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AN ECOLOGICAL ASSESSMENT OF ENERGY AND CARBON PATHWAYS IN SWARDS OF *Bromus tectorum* L. ON CONTRASTING SLOPE EXPOSURES

Battelle
Pacific Northwest Laboratories
Richland, Washington 99352

AUGUST 1974

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by
W. T. Hinds

August 1974

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University of Washington

Abstract

AN ECOLOGICAL ASSESSMENT OF ENERGY AND CARBON PATHWAYS IN SWARDS OF BROMUS TECTORUM L. ON CONTRASTING SLOPE EXPOSURES

by Warren Ted Hinds

Chairman of Supervisory Committee: Dr. Roger Del Moral
Department of Botany

The biotic and abiotic fates of incident energy have rarely been considered together in detail, so little is known about where or whether any energy or carbon relations remain constant in contrasting energy environments. An experiment to determine the fates of energy and carbon was carried out on steep (40°) north- and south-facing slopes on a small earth mound, using small lysimeters to emulate swards of cheatgrass (Bromus tectorum L.). Meteorological conditions and energy fluxes that were measured included air and soil temperatures, relative humidity, wind speed, incoming 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 analysis of the plant tissues into mineral nutrients, 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.

Ordinary climatological measurements did not reveal notable differences between slopes. However, all terms in the average radiation balance were significantly larger on the south exposure (650 compared to 470 cal cm^{-2} day^{-1}), and the estimated average radiative surface temperature was higher on the south exposure (about 40°C compared to about 30°C on the north exposure), leading to much greater sensible heat flux to the atmosphere on the south exposure than on the north. The energy-rich 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 all showed an abrupt decrease in their slopes as a function of time, occurring simultaneously at about -14 bars average cm water potential in the 60 cm active soil profile (∿10% by weight), 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 a period about 50% 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 appreciably different on the two exposures, because the greater magnitude 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 (0.43%) than the north exposure (0.67%) in converting sunlight energy into chemical energy stored in plant tissues.

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

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 a decrease in soluble components, probably starches in the endosperm. Crude protein content was almost identical--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 strong) > seed composition (strong) > shoot and root composition (moderately strong) > average seed weight = shoot production (moderate) > seed number (weak) > total root and seed production (none noticeable).

I. INTRODUCTION

Fools and angels both rush about.....
the significant difference is where, not how fast.

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 is devoted to tracing biochemically fixed energy through trophic transfers. Concerted and comprehensive measurements of the "fate and effects" of energy in an ecosystem are rare; in fact, I found none that considered simultaneously the meteorological disposition of energy income and physiological disposition of assimilated energy in comparable detail. Energy relations are not yet typical concerns of autecological studies (West, 1968), but this oversight will probably be corrected as ecological analyses penetrate organism/environment relationships.

Two factors come immediately to mind when pondering how best to study the importance of ecoenergetics: first, the species to be studied, because the results are almost certain to be species specific in important ways; and second, whether the study ought to be observational or experimental.

I feel that ecological work must emphasize field work, for most communities do not flourish under roofs. Still, the advantages of experimentally controlling several variables while changing others in a known fashion has much to recommend it. Ultimately, the courses of action from which to choose depend upon the species chosen, for liverworts and cypress differ in more than stature. An obvious choice was cheatgrass, _Bromus tectorum_ L.*, a moderate-sized annual grass well adapted to the climate of south-eastern Washington, and an important species to range management and waste management alike, for both are concerned with perturbed stable communities, allowing cheatgrass a potential foothold.

Several methods have been used to alter energy relations, 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 the most meaningful ecological alteration for a sward of cheatgrass seemed to be alteration 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 would guarantee contrasts if the slopes were steep enough.

Therein lay a prickle; the literature on slope effects is almost entirely devoted to species presence and abundance. From Potzger (1939) on a ridge in Indiana, concealing atmometers from transient hunters, to Ayyad and Dix (1964), on prairie slopes in Saskatchewan, scoring and ordinating many stands, the emphasis lay on taxonomy. All agreed it was more or less warmer and drier on the south slopes. Finally, I arranged to have small artificial slopes constructed as steep as possible, and hoped for the best.

