60 cm depth. Wind speeds were measured with totalizing anemometers with a starting speed of about 1.5 m s⁻¹; the cups were centered 35 cm above the surface, about 20 cm above the maximum height of the grass. Precipitation was measured with six (three each slope) small rain gauges with 5-cm diam. and 15-cm capacity, buried in the soil with their opening parallel to and at the surface, in relatively open areas of the mound. The gauges were systematically arranged to account for possible changes in interception with location on the mound.

Insolation was measured with pyranographs, set parallel to the slopes after calibration against an Eppley pyranometer at the Hanford Meteorological Station. Net radiation was measured with Dirmhirn design thermopile radiometers situated 50 cm above (Idso and Cooley 1971, 1972) and parallel to the sloping surfaces of the earth mound. All continuous recordings were averaged over daytime and nighttime hours separately. Daily totals of incident shortwave and net radiation were determined by planimetering the area under the trace.

Reflected shortwave radiation was estimated by periodic measurements of reflected flux at different seasons and solar elevations with a small hand-held
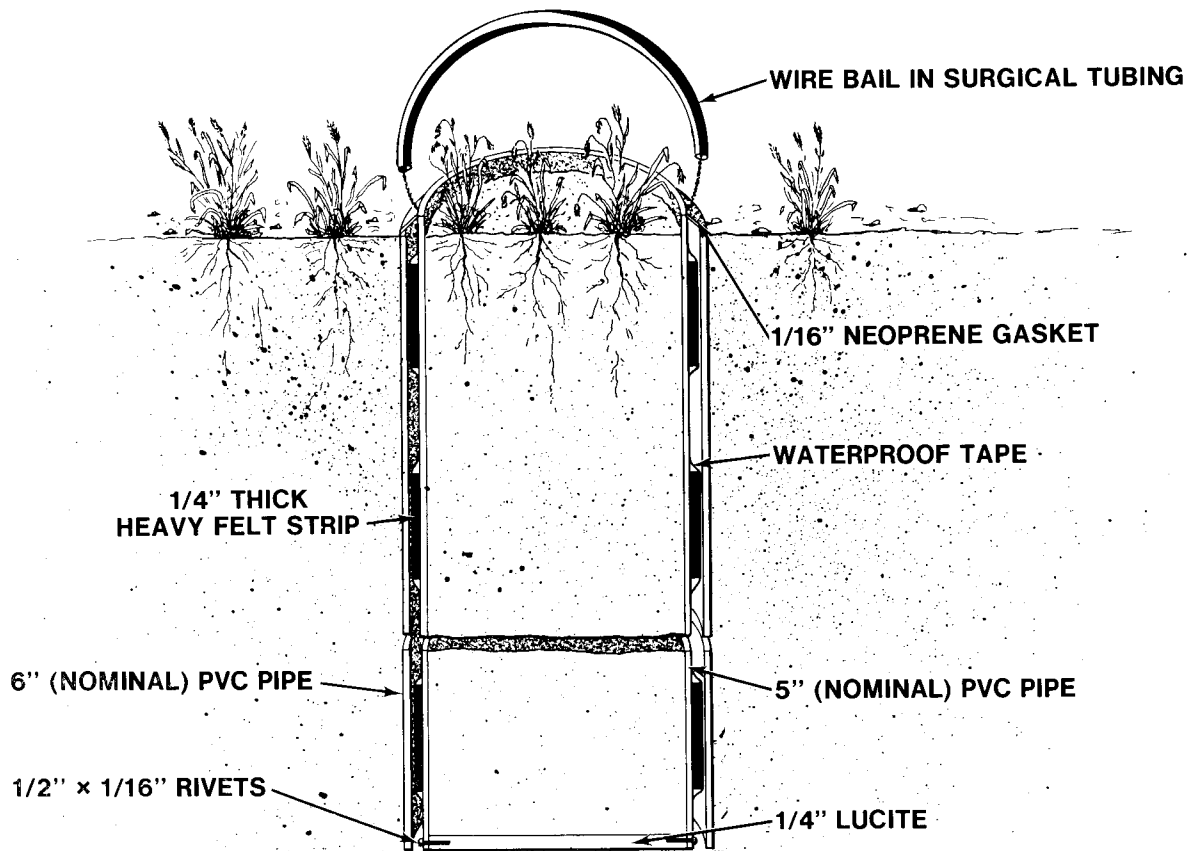
FIG. 4.   Details of the construction of the small lysimeters.

pyranometer. Calculation of daily fluxes followed, using hourly solar elevations and azimuths (List 1951).

Sensible heat flux to the soil was calculated using well known relations between temperature profiles and heat flux in solids (Sellers 1965).

Sensible heat flux to the atmosphere was estimated by difference in the energy equation: $H = R_n - G - LET$. Calculated in this manner, all errors from the other measurements were lumped into this flux.

Evapotranspiration was measured with small lysimeters developed during the past 3 yr (Hinds 1973) from a Russian design (Konstantinov 1966). The construction of the small lysimeters is shown in Fig. 4. The lysimeters were fabricated from 5-in (nominal) diam. PVC (polyvinyl chloride) irrigation pipe, 60 cm long, with a Plexiglas® bottom riveted and glued in, and with a wire-in-surgical-tubing handle. The outer casing (sleeve) of the lysimeter installation was 6-in (nominal) diam. pipe, which fit snugly in a hole drilled by a 7-in diam. power earth auger. The tops of both the lysimeters and the sleeves were cut to parallel the slope. An annular gasket of pliable 1.5-mm thick neoprene covered the gap between the

lysimeter and the sleeve, and four felt gaskets about 6 mm (¼ in) thick taped around the lysimeter provided baffles to prevent vertical air motions along the outer surfaces of the lysimeter. Temperature profiles inside the lysimeter were indistinguishable from those in the field, and comparisons of water loss and cheatgrass production with field data showed no significant differences (Hinds 1973). The lysimeters were weighed at 4- to 8-day intervals on a portable scale to ± 5 g (± 0.4 mm water); more frequent weighings are not optimal for soil water budget methods (Rouse and Wilson 1971/1972).

The plants to be used in the experiment were transplanted into the lysimeters. Soil cores 20 cm deep selected randomly from a uniform west-facing hillside were inserted into 34 partially filled lysimeters (17 each exposure), thus preserving root structure, phenological advancement, and the surface mulch of dead plants developed over the past years in the hillside community. I estimated evaporation from nontranspiring surfaces by plucking the green plants from the surface of 8 lysimeters (4 each exposure); the plucked shoots were added to the mulch. The mass of the plucked shoots was about 130 g/m², but

Fig. 5. The north exposure of the experimental earth mound, 15 May 1972.

of the mulch, about 1,200 g/m², so this addition made little difference. Transpiration was estimated as the difference between the evapotranspiration lysimeters with green plants, and the evaporation lysimeters without green plants.

Figure 5 shows one experimental site and part of the instrumentation.

### Biotic fluxes

Heats of combustion (caloric content) of the plant materials were determined by an adiabatic bomb calorimeter. The dried plant materials were ground to pass a 40-mesh screen; about a third of a gram was placed loosely in a combustion cup and ignited in 30 atm of $O_2$. Correction for $NO_2$ formation was performed, but not for $SO_2$.

I estimated standing crops of roots at the beginning of the experiment using randomly chosen cores from the community providing the lysimeter transplants. Two depths (0–10 cm, and 10–20 cm) were removed for each sample to verify initial root distribution (which was 90% ± 2%, in the upper decimeter). The soil cores were washed with water spray, and the root material was floated and collected, then dried for 48 h at 60°C, weighed, ground to pass a 40-mesh screen, and separated into subsamples for ashing, chemical analysis, and heat of combustion determination. At the end of the experiment, the soil was washed out of the lysimeters with a high-pressure water spray, through a 20-mesh soil screen. The root material was again collected, washed, dried, and ground as before.

I estimated shoot standing crops at the beginning and end of the experiment by clipping all standing *B. tectorum* shoots at the soil surface (under the mulch of dead material). The green material was dried, weighed, ground, and ashed as was the root material.

Seeds presented a problem. The fruit includes both caryopsis and glumes; one glume (the lemma) possesses an awn about 10 mm long. To estimate the weight and constitution of the "seed," I removed the lemma and its awn from the fruit, but left the palea attached to provide a physical support for the tiny caryopsis during handling.

Seeds were separated from mature shoots before harvest of the shoots. The seeds were gathered separately from tall culms, i.e., the dominant tillers in the stand, and short culms, or the suppressed tillers. The difference between dominant and suppressed culms was arbitrarily set at those rising 8 cm above the flag leaf (a nearly horizontal leaf attached about midheight on each culm) to the top of the panicle in normal (nodding) position. Generally, only the tall culms nodded significantly. The culms involved in in each size category were counted and the seeds were weighed both as a total for each size category, and in lots of 200 for individual seed weight estimates.

All biomass measurements refer to ash-free weights after combustion at 600°C.

The procedures involved in proximate analysis are described in the publications of the Association of Official Agricultural Chemists (1965), but the actual analyses reported here were performed by United States Testing Co., Richland, Wash.

Two soils were used in this experiment: Ritzville silt loam for the rooting medium in the bottom of the lysimeters; and Scooteney graveley silt loam which was substrate for the stand of cheatgrass transplanted into the lysimeters (Hajek 1966). Two soils were necessary because the steep hillside providing transplants was too small to provide the soil necessary to fill the lysimeters. Physical and chemical analyses of the two soils are summarized in Table 1. The Ritzville soil had a relatively low nitrogen content, 6 ppm (nitrate + ammonia form), compared to the Scooteney soil of the hillside community used for transplants (17 ppm nitrogen). The high nitrogen content for the Scooteney soil apparently is due to its history; it was an old sheep-holding site and is now quite fertile.

### Imprecision and statistics

Estimates of imprecision were based on standard errors (Snedecor and Cochran 1967), whether from primordial measurements or their linear combinations. Statistical tests of differences were performed on all measurements where such tests were appropriate. However, geometric combinations of mea-

TABLE 1. Soil physical and chemical characteristics for Scooteney and Ritzville silt loams

| Character | Unit | Scooteney | Ritzville |
|---|---|---|---|
| Sand | % | 54 | 42 |
| Silt | % | 42 | 54 |
| Clay | % | 4 | 4 |
| pH | ... | 6.9 | 7.0 |
| Organic matter | % | 1.9 | 1.0 |
| NO$_3$–nitrogen | ppm | 2 | 1 |
| NH$_4$–nitrogen | ppm | 15 | 5 |
| Phosphorus | ppm | 34 | 18 |
| Potassium | ppm | 900 | 320 |
| Calcium | meq/100 g | 6 | 7 |
| Total bases | meq/100 g | 12.5 | 12.5 |
| Cation exchange capacity | meq/100 g | 13.5 | 14.5 |

surements (multiplication or division) skew the distribution of errors to a non-normal form, so tests of significance based on SE may be misleading. I made estimates of precision in these cases by adding and subtracting the SE to the factors involved, giving two estimates of the product (or quotient) with maximal difference (e.g., $[x + e] [y + e] - [x - e] [y - e]$). The difference between these two estimates was divided by 2 to form an "estimated error" which gauges precision in the results but is not appropriate for statistical tests such as a $t$-test.

Most measurements, such as lysimeter weights, standing crop, or seed numbers, involved replicated estimates of an average, to which the above considerations apply. However, the measurements of radiation flux densities (shortwave and allwave) were different. For them, the total variability between any two dates for a given slope was the sum of three components: the overall average, day-to-day weather changes, and the random error of imprecise measurement. The day-to-day differences between slopes formed the essence of the experimental alterations of environment, but a straightforward calculation of an average and standard error placed the day-to-day variability (due to macroscale weather conditions) in the error term rather than in a category related to weather. Consequently, I performed a two-way fixed-effects analysis of variance (without replication) on the radiation data, using slope and date as the two treatments. This approach relegated to the error term only that variability not attributable to the linear model for the analysis of variance between slopes and dates (Guenther 1964).

### Units of measurement

Currently, the scientific community is encountering a change in acceptable units for measurement, away from the traditional centimeter-gram-second Celsius system to the meter-kilogram-second Celsius system (the so-called SI, or Systeme International units). In the SI scheme, the unit of energy is the joule

rather than the calorie (4.18 J cal$^{-1}$) and the unit of energy flux is the watt ($=$ joules per second) (1 W m$^{-2}$ = 0.00143 cal cm$^{-2}$ · min$^{-1}$). Meteorological fluxes are now relatively familiar in terms of watts meter$^{-2}$, but ecological energy equivalents (particularly fluxes) in terms of joules are foreign to nearly all ecologists because of the orders of magnitude differences. I have therefore used duplicate units for some abiotic fluxes while reporting gross energy balances and biological measurements in the traditional units.

### RESULTS AND DISCUSSION

#### Microclimates and abiotic energy budgets

The immediate environment in which plants grow has traditionally been characterized as the microclimate, that is, the climate of the (small) space surrounding organisms, as opposed to the regional climate in which a community or an ecosystem exists. Broadbent (1951) proposed to differentiate between an unmeasurable "microclimate" that plants experience and an "ecoclimate" that instruments actually measure. This distinction is unprofitable, at best, because a basic tenet of science is measurement: unmeasurables are metaphysical. Geiger (1965) used "ecoclimate" to describe the climate near the ground, where plants and animals live, and pointed out on the first page of his classic monograph that radiant fluxes were essential considerations. The smaller the habitat under investigation, the more essential it is to consider radiation budgets: the atmosphere requires fairly extensive time and space intervals to adjust its temperature or humidity profiles to changes in boundary conditions (cf. Rider et al. 1963), but radiant fluxes can change sharply in only a few millimeters.

This experiment amply demonstrated a thermal inertia for the atmosphere, in that temperature contrasts between north- and south-facing exposures were almost nonexistent. Figure 6 illustrates averages of air temperatures, soil temperatures, vapor pressure deficits, wind speeds, and sky cover, along with rainfall and frontal passages, during the period between 31 March and 31 May 1972. Continuous recordings (averaged over the time periods between weighings of the lysimeters) showed that average air temperatures at 10-cm height rarely were so much as 1°C apart, day or night, although soil temperatures on the south exposure were consistently 2°–4°C warmer throughout the profile (apparently because it started to warm up earlier). Vapor pressure deficits, like air temperatures, were very similar on the two exposures. However, wind speeds were consistently higher on the south (windward) slope, particularly during the latter part of May when vigorous frontal passages brought high wind speeds. Nighttime wind
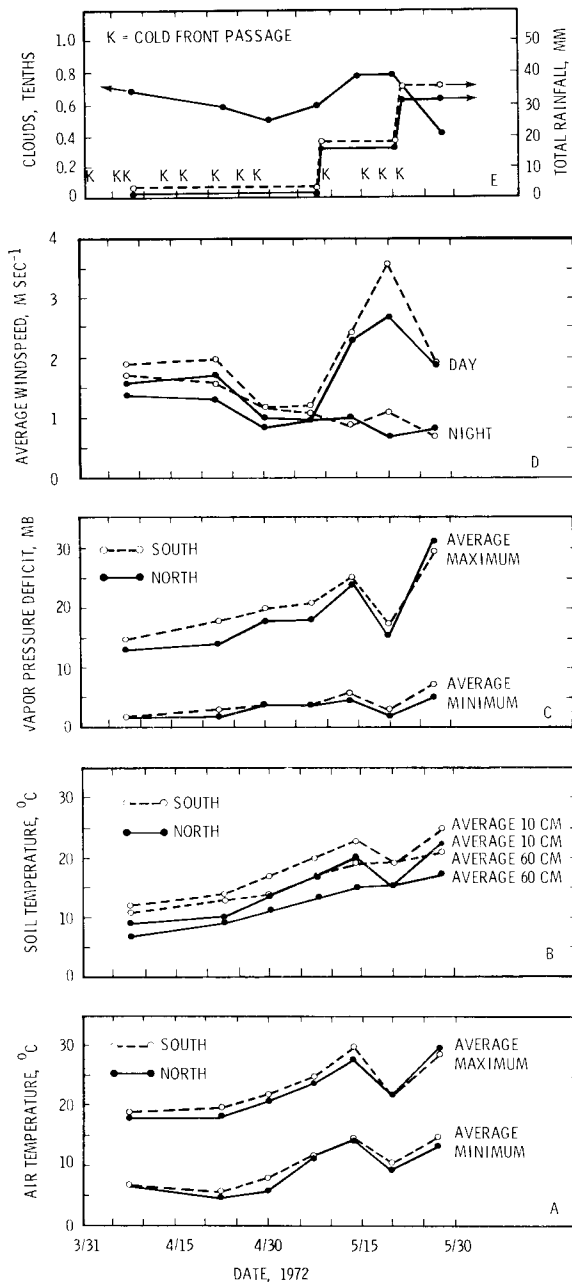
FIG. 6. Average microclimatic conditions between weighings of the small lysimeters.