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* All formal taxonomic nomenclature follows Hitchcock and Cronquist (1973)

It should be noted that the approach I have taken to study energy relations is diametrically opposed to that of Gates (1968). I have begun with a community, and later deduced some elementary relations for individual components of the plants as average contributors to the community, whereas Gates expresses the idea of determining relationships for individual leaves, then integrating over all leaves on a plant, then over all plants in a community, to arrive at community energetics. Clearly his approach is best adapted to mathematical simulations.

The following text aims to weld together an amorphous mass of literature and ideas into a meaningful description of energy pathways in 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 in turn upon the relation between microclimates and energy balances, interpretation of abiotic energy balances, photosynthetic efficiency, carbon pathways in maturing cheatgrass, and environmental influences on production and reproduction in *Bromus tectorum* L.

II. THE LITERATURE IN PERSPECTIVE

A skilful canoeist leaves glints and sparkles, not a wake.

BROMUS TECTORUM L.

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 and has generated a substantial literature that is well reviewed by Stewart and Hull (1949) and Klemmedson and Smith (1964). Much of the early literature was concerned with reducing stands of cheatgrass and encouraging regrowth of the native perennial grasses (see Leopold, 1949). However, recent years have seen some of the cheatgrass communities invaded by an even more agressive and obnoxious species, medusahead rye (Elymus caput - medusae L. in Hitchcock and Cronquist (1973); synonymously, Taeniatherum asperum (Sim.) Nevski) (see West, 1968), and some recent work now is aimed at maintaining existing cheatgrass stands against this invader (Young, et al., 1971).

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 and a great deal of taxonomic and autecological information was reported by Hulbert (1955). The ensuing paragraphs point out some important results reported since.

Cheatgrass seeds germinate rapidly in laboratory tests; usually, all viable seeds have germinated within three or four 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 only competitive if existing climax vegetation is disturbed--cheatgrass makes few inroads into perennial grasslands otherwise (Leopold, 1949; Harris, 1967).

The phenology and phenotypic expression 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 three centimeters 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 and for nitrogen and sulfur amendments (Eckert and Evans, 1963). However, yields are about six times as sensitive to water relations as nutrition (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 (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 is known to form a major part of the diet of chukar partridges in the fall, (Weaver and Haskell, 1967) and in fall and spring both 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 (Daubenmire, 1970) of the ecosystems in western United States, 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 TRANSFERS IN AND AROUND A PLANT COMMUNITY

In the broadest sense, energy enters the community as radiation (shortwave, from the sun) and leaves the community (earth) as radiation (longwave, to space). Between these two radiant fluxes are many energy transformations inextricably wound up in a web of bioenergetics. However, the transformations that take place in the environment surrounding a plant community often can be conveniently separated from the transformations taking place within the biota (the community proper). Figure 1 is a diagram of the major biotic and abiotic pathways for energy transfers and transformations, and the next several paragraphs provide an interpretation and perspective for the fluxes and storages noted there, beginning with the abiotic fluxes, then returning to the fate of radiant energy captured by the plants via photosynthesis.

ABIOTIC ENERGY TRANSFERS AND STORAGES

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

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

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

where S = insolation (0.2 to 3.2 micron wavelengths)

r = reflectivity

I_d = atmospheric longwave radiation (6 to 25 micron wavelengths)

I_u = longwave radiation 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 transportation