FIG. 7. Average daily solar elevation angle with respect to 40° slopes, spring season.

speeds showed a persistent tendency to decrease as the season progressed, probably because of the damping of turbulence as radiation cooling at night created stronger temperature inversions in clearer skies. Daytime sky cover decreased somewhat, from 0.7 in early April to 0.5 in early May, but then increased because of vigorous frontal passages. The south-facing slope, being windward, intercepted about 10% more rainfall than the north-facing slope. The final week of the experiment was characterized by warm
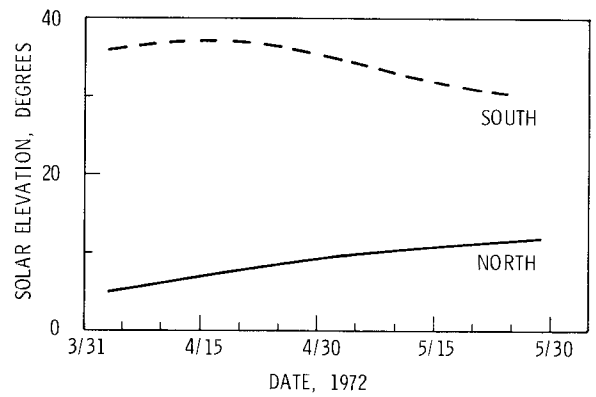
temperatures (near 30°C), clear skies (< 0.4 sky cover), large vapor pressure deficits (> 30 mbars) and moderate winds ($\approx 2$ m s$^{-1}$), providing strong contrasts with the rather wet and cool conditions that prevailed during the preceding weeks, but still without provoking temperature contrasts between exposures.

The small size of the experimental earth mound thus precluded formation of significant atmospheric modifications such as reported for ridges (Jackson 1966) or mountains (Cantlon 1953). However, the sloping surfaces made radically differing angles with incident solar radiation, causing differences in energy absorption that created several energetic contrasts on the two slopes. This is illustrated in Fig. 7, which shows the solar elevation with respect to each slope, averaged over all daylight hours. Although the average elevation angle declined on the south exposure after about mid-April, the typical angle was about 35°, whereas on the north exposure it was less than 10°. This contrast was accentuated in the early part of April, because the sun could shine on the north exposure only between about 1100 and 1300 h.

Figure 8 shows the observed sequence of insolation on the two exposures, along with reflection and net radiation. In early April, insolation averaged nearly 600 cal cm$^{-2}$ · day$^{-1}$ on the south exposure, compared to about 350 cal cm$^{-2}$ · day$^{-1}$ on the north exposure. Net radiation similarly was greater on the south, 260 cal cm$^{-2}$ · day$^{-1}$ compared to about 150 cal cm$^{-2}$ · day$^{-1}$ on the north, but the difference between slopes for both fluxes decreased substantially by mid-May. The reflected portion of incoming solar radiation was not greatly different on the two exposures, because the reflection coefficient increases with declining solar elevation (Monteith and Szeicz 1961, Hinds 1974).

Table 2 lists the total incoming solar radiation on the two exposures for April and May along with the

TABLE 2. Growing season insolation on experimental surfaces in relation to a horizontal surface

|  | North | South |
|---|---|---|
| Insolation (kcal cm$^{-2}$) |  |  |
| April | 12.4 | 19.8 |
| May | 16.6 | 20.7 |
| Total | 29.0 | 40.5 |
| Deviation from horizontal |  |  |
| April | − 24% | + 22% |
| May | − 11% | + 12% |
| Total | − 17% | + 16% |



FIG. 8. Average radiant flux densities on north- and south-facing slopes, spring 1972.

corresponding deviations from a horizontal surface. April was the month of strongest slope effect, causing deviations of about ± 20% due to slope; May produced deviations of about 10%. As a whole, the slope effect produced about equal energetic augmentation on the south and diminution on the north. This would not have been perceived by calculating direct beam reception on the slopes (as recommended by Garnier and Ohmura 1968, for example), because the very significant effect of diffuse radiation would not then be considered (a recent and more complicated computation proposed by Williams et al. 1972 might provide reasonable estimates of both direct and diffuse fluxes). The significance of diffuse radiation was implicit in Fig. 6, which shows that the daytime sky cover averaged over 60% throughout the spring; overcast skies often have no direct beam component of insolation.

Sensible heat fluxes are listed in Table 3, showing that the high solar radiation intensities incident on the south exposure were associated with very much higher sensible heat fluxes to the atmosphere, but not to the soil, an indication that most of the insola-
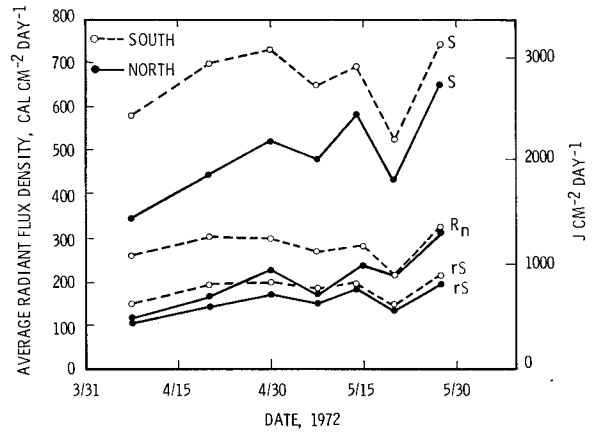
tion was intercepted by the cheatgrass community. Sensible heat flux to the soil was actually somewhat greater than shown here, particularly on the south exposure, because temperatures were increasing with time at the bottom of the lysimeters. This error is small: about a tenth of the estimated soil fluxes.

Latent heat fluxes, also listed in Table 3, show that the rate of transpiration continued to increase on the north exposure long after it had declined on the south exposure. The total latent heat flux (evapotranspiration) remained much more nearly constant throughout the experiment on the south exposure than on the north, but the maximum rate of both evaporation and transpiration occurred on the north, following late season rains.

### Water relations

Only one significant flux in the energy budget (Table 3) did not total to a difference between

TABLE 3. Average energy budgets ($\bar{x} \pm$ SE) for *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes, spring 1972