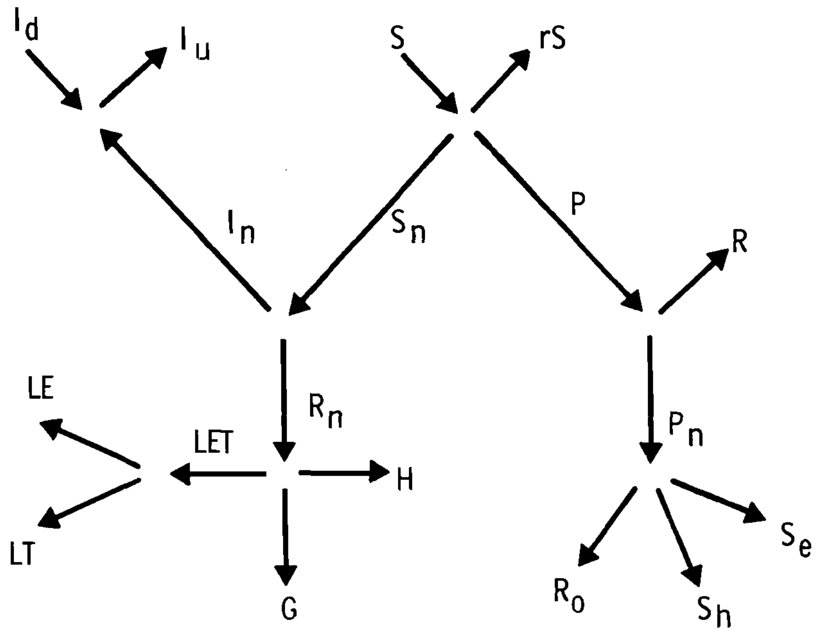
G = sensible heat flux to the soil

H = sensible heat flux to the atmosphere

P_n = net photosynthesis

Equation 1 shows that net (all-wave) radiation is the energy that undergoes transformation to stored forms of energy at or in the community. Equation 2 shows that the energy flux incident upon the plant community is a function of large scale processes -- cloudiness, air temperature, season -- whereas the fate of the incident energy is determined strictly 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 is often termed "insolation," and 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 between the two fluxes is that diffuse radiation usually shows a maximum at shorter wavelengths than direct radiation. No significant loss of information



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 TRANSPIRATIONS
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

Figure 1. Energy Flows in a plant community and its environment.

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; both terms refer to orientation with respect to compass direction), season, climate, and so on. The effect of each of these factors on shortwave radiation is well understood and discussed in standard reference works (List, 1957; Geiger, 1967; Sellers, 1965).

The first energy transfer in a plant community is the reflection of shortwave radiation back to space. The proportion reflected varies with the surface properties of the community and the angle of incidence of the radiant flux. Monteith (1960) discussed reflection extensively, showing that some species reflected much more incident shortwave radiation than others. For example, Eurotia lanata (Pursh.) Moq., a desert shrub with grey pubescent leaves, reflected about 35% of the incident radiation, whereas typical plants with green leaves reflected about 25%. Figure 2 indicates that Bromus tectorum is a typical species, showing that reflection increases markedly at large angles of incidence (Idso, et al. 1969; Monteith and Szeicz, 1961). Reflected radiation, like insolation, has both direct beam and diffuse components, both of which are lumped here into a single flux.

Longwave radiation directed downward arises primarily from atmospheric water vapor and carbon dioxide. The emission spectra of