| Flux | Exposure | 3-31 4-17 | 4-18 4-25 | 4-26 5-3 | 5-4 5-11 | 5-12 5-15 | 5-16 5-23 | 5-24 5-31 | Season average | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Net radiation | North | 114 ±10 | 163 ±10 | 227 ±15 | 179 ±13 | 241 ±12 | 218 ±12 | 324 ±12 | 192 ± 7 | 11,900 ±400 |
|  | South | 260 ±11 | 301 ±11 | 302 ±15 | 275 ±13 | 286 ±12 | 212 ±12 | 326 ±12 | 277 ± 7 | 17,200 ±400 |
| Evaporation | North | 39 ±10 | 5 ± 3 | 12 ± 4 | 17 ± 3 | 99 ±29 | 23 ±17 | 68 ± 5 | 34 ± 2 | 2,060 ±100 |
|  | South | 40 ± 4 | 27 ± 7 | 9 ± 3 | 64 ± 4 | 41 ±11 | 55 ±12 | 46 ±25 | 40 ± 2 | 2,460 ±100 |
| Transpiration | North | 42 ± 6 | 74 ± 4 | 74 ± 6 | 99 ± 5 | 113 ±15 | 48 ± 8 | 57 ± 6 | 66 ± 3 | 3,980 ±160 |
|  | South | 72 ± 6 | 106 ± 6 | 91 ± 5 | 50 ± 8 | 92 ±12 | 6 ± 7 | 51 ±15 | 70 ± 4 | 4,260 ±230 |
| Sensible, to soil | North | −5 | 4 | 13 | 0 | 14 | −10 | 35 | 4 | 850 |
|  | South | −5 | 4 | 12 | 0 | ·13 | −9 | 35 | 4 | 850 |
| Sensible, to atmosphere | North | 38 ±11 | 80 ±12 | 128 ±17 | 63 ±14 | 15 ±16 | 157 ±13 | 164 ±13 | 88 ±14 | 5,000 ±850 |
|  | South | 153 ±12 | 164 ±13 | 190 ±18 | 161 ±18 | 140 ±13 | 160 ±13 | 194 ±13 | 163 ±14 | 9,600 ±880 |
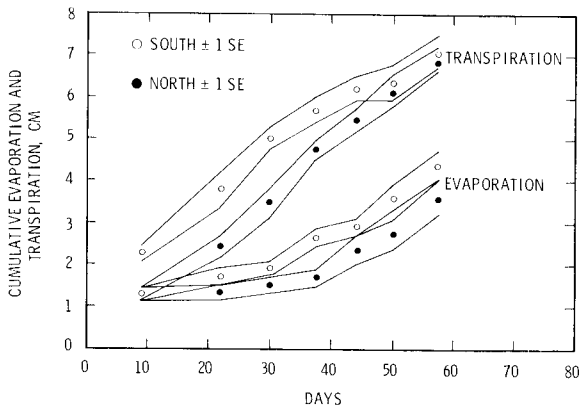
FIG. 9. Cumulative evaporation and transpiration on north- and south-facing slopes as a function of time after 31 March 1972.

exposures: transpiration. As shown in Fig. 9, the south exposure started with the same evaporative flux as the north, but as the season progressed, the total evaporation from the south exposure exceeded that from the north, i.e., these two curves in Fig. 9 diverge. Transpiration, however, was quite the opposite: the curves converge. The south exposure began with a higher rate, which declined later in the season; the final total of transpired water was practically identical on both exposures.

A change in transpiration rate on both exposures was related to the amount of soil water remaining in the profile. Figure 10 shows the temporal coincidence on each exposure of a change of rate of transpiration with a change in the fraction of available energy used for transpiration at the same soil-water content (in the 60-cm profile) of about 7.5 cm³ cm⁻², or 10%, using a bulk density of 1.25 g cm⁻³ (Hinds 1973). Ritchie et al. (1972) described similar results for corn and cotton, but with the ratio of evapotranspiration to net radiation near unity, rather than about 0.4 as in Fig. 10B—i.e., a subhumid climate as opposed to a semi-arid climate.

The course of events leading to the relatively abrupt change in transpiration rate (and imposition of water stress) on the south exposure can be put in perspective by the following approximate analysis. A soil-water content of 10%, if uniformly distributed through the 60-cm profile, would correspond to a soil-water potential of about −14 bars (T. R. Garland, *pers. comm.*). Likewise, a soil-water content of about 11% would correspond to a water potential of about −10 bars; this soil-water content was attained about 8 or 10 days before the rate of transpiration changed sharply, on both exposures. If, as Lawlor (1973) noted for wheat, cheatgrass roots grew but slowly in soils characterized by −10 bars water potential, then the aging roots in the lysimeters might not have been able to absorb efficiently the increasingly
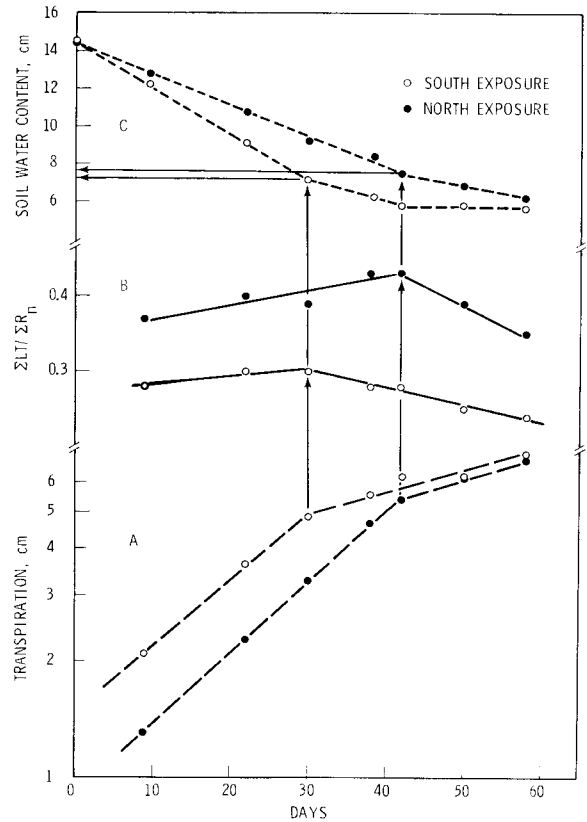


FIG. 10. A. Cumulative transpiration (log scale). B. Fraction of available energy used in transpiration. C. Soil water content in the profile (60 cm deep), as a function of time.

rarified soil water. At a soil-water content typified by −14 bars, then, the total availability of water to the plants had decreased sufficiently to alter the rate of transpiration.

These estimates of water potentials, derived as they were from profile totals of water content, cannot be closely interpreted, because the rate of water uptake depends upon the distribution of water throughout the profile. However, the estimates are probably representative of the stresses to which the plants were subjected, and they are close to traditional levels for "wilting point," about −15 bars.

The close parallelism among the curves in Fig. 10 suggests that the principal difference in water relations on the two exposures was merely the rate of water use. Soil water available for transpiration apparently was initially removed at rates corresponding to the energy available, with resistance to water movement primarily in the plants and atmosphere. However, after the water content in the profile had decreased sufficiently, an additional resistance intruded into the water pathway, possibly a soil hydraulic resistance, that reduced transpiration immediately, more or less as postulated by Penman (1956). The

TABLE 4. Phenological progression of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes, spring 1972 (sample size = 13)

| Milestone | North | South |
|---|---|---|
| | Date | |
| Exposed (all vegetative) | 31 Mar | 31 Mar |
| 10% in flower | 12 May | 11 May |
| 50% in flower | 15 May | 13 May |
| 90% in flower | 18 May | 15 May |
| End experiment | 31 May | 31 May |
| | Phenological stage on 31 May | |
| Green culms, % | 16 ± 2.0 | 12 ± 2.0 |
| Red culms, % | 21 ± 2.0 | 20 ± 1.6 |
| Dead culms, % | 63 ± 4.0 | 68 ± 3.6 |

TABLE 6. Root-to-shoot and seed-to-shoot ratios of spring production and at peak standing crop of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes (sample size = 13). Numbers following ± are estimated error (see "Imprecision and Statistics," Methods section)

| Exposure | Root:shoot ratio | | Seed:shoot ratio | |
|---|---|---|---|---|
| | Peak standing crop | Spring production | Peak standing crop | Spring production |
| North | .40 ± .04 | .56 ± .08 | .34 ± .03 | .56 ± .06 |
| South | .31 ± .02 | .41 ± .05 | .24 ± .02 | .39 ± .04 |

transition from a freely transpiring regime to the parsimonious era occurred after 30 days on the south exposure, and after 45 days on the north exposure, giving the north a fortnight longer without severe water stresses. It will be shown in the next section that root and seed biomass production was much less on the south exposure than on the north, probably because of this shortening of the growing season on the south exposure.

## Production and energy fixation

Ordinarily, changes in phenological progression on contrasting exposures form a significant dimension of slope effects (Cantlon 1953, Jackson 1966). Cheatgrass is especially plastic in this respect; observations on other earth mounds have indicated as much as 1 mo difference in phenological milestones of cheatgrass on north and south slopes (Rickard et al. 1971). However, direct comparisons between north and south slopes in this experiment required the plants to be at the same phenological stage. This was indeed the case, as shown in Table 4. Although plants on the south slope began flowering a day or two sooner (11 May, compared to 12 May on the

north) and at a slightly faster rate (4 days, compared to 6 days on the north to complete flowering), still, by the end of the experiment, the distribution of maturity of the culms was not significantly different. The slope effect on phenology was minimized here by three factors: temperature differences were slight; the plants were exposed to the experimental conditions for only a relatively short time (60 days); and they began the experiment in identical condition on both slopes. Seedling history appears to be very influential for development of maturing cheatgrass.