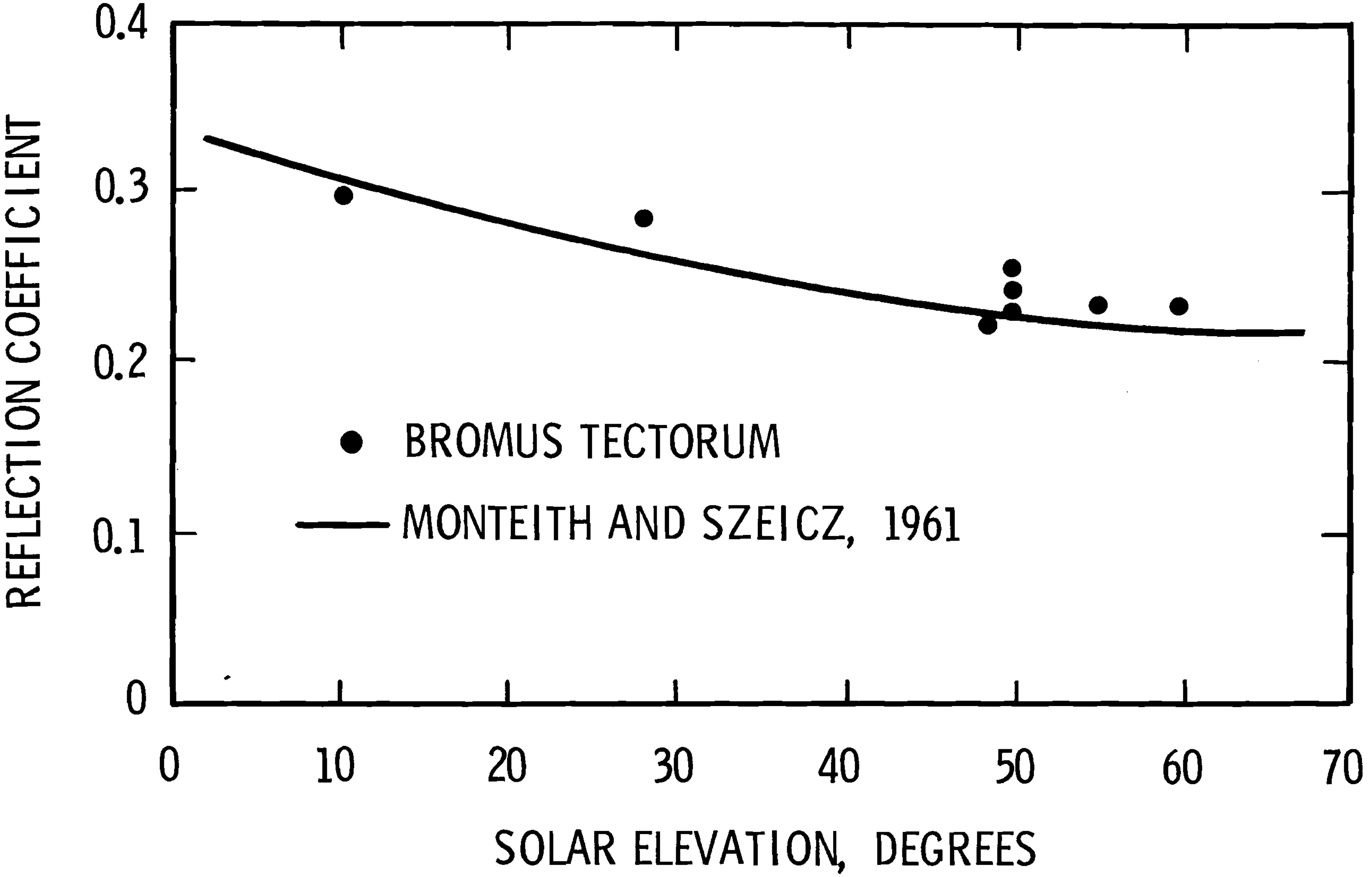


Figure 2. Reflectivity of Bromus tectorum as a function of solar elevation angle. Solid line is a suggested average for several species.

these two molecules are so intense in most wavelengths between 6 and 25 microns that the longwave radiant flux density at the earth's surface often arises almost exclusively from water and carbon dioxide in the lower few hundred meters (Gates, 1962). Consequently, downward radiation can be estimated in terms of ordinary meteorological parameters. Recent analyses (Swinbank, 1963; Idso and Jackson, 1969) attributes the radiation to air temperature alone if the sky is clear and the atmosphere near neutral--typically, daytime conditions. Most terrestrial surfaces act very nearly as black bodies with respect to longwave radiation (Buettner and Kern, 1965), so angle of incidence and reflectivity are of little consequence.

Radiative fluxes emitted from the earth's surfaces are also very nearly a function of surface temperature alone, again because terrestrial surfaces appear nearly black at these wavelengths. This component plays the major role in the energy balances of leaves: about two-thirds or more of the energy absorbed by leaves is reradiated as longwave radiation (Idso and Baker, 1967).

Warming of the soil by sensible heat flux during the spring and summer seasons stores significant amounts of energy. Annual cycles of soil temperatures reach deep into the soil, 15 or 20 meters, and daily cycles of soil temperature often reach depths approaching half a meter (Sellers, 1965). However, the magnitude of the soil heat flux is small in relation to insolation, and soil heat flux decreases rapidly in importance relative to other fluxes as time periods increase. Its importance to the ecosystem lies in its direction (warming or cooling), and in the associated changes of soil temperatures, which provide relatively favorable or unfavorable conditions for plant growth.

Sensible heat fluxes to the atmosphere arise by convection from surfaces of the earth or plant communities warmed by absorption of solar radiation. The amount of energy stored in the atmosphere in this fashion is a very significant proportion of the incident energy, especially in arid regions where the competitive process of evaporation may be small. Ordinarily, air temperatures change slowly through a large depth, because the heat capacity of the air is very small and convection is an efficient process that minimizes temperature gradients in comparison with conduction.

Energy stored in the environment due to change of phase of water is termed the latent heat flux, i.e., without temperature change. Two common pathways exist: evaporation and transpiration. A recent critique of the extensive literature on evaporation (Stanhill, 1973) found good reason to keep these two components of the latent heat flux separate: transpiration is mediated by biotic mechanisms in addition to abiotic constraints.

Evaporation (from non-living substrates) typically occurs from 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 conserve water in the profile to depths of 30 centimeters, compared to a bare surface. However, soil texture (e.g., sands compared to clays) had little effect on the depth to which soil water can be lost (Alizai and Hulbert, 1970).

Transpiration is very significant, because it affects water deep in the soil that otherwise would remain unmoved; in situations 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 inordinately 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.

BIOTIC ENERGY TRANSFERS AND STORAGES

Energy enters the community via photosynthesis, which is connected to abiotic energy transfers by net shortwave flux. The fate of photosynthetically fixed energy is only indirectly related to the environment, being directly related to the structure and function of the plants in the community. Several pathways exist for photosynthetic energy fixation; the commonest involves formation of triose phosphates (Rabinowitch and Govindjee, 1959). This, the C_3 pathway, is the major process in most green plants. However, a few species, particularly grasses of tropical origin, have a very different sequence for most of their carbon uptake, which involves formation of a four-carbon acid (Hatch and Slack, 1968). This, the C_4 pathway, is associated with high efficiencies, net productivity proportional to insolation, and a very low or nonexistent rate of photorespiration (Zelitch, 1971). However, dogmatic separation of species into groups according to carbon reduction pathways is 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 carbon fixation 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 productivity typical of the C_4 pathway species.

Photosynthesis via the C_3 pathway exhibits a typical enzyme saturation response curve as 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 usually increases with increasing energy availability (Hesketh and Baker, 1967).

Energy fixation within a stand depends upon the absorption of radiant energy throughout the leaf profile, so considerable effort has been devoted to analyzing the absorption profile of radiant energy. The basic phenomenon is a more or less exponential decrease of flux density from the top of the canopy downwards (a purely exponential decrease would imply a Beer's law absorption process, requiring a uniformly dispersed homogeneous assemblage of small leaves and monochromatic radiation). For example, Impens and Lemeur

(1968) showed that the log of the fraction of net radiant flux remaining at any height in a corn canopy was actually a quadratic polynomial rather than a linear (Beer's law) function, and that the extinction coefficients were not constant throughout the day.

Theoretical light absorption profiles in plant canopies abound, and useful insights can be gleaned from several analyses. Anderson and Denmead (1969) examined the differences between direct beam and diffuse radiation. They showed that dramatic differences exist in radiant flux densities incident upon different leaves within the canopy; the highest flux densities occur from direct beam radiation on nearly vertical leaves at low solar elevations. Foliage inclination means little under diffuse radiation. Monteith (1965) concluded that for leaf areas per unit of ground surface (leaf area index) less than three, photosynthesis would decrease as leaf angle increased from horizontal, whereas for leaf area indices greater than five, photosynthesis would increase with steeper leaf angle. Cowan (1968) separated his analyses of radiant fluxes into five wavebands with rather different profiles of absorption, but his analysis showed that the absorption profiles for both all-wave and visible radiation were very similar, basically because absorption in the far infra-red of the solar spectrum (1.2 to 5.5 microns) was largely compensated by net loss of thermal (longwave) radiation.