The biomass of the cheatgrass at the beginning of the experiment (31 March) and at the end (31 May) is tabulated in Table 5. The final standing crop (aboveground plus belowground) was not significantly different on the two exposures, 608 g m$^{-2}$ on the north and 564 g m$^{-2}$ on the south. Neither was the springtime production of stems and leaves: 214 g m$^{-2}$ on the north and 228 g m$^{-2}$ on the south. However, the springtime production of roots and seeds were both significantly higher on the north exposure: 121 compared to 94 g m$^{-2}$ for roots and 119 compared to 88 g m$^{-2}$ for seeds. Still, total springtime production was only marginally different, 454 compared to 410 g m$^{-2}$.

The standing crop of leafy tissues provides the

TABLE 5. Biomass production (g/m$^2$ ash-free) of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes between 31 March and 31 May, 1972 (*n* is sample size; numbers following ± are SE; *p* is probability of the difference occurring by chance)

| Part | Exposure | 31 Mar | *n* | 31 May | *n* | Net production |
|---|---|---|---|---|---|---|
| Root | North | 18 ± 2 | 16 | 139 ± 11 | 13 | 121 ± 13 |
| | South | 18 ± 2 | 16 | 112 ± 8 | 13 | 94 ± 10 |
| | *p* | | | .009 | | .04 |
| Shoot | North | 136 ± 9 | 15 | 350 ± 19 | 13 | 214 ± 34 |
| | South | 136 ± 9 | 15 | 364 ± 16 | 13 | 228 ± 31 |
| | *p* | | | .4 | | .50 |
| Seeds | North | . . . | . . . | 119 ± 7 | 13 | 119 ± 7 |
| | South | . . . | . . . | 88 ± 7 | 13 | 88 ± 7 |
| | *p* | | | 10$^{-1}$ | | 10$^{-1}$ |
| Total | North | 154 ± 11 | . . . | 608 ± 37 | 13 | 454 ± 54 |
| | South | 154 ± 11 | . . . | 564 ± 31 | 13 | 410 ± 48 |
| | *p* | | | .2 | | .1 |

TABLE 7. Heats of combustion (kcal/g, ash-free[a]) of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes. Numbers following ± are SE. *N* = sample size

| Date | Part | Exposure | N | Heat of combustion |
|------|------|----------|---|--------------------|
| 31 Mar | Root | . . . | 4 | 4.32 ± .02 |
| | Shoot | . . . | 6 | 4.66 ± .07 |
| 31 May | Root | North | 13 | 4.09 ± .08 |
| | | South | 13 | 4.08 ± .07 |
| | Shoot | North | 13 | 4.36 ± .03 |
| | | South | 13 | 4.38 ± .09 |
| | Seed | North | 13 | 4.22 ± .02 |
| | | South | 13 | 4.23 ± .06 |

[a] 1 kcal/g = 4.184 J/mg

TABLE 9. Proximate analysis (% ash-free) of immature *Bromus tectorum* plants, 31 March 1972. *N* = sample size, $\bar{x}$ ± SE

| Part | N | Crude protein | Crude fat | Crude fiber | Nitrogen-free extract |
|------|---|---------------|-----------|-------------|-----------------------|
| Root | 4 | 12 ± 0.4 | 1.3 ± 0.14 | 22 ± 0.9 | 65 ± 1.1 |
| Shoot | 6 | 24 ± 1.3 | 2.9 ± 0.2 | 18 ± 0.5 | 56 ± 2.7 |

photosynthetic activity to support the rest of the plant, so an indication of the relative efficacy of leaf activity on the two exposures is the growth of nonphotosynthetic tissues supported during the season by the leafy tissues. Table 6 shows the ratios of roots to shoots, and of seeds to shoots, measured on the north and south exposures. The ratios in terms of standing crops at the end of the experiment were variable, with the north exposure being somewhat the greater. However, in terms of springtime growth only, constant ratios resulted for both root/shoot and seed/shoot ratios: 0.56 on the north, and 0.40 on the south. This indicates that each gram of spring-grown shoot tissue from the north supported the growth of 1.12 g of nonproductive tissues, as opposed to only 0.8 g by the south shoots, a striking 40% increase on the north.

The energy fixed in plant tissues and measured as heat of combustion was very similar on the two exposures, as shown in Table 7, but it differed significantly between plant parts, and, for both roots and shoots, decreased with maturity. The

heats of combustion in Table 7 are somewhat lower than expected from literature values for grasses in general; Hunt (1966) suggested 4.9 kcal g⁻¹ ash-free as an appropriate average for grasses, substantially higher than the 4.36 kcal g⁻¹ (= 18.2 J/mg) for mature shoots in Table 7. Hunt possibly was referring to relatively young, green tissues, but his suggestion is still higher than the 4.66 kcal g⁻¹ (= 19.5 J/mg) I found for immature cheatgrass shoots. Other workers have reported higher values for cheatgrass than I found here, particularly for seeds: for instance, R. K. Schreiber (*pers. comm.*) determined heats of combustion of cheatgrass seeds from a different site on the Hanford Reservation to be about 4.7 kcal g⁻¹ (= 19.7 J/mg). These differences are currently inexplicable.

The photosynthetic efficiencies for the two exposures are summarized in Table 8. The overall efficiency was calculated on the basis of total incoming solar radiation and ash-free biomass production, resulting in an efficiency of 0.67% on the north and 0.43% on the south. This efficiency resulted from (1) approximately equal biomass production on the two exposures, (2) equal heats of combustion, and (3) unequal solar fluxes; it is not related to the efficacy of leafy biomass in supporting other tissues, as discussed earlier. The term "efficacy" related to partitioning, or allocation, of biomass,

TABLE 8. Net (ash-free) photosynthetic efficiency of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes (sample size = 13). Numbers following ± are SE; *P* is probability of the difference occurring by chance

| Parameter | Exposure | Root | Shoot | Seed | Total |
|-----------|----------|------|-------|------|-------|
| Net production (g/m²) | North | 120 ± 11 | 214 ± 21 | 119 ± 6.6 | 453 ± 32 |
| | South | 93 ± 8 | 228 ± 19 | 88 ± 6.9 | 409 ± 24 |
| | *p* | .009 | .50 | .0001 | .1 |
| Heat of combustion (kcal/g) | North | 4.09 ± .083 | 4.36 ± .026 | 4.22 ± .023 | . . . |
| | South | 4.08 ± .072 | 4.38 ± .010 | 4.23 ± .056 | . . . |
| | *p* | .009 | .50 | .0001 | .1 |
| Photosynthetic energy fixation (kcal/m²) | North | 491 ± 46 | 933 ± 91 | 502 ± 28 | 1926 ± 106 |
| | South | 379 ± 33 | 999 ± 83 | 372 ± 29 | 1750 ± 94 |
| | *p* | .009 | .4 | .0001 | .09 |
| Incident shortwave radiation (kcal/cm²) | North | . . . | . . . | . . . | 29.0 ± 0.60 |
| | South | . . . | . . . | . . . | 40.5 ± 0.60 |
| Net photosynthetic Efficiency (%)[a] | North | 0.17 ± .02 | 0.32 ± .04 | 0.17 ± .01 | 0.67 ± .05 |
| | South | 0.093 ± .009 | 0.24 ± .02 | 0.093 ± .009 | 0.43 ± .03 |

[a] Numbers following ± are estimated error ("Imprecision and Statistics," in Methods section).