Verhagen et al. (1963) presented an analysis of several theoretical types of foliage distributions. In an ideal foliage (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, but not *Bromus tectorum*. Further, they showed that the light emerging from the base of an ideal (i.e., maximally productive) foliage exceeded the light emerging from a foliage with the bottom leaves at compensation point. That is, maximum productivity is not associated with maximum absorption measured on horizontal planes, because it is the light absorbed by the leaves that is critical. Thus, the attractive idea of defining photosynthetic efficiency in terms of intercepted light, as proposed by Botkin and Malone (1968), and Hesketh and Baker (1967), must be foregone. Botkin and Malone recognized the important difference between absorbed light and transmitted light; but even so, the proper base for efficiency calculations should be insolation incident on the top of the foliage, thus removing any effect of variable inclination of the foliage.

Ecological aspects of these insolation absorption phenomena are related to the experiment at hand as follows: the radiant flux density incident upon the top of the cheatgrass canopy will be much higher on the south than on the north, due to the angle of incidence on the slope, but the total leaf area traversed by the parallel beam radiation will be much less on the south than on the north. Consequently, the fraction of the direct beam radiation absorbed during passage through the foliage may be lower on the south. Diffuse radiant flux will be approximately the same on the two exposures. This is in contrast to other experiments (Campbell et al., 1969, for example) where shade cloth was used to reduce radiant flux density, because cloth shading tends to attenuate direct beam radiation and increase diffuse radiation.

Carbon Pathways

Plant responses to contrasting energy relations in the community may be reflected in either (or both) the proportion or total of photosynthetically reduced carbon allocated to each of thousands of biochemicals associated with life. A suitable base for generalizing carbon pathways is a carbon balance diagram by Mooney (1972), which is presented in a very simplified form in Figure 3. Several endpoints appear in this diagram: saccharides for storage and construction; aromatic and phenolic compounds for function and control purposes; proteins; and fatty acids. The number of compounds associated with the function and control (shikimic acid) group is very large, but the mass of materials associated with each of them is often small because the concentrations required are small. The other end points in the diagram can be roughly thought of as containing relatively small numbers of compounds in relatively high concentrations.

To presume 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 common lumping procedure useful in biochemistry is to differentiate