TABLE 10. Proximate analysis (% ash-free) of mature *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes, spring 1972. Numbers following ± are SE; *P* is the probability of the difference occurring by chance. *N* = sample size

| Part | Exposure | *N* | Crude protein | Crude fat | Crude fiber | Nitrogen-free extract |
|------|----------|-----|---------------|-----------|-------------|----------------------|
| Root | North | 5 | 11.3 ± 0.3 | 0.75 ± 0.10 | 29 ± 1.3 | 59 ± 2.0 |
|      | South | 3 | 10.4 ± 0.3 | 0.77 ± 0.15 | 26 ± 1.9 | 63 ± 1.9 |
|      | *p*   |   | .05 | .23 | .1 | .84 |
| Shoot | North | 13 | 6.6 ± 0.4 | 3.3 ± 0.4 | 32 ± 0.6 | 57 ± 0.5 |
|       | South | 13 | 8.3 ± 0.15 | 3.0 ± 0.15 | 32 ± 1.1 | 56 ± 1.3 |
|       | *p*   |   | $10^{-5}$ | .33 | 1.0 | .28 |
| Seed | North | 5 | 11.7 ± 0.3 | 1.3 ± 0.2 | 17 ± 0.6 | 70 ± 0.9 |
|      | South | 3 | 13.1 ± 0.2 | 1.0 ± 0.9 | 16 ± 0.4 | 70 ± 0.7 |
|      | *p*   |   | .005 | .08 | .09 | 1.0 |

whereas the efficiency calculated in Table 8 was derived from production and energy availability.

The efficiencies in Table 8 are somewhat lower than corresponding efficiencies reported in other climates or for other species. Botkin and Malone (1968) summarized results from several climates and communities, mostly reporting efficiencies under 1% for aboveground production alone. However, gross efficiencies for (nonagricultural) oligospecific communities are usually lower than those for multi-specific communities; for example, the efficiency reported here is comparable to the 0.3% to 0.4% reported by Golley (1965) for an old-field dominated by broomsedge.

### Carbon pathways

The distribution of photosynthetically fixed carbon in cheatgrass roots and shoots at the beginning of the experiment is listed in Table 9; it is quite comparable to that found for many other immature grasses: high in crude protein, low in crude fiber (McIlroy 1967, National Academy of Sciences 1969). The analysis of mature root, shoot, and seed biomass at the end of the experiment is shown in Table 10. Significant differences between exposures were found

only in crude protein content. Aboveground, the south exposure had the higher crude protein content, 8.3%, compared to 6.6% in shoots, and 13.1% compared to 11.7% in seeds; belowground, the north had the higher content, 11.3% compared to 10.4% on the south. All other categories were not significantly different between slopes.

Compared to the analysis of juvenile cheatgrass (Table 9), the mature grass (Table 10) had much less crude protein content, and much more crude fiber content. Rapid nitrogen uptake by juvenile plants is a fundamental aspect of plant physiology; it occurs even when nitrogen is severely deficient (Langer 1966) or when water is deficient (Johnson and Nichols 1969). The crude fiber content, on the other hand, continually increases as structural tissues are progressively matured and lignified (McIlroy 1967), ultimately providing the strength required to support heavy seed panicles on very slender columns.

A detailed analysis of the relative importance of the various carbon pathways for springtime aboveground growth of cheatgrass is provided in Table 11. The pathways are identified according to proximate analysis, so there is probably a significant overlap

TABLE 11. Allocation of assimilation among four carbon pathways in springtime production of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes. Numbers following ± are estimated errors ("Imprecision and Statistics," in Methods section)

| Pathway | Exposure | Root g/m² | Root % | Shoot g/m² | Shoot % | Seed g/m² | Seed % | Total g/m² | Total % |
|---------|----------|-----------|--------|------------|---------|-----------|--------|------------|---------|
| Crude protein | North | 14 ± 2.3 | 12 | −10 ± 6 | −5 | 14 ± 1.2 | 12 | 18 ± 10 | 4 |
|               | South | 10 ± 1.5 | 10 | −3 ± 5 | −1 | 12 ± 1.1 | 13 | 19 ± 8 | 5 |
| Crude fat | North | 0.8 ± 0.2 | 1 | 8 ± 2 | 4 | 1.6 ± 0.3 | 1 | 10 ± 2 | 2 |
|           | South | 0.7 ± 0.2 | 1 | 8 ± 2 | 4 | 0.9 ± 0.2 | 1 | 10 ± 2 | 2 |
| Crude fiber | North | 36 ± 6 | 30 | 88 ± 10 | 42 | 20 ± 1.9 | 17 | 140 ± 18 | 31 |
|             | South | 26 ± 5 | 27 | 92 ± 12 | 44 | 14 ± 1.5 | 16 | 130 ± 18 | 32 |
| Nitrogen-free extract | North | 70 ± 11 | 58 | 125 ± 21 | 59 | 84 ± 6 | 70 | 280 ± 38 | 62 |
|                       | South | 58 ± 8 | 61 | 129 ± 22 | 57 | 62 ± 6 | 70 | 250 ± 36 | 61 |

TABLE 12. Nutrient content (% ash-free) of *Bromus tectorum* shoots grown in small lysimeters on north- and south-facing slopes (sample size = 13). Numbers following ± are SE, $p$ is the probability of the difference occurring by chance

| Exposure | N | P | K | Ca |
|---|---|---|---|---|
| North | 1.06 ± .06 | .16 ± .01 | 1.09 ± .10 | .78 ± .01 |
| South | 1.33 ± .02 | .20 ± .01 | 1.34 ± .09 | .92 ± .05 |
| $p$ | $10^{-5}$ | .008 | .02 | $10^{-4}$ |

in some of the biochemicals involved, particularly for the division of carbohydrates into "celluloses" (crude fiber) and "starches" (nitrogen-free extract, NFE), because of failings of the proximate analysis technique (Van Soest 1967).

Nonetheless, useful ecological insights devolve from Table 11. A negative production of crude protein in shoot material is indicated, which can only mean a net export from the juvenile plant to new growth during the spring; this seems more likely to be a real translocation in grass from the north exposure than from the south. High temperatures rapidly increase the rate of denaturation of proteins (cf. Morowitz 1968:115), so higher leaf surface temperatures on the south exposure (deduced from the greater sensible heat flux to the atmosphere) might have precluded export of nitrogenous compounds to other tissues because of a metabolic demand for restructuring existing proteins. Production of crude fat, crude fiber, and NFE was very similar on the two exposures in shoot material but differed in root material because of greater root biomass production on the north exposure. Differences appeared in total production of seed material in all categories: fruits from the north exposure totaled to a higher biomass, but with a percent composition similar to that of south exposure seeds.

Comparison of mature and immature cheatgrass showed phenological alteration of carbon pathways

to be very similar on the two exposures. The crude protein pathway was not strongly represented during spring growth, being about an order of magnitude less important (and of opposite sign) during the spring than in the seedling growth of the juvenile plants (−1% to −3% in the spring, compared to 24% in the juvenile plants). The crude fat pathway was essentially unchanged between juveniles and springtime growth: nearly 3% in both cases. Likewise, the NFE pathways were similar between exposures and between ages: about 60% in all cases. However, the crude fiber pathways made a strong contrast between ages: 18% for the young plants, and 38% for the springtime growth, similar to that noted by McIlroy (1967) for grasses in general. Table 11 thus shows that for cheatgrass, at least, phenologically induced changes in carbon pathways were largely decoupled from environmental stress or abundance. The phenological plasticity for which cheatgrass is noted must be accompanied by a sturdy and homeostatic physiology of adult growth and development.

### Mineral nutrients

Greenhouse trials indicated a difference between soils in reaction to fertilization, with the soil used in the bottom 40 cm of the lysimeters more responsive than the soil in which the transplanted grass was naturally rooted. However, the greenhouse trials indicated little difference between soils for control treatments.