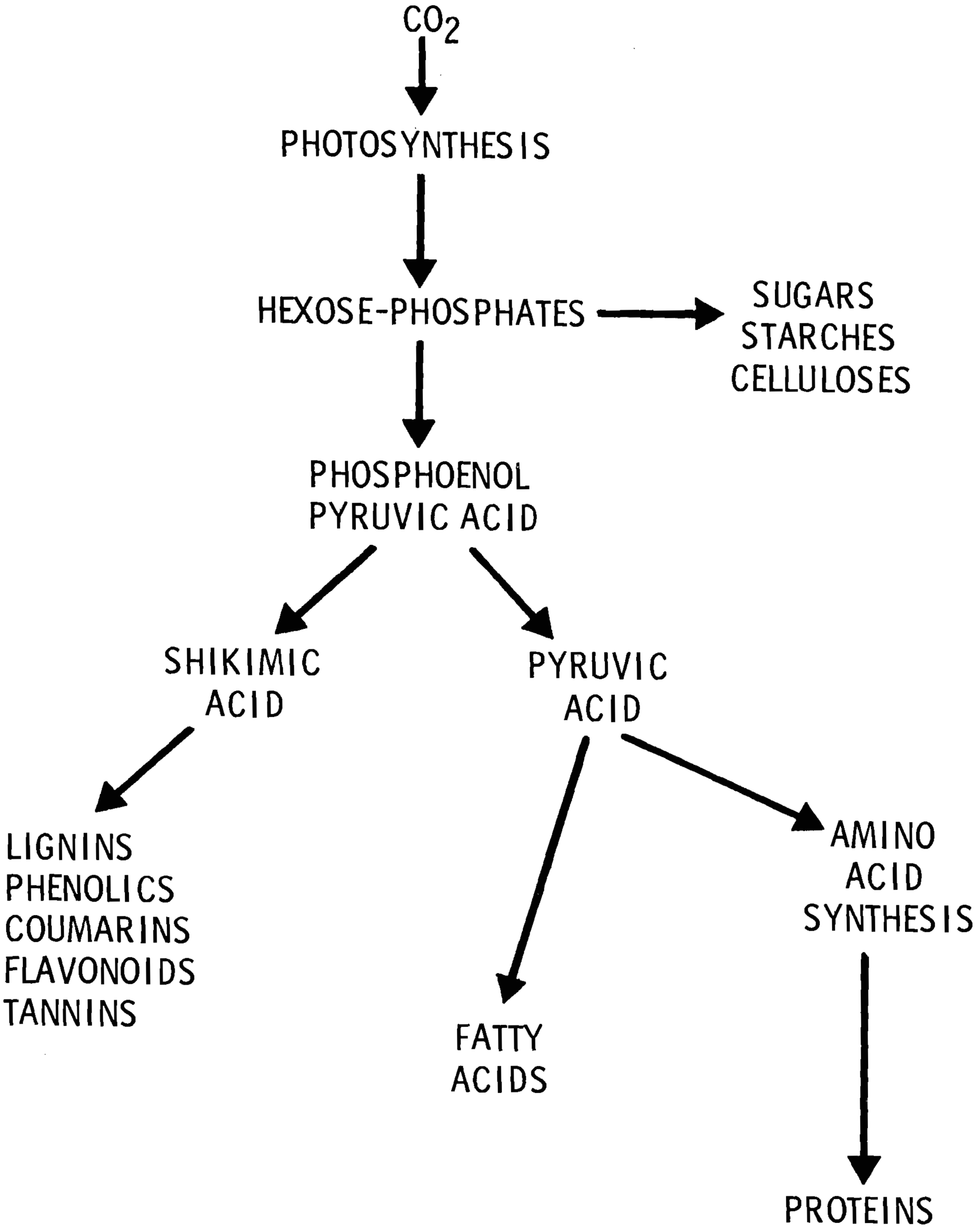


Figure 3. Carbon pathways in typical green plants (after Mooney, 1972).

between carbohydrates, lipids, and proteins, three categories that coincide roughly with three of the four endpoints in Figure 3. A scheme of plant tissue analysis that approximates this subdivision is the Proximate Analysis Technique developed by workers at the Weende Experiment Station in Germany in 1865 (Crampton and Lloyd, 1969). Proximate analysis differentiates nitrogen-bearing compounds (called crude protein), ether-soluble compounds (called crude fat), substances insoluble in dilute acid followed by dilute base (called crude fiber), the remaining soluble compounds (called nitrogen-free extract) and mineral constituents (called ash) (Figure 4).

Nitrogen-bearing substances in green plants are almost entirely proteins or their precursors, amino acids. Some nitrogen may occur as nitrate, but usually only in very heavily (overly) fertilized soils (Duncan et al. 1970). Other nitrogenous substances occur, but usually in small concentrations (alkaloids, for example). The term crude protein thus reflects the predominance of proteinaceaous matter in the nitrogen economy of the plant, but it does not reflect the relations between true proteins, amino acids, and other nitrogen-containing compounds.

Many substances soluble in an organic solvent such as ether are derived from fatty acids -- oils, fats and waxes are principal examples. However, other compounds soluble in ether are not fats, such as hormones and vitamins. The term lipid, often substituted for fat, also refers to fatty-acid compounds, not to the heterogeneous ether-soluble substances lumped under the term crude fat.