The nutrient content of the shoots of mature plants at the end of the experiment is summarized in Table 12. The mineral contents tended to be greater in young plants grown in greenhouse trials than in mature plants, reflecting a rapid uptake common in juvenile plants (Langer 1966). Calcium contents were higher in the field-grown plants. However, comparisons involving greenhouse and field-grown plants are ambiguous at best (Stefanson and Collis-

TABLE 13. Reproductive success of dominant and suppressed tillers of *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes. (Dominant tillers stood higher than 8 cm above their flag leaf.) Numbers following ± are SE, $p$ is the probability of the difference occurring by chance. $N$ = sample size

| Tiller size | Exposure | N | Culms/m² | Seeds/ culm | Wt/seed (mg) | (Seeds × 1,000)/m² | Total seed biomass (g/m²) |
|---|---|---|---|---|---|---|---|
| Dominant | North | 13 | 640 ± 60 | 45 ± 2.4 | 2.48 ± .07 | 24 ± 3 | 70 ± 7 |
| | South | 8 | 480 ± 53 | 43 ± 4.6 | 2.32 ± .11 | 22 ± 4 | 50 ± 7 |
| | $p$ | | .01 | .6 | .09 | .06 | .011 |
| Suppressed | North | 13 | 2,600 ± 250 | 10 ± 0.7 | 1.98 ± .06 | 25 ± 2.4 | 49 ± 4 |
| | South | 8 | 2,900 ± 120 | 7 ± 0.8 | 1.89 ± .10 | 20 ± 2.6 | 39 ± 7 |
| | $p$ | | .12 | .0007 | .28 | .06 | .08 |
| All | North | 13 | 3,300 ± 220 | . . . | 2.22 ± .05 | 54 ± 3.4 | 119 ± 7 |
| | South | 13 | 3,400 ± 120 | . . . | 2.07 ± .05 | 43 ± 3.1 | 88 ± 7 |
| | $p$ | | .56 | | .006 | .002 | .0001 |

TABLE 14. Average composition of seeds from *Bromus tectorum* grown in small lysimeters on north- and south-facing slopes. Numbers following ± are estimated errors ("Imprecision and Statistics," in Methods section). All values expressed in milligrams

| Exposure | Crude protein | Crude fat | Crude fiber | Nitrogen-free extract | Average seed weight |
|---|---|---|---|---|---|
| North | .26 ± .01 | .03 ± .005 | .38 ± .02 | 1.55 ± .05 | 2.22 ± .05 |
| South | .27 ± .01 | .02 ± .002 | .33 ± .02 | 1.45 ± .04 | 2.07 ± .05 |

George 1974b); ecological significance is best attached to the differences between mature plants on the north- and south-facing exposures (Table 12): all nutrient contents were about 20% greater on the south (warm, dry) exposure. This uniform differentiation between slopes was in response to environmental conditions, rather than soil conditions or root distribution, which were optimal for the grass (cf. Stefanson and Collis-George 1974a).

### Reproduction

The response of cheatgrass to environmental conditions, insofar as production of reproductive organs is concerned, forms an important part of the natural history of this grass. Cheatgrass is a good example of a colonizer species: it is an annual that allocates a large amount of each year's growth to seed production, and it produces a large number of small seeds, maximizing the chances for germination of viable seeds. Table 13 summarizes some pertinent data regarding seed numbers and production from the north and south exposures.

The number of dominant culms was much higher on the north, 640 $m^{-2}$ compared to 480 $m^{-2}$ on the south, but the much more numerous suppressed culms were marginally fewer (2,600 $m^{-2}$ on the north and 2,900 $m^{-2}$ on the south). The preponderance of suppressed culms allowed no significant difference to arise in total density of culms on both exposures: about 3,300 $m^{-2}$ on both (toward the high side of the densities studied by Hulbert 1955). Differential mortality between slopes therefore was nonexistent; instead, more plants on the north grew vigorously, producing more dominant culms.

The number of seeds per dominant culm was very similar (45 on the north, 43 on the south) but the number of seeds per suppressed culm was about 50% greater on the north, 10 compared to 7 on the south. Individual seed weights were uniformly larger from the north exposure, and larger from the dominant culms, decreasing in the order 2.45 mg (dominant, north), 2.32 mg (dominant, south), 1.98 mg (suppressed, north), and 1.89 mg (suppressed, south). A one-way analysis of variance and the Studentized Range test (Snedecor and Cochran 1967:272) indicated all weights were significantly different at $p < 0.01$. The total number of seeds

was significantly greater on the north, both from dominant and suppressed categories, and also as a total, 54,000 $m^{-2}$ on the north, compared to 43,000 $m^{-2}$ on the south. The total seed biomass from dominant culms was significantly higher from the north exposure (70 g $m^{-2}$ compared to 50 g $m^{-2}$ from the south), but the difference in biomass of seeds from the suppressed culms, like the number of suppressed culms, was only marginally different (49 g $m^{-2}$ on the north, 39 g $m^{-2}$ on the south). Total seed biomass was highly significantly different, 119 g $m^{-2}$ from the north and 88 g $m^{-2}$ from the south.

The season ultimately revealed a very successful reproductive effort on the north exposure compared to a noticeably less robust effort on the south, particularly for the suppressed culms. However, there is more to reproductive success than merely biomass or numbers. Both exposures produced a glut of seeds; even the south exposure produced more than 4 seeds/$cm^2$, whereas the parent culm density was less than a tenth as high: 0.3 culms/$cm^2$. Both exposures therefore produced much more than mere replacement numbers, implying that the seedlings would face severe intraspecific competition the following year.

Table 14 lists the composition of an average seed from north and south exposure plants. Although the seed weight was greater from the north exposure, the weight of crude protein in an average seed was almost identical. This probably was an important compensation. Seedling survival in wheat has been directly correlated with the amount, not the concentration, of nitrogen in wheat seeds (Lowe and Ries 1973, Ries and Evanson 1973); the same may well be true for cheatgrass, which resembles wheat both taxonomically and phenologically.

Crude fat, crude fiber, and nitrogen-free extract in an average seed were all reduced in seeds from the south exposure, with unknown importance for germination and seedling survival. The clearest interpretation lies in the reduction in nitrogen-free extract, which probably represents starches in the endosperm; a north exposure seed apparently had about 8% more inventory to supply the seedling during the early stages of germination and growth. The importance of this excess (compared with seeds from

the south exposure) in conjunction with the identical crude protein content is unknown at this time.

Germination success (in soil) of the seeds from the various culms, from four tests with 15 replications of 16 seeds each, showed the seeds to be highly viable, about 90%, as reported by others (Hulbert 1955, Rickard et al. 1971), with no differences between seed sources.

The homeostatic natures of seed weight and composition are well known (Harper et al. 1970) and were amply demonstrated in this experiment. Homeostasis in seed characteristics on the two slopes decreased in the following order: viability (very strong) > composition (strong) > weight (moderate) > numbers (none noticeable).

## CONCLUSIONS

Temperatures and humidities on the contrasting north- and south-facing exposures were much more similar than the magnitude and disposition of energy fluxes on the two slopes. Average daytime temperatures and vapor pressure deficits were quite similar, as were total rainfall and wind speeds, perhaps leading to a conclusion that little difference redounded from slope exposure. This would be false, for the energy-rich south exposure had specific modes of energy transfer exaggerated in comparison with the north exposure (Fig. 11), the most important of which was sensible heat transfer to the atmosphere. Plants growing on the south exposure had about a third again as much energy impinge upon them in the form of net radiation as did the north-exposure plants; of this excess, about 80% went into heating the atmosphere, and about 20% into evaporation of water from soil (not plant) surfaces. This was just about the excess rainfall intercepted by the south exposure because of its windward orientation.

Water played a passive role in the energy budgets of the cheatgrass; so long as soil water remained readily available (an average of more than 10% by weight through the 60-cm profile), transpiration continued at a rate determined by energy availability. However, after the soil had dried out to an average water content of less than 10%, the rate of transpiration decreased sharply below the preceding freely transpiring rate. The decrease in rate of water use occurred near day 30 on the south, about 10 days before flowering, but near day 45 on the north, after initiation of flowering; apparently this timing was peculiarly difficult for the south-exposure plants, inducing decreased seed and root production.

Biomass production of shoot material (leaves and stems) was not very different on the two exposures, in spite of the apparent difference in length of growing season; this suggests a more rapid growth rate for leafy tissues on the south exposure, considering the shorter interval of water availability. However,
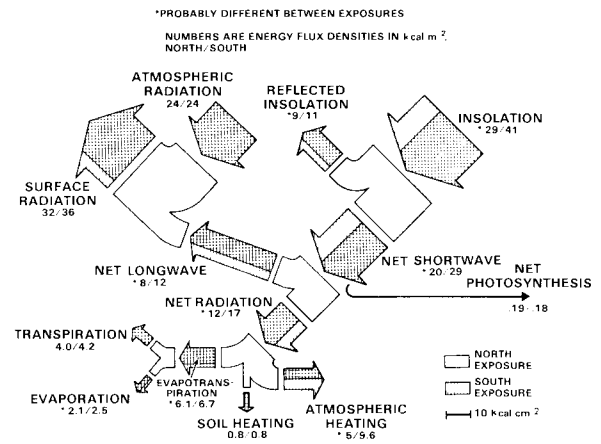


FIG. 11. Flow sheet of energy in the environment on north- and south-facing slopes, spring 1972.

both root and seed production were greater on the north exposure (Fig. 12). If, like wheat, cheatgrass slowed or ceased root growth in relatively dry soils, then the longer growing season on the north would indeed allow greater root production. Similarly, the relatively favorable water conditions at flowering for the north-exposure plants would have allowed formation of a greater number of fertile florets during flowering. Consequently, the rate of water use was limiting, rather than the total amount available, because there was no difference between total transpired water on the two exposures.

The upshot of these two water-related phenomena was a substantially greater production of both roots and seeds on the north with essentially equal shoot production: 1 g of new shoot tissue supported 1.12 g of nonproductive tissues (roots and seeds) on the north, but only 0.8 g on the south exposure, a difference of 40%. However, efficiency (defined as energy captured as biomass per unit insolation energy) was 0.43% on the south, and 0.67% on the north, nearly 60% greater on the north, because of two factors: more production, and less insolation, on the north.

The juvenile plants at the beginning of the experiment were high in crude protein (20%) and low in crude fiber (18%). However, during the spring period of growth, the mass of crude protein in the shoots actually declined, indicating translocation to other tissues, more so on the north (about 33% of the initial inventory) than on the south (about 5% of the initial inventory). The fraction of mass allocated to crude fiber increased from about 18% in juvenile plants to about 40% during spring growth on both exposures. Ultimately, the mature shoots on both exposures were closely similar in crude fat, crude fiber, and nitrogen-free extract, differing only in crude protein.

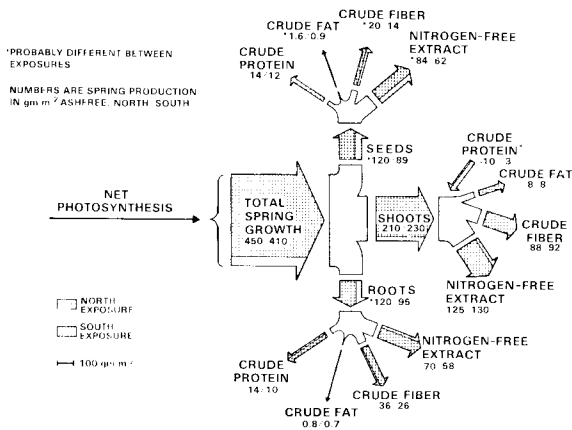Root production (g m$^{-2}$) on the two exposures

FIG. 12. Fate of assimilated carbon during the spring growth phase of *Bromus tectorum*, on north- and south-facing slopes, spring 1972.



| STRONG | | % DIFFERENCE |
|---|---|---|
| | AVERAGE SEED VIABILITY | ~ 0 |
| | TOTAL, SEED COMPOSITION | ~ 5 |
| | TOTAL, ROOT COMPOSITION | ~ 5 |
| | TOTAL, SHOOT COMPOSITION | ~ 5 |
| MODERATE | SHOOT PRODUCTION | ~ 10 |
| | AVERAGE SEED WEIGHT | ~ 10 |
| | AVERAGE SEED COMPOSITION | ~ 10 |
| | SEED NUMBERS | ~ 25 |
| | ROOT PRODUCTION | ~ 25 |
| | SEED PRODUCTION | ~ 30 |
| WEAK | INSOLATION | ~ 30 |

FIG. 13. Degrees of homeostasis observed in *Bromus tectorum* growing on north- and south-facing slopes, in terms of deviation from averages of the two exposures.

was significantly different, greater on the north, but the fractionation (percent composition of crude protein, fat, fiber, and NFE) differed only for protein. Seed production was also very different on the two exposures, being greater on the north for biomass, numbers, and production of crude protein, fat, fiber, and NFE, and percent crude fat, fiber, and NFE. However, the total protein content of an average seed from the two exposures was the same, potentially a significant compensation for viability, because overall, an average seed from the south exposure was about 10% lighter than one from the north.

Mineral uptake was also significantly different between exposures: nitrogen, phosphorus, potassium, and calcium were all about one-fifth greater (as percent of shoot biomass) on the south exposure. Greenhouse studies showed this difference was probably due not to different patterns of uptake from the two soil layers used in the small lysimeters, but to environmental conditions and plant responses. The specific environmental variable(s) responsible were unidentifiable in this experiment.

Two general conclusions seem appropriate. First, ecologists must be wary of the important differences between climates considered with, and considered without, energy fluxes. On a microscale, temperatures and humidities can be similar, while the disposition of incident energy can be quite different, exemplified here by strong contrasts in sensible and radiant heat fluxes with very similar air temperatures. Second, transpiration can be considerably more variable between habitats than radiant fluxes. For example, the ratio (north:south) of net radiation varied between 0.44 early in the season to near 1.0 late in the season, about a factor of 2. By contrast, the ratio of transpiration fluxes varied from 0.58 to 8.0, more than a factor of 10. The bond
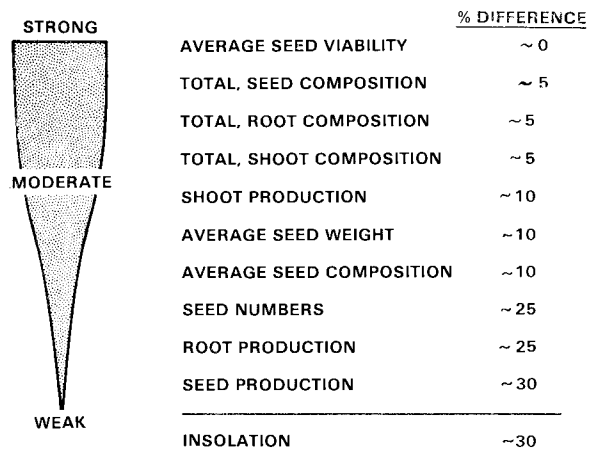
between energy and water relations is often close, but soil water remains the ultimate arbiter.

Environmental contrasts produced several reactions in the cheatgrass stands. First, the time available for growth was different, since it was determined by environmental conditions. This poses a question: what would it profit a sward if it grew rapidly, but briefly? In this experiment, nothing. The imputed rapid growth rate for shoots on the south exposure ultimately led to fewer, smaller seeds, a poor trade-off for an annual with colonizer traits.

Second, the distribution of assimilates between alternate carbon pathways in cheatgrass was apparently decoupled from environmental rigors, at least to a first-order approximation. The allocation of photoreduced carbon to proteins was the only process strongly affected by environment; for fatty, structural, and storage biochemicals, any differences were too subtle for the crude analyses employed here.

Third, development was decoupled from the environment far more than was production for these plants with identical seedling histories. Phenological progression to maturity proceeded apace on both exposures, along with nearly identical carbon distributions (albeit in differing biomasses).

Fourth, homeostasis was variably evident in several aspects of the cheatgrass stand (Fig. 13): greatest for composition and viability of seeds, and for leafy production; less for allocation between the various biochemical categories measured here; and least for seed production and numbers, root production, and mineral uptake.

Fifth, more than half of each community's total reproductive resources ended up in the reproductive potential of only 15% of the stems, in both environments. However, this accretion of resources produced no obvious advantage for seeds so endowed, in

comparison with seeds from the masses of the suppressed stems. This is indeed an adaptive trait for a colonizing annual: maintaining growth potential in succeeding generations without penalty for depauperate conditions in earlier generations.

This experiment aimed to provide an unusually detailed accounting of the dissimilar fates of energy and carbon in two simple communities, to illustrate ecological insights made available by including energy relations (other than photoperiodism) in autecological or general ecological investigations. Energy relations were particularly valuable for apprehending interrelations between temperatures, radiant fluxes, atmospheric heating, and transpiration, and for understanding relations between water stresses, phenology, productivity, and reproduction. However, the most valuable aspect of the experiment probably follows from the describing of a wide range of homeostasis in several ecologically pertinent attributes of this grass. This grass may well require opposing considerations for vegetation—as opposed to trophic—dynamics: differences in biomass production on thet one hand, and similarities in composition on the other.

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