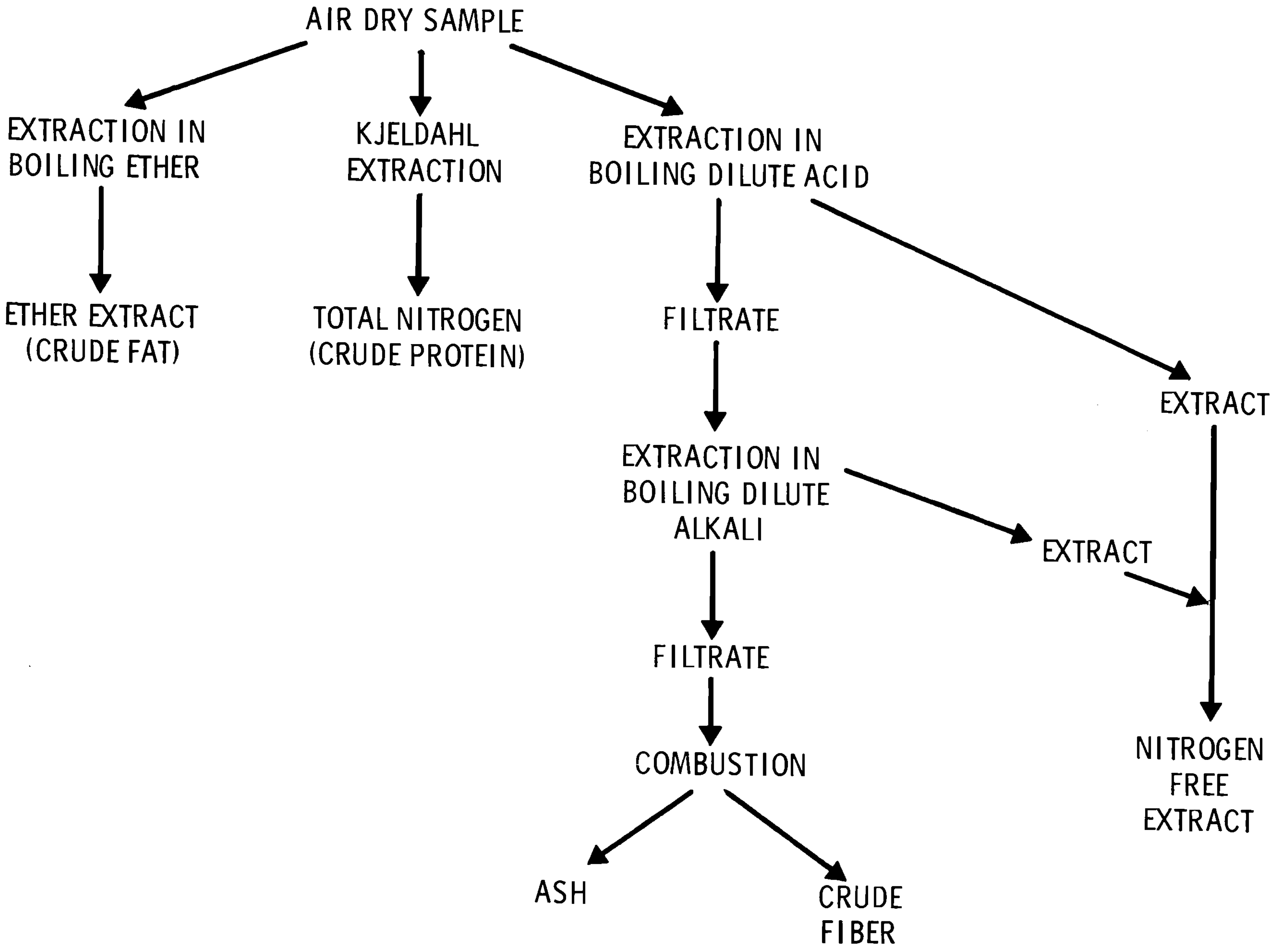


Figure 4. Flow sheet for the Weende proximate analysis scheme (after Crampton and Lloyd, 1959).

The insoluble substances left after digestion of plant tissues in dilute acid and base is termed crude fiber, consisting mostly of cellulose and lignin.

The soluble sugars and starches, organic acids, coumarins, flavonoids, alkaloids, and water-soluble compounds of all types, indicated in Figure 3 as branching from the shikimic acid path, are subsumed into a heterogeneous group called nitrogen-free extract (NFE). The bulk of this group is mono- and poly-saccharides (sugars and starches), but NFE reflects many more functions than just translocation and storage. A small but variable proportion of cellulose and lignin also ends up in this fraction, one of the most serious criticisms to be made against proximate analysis, because structural materials (cell walls) are not completely separated from functional materials (cell contents) (Van Soest, 1967).

PLANT - ENVIRONMENT INTERACTIONS

The field of study that comprises interactions between plants and their environment includes nearly all of plant ecology, and even restricting attention to the abiotic aspects of the interaction requires a book for adequate treatment (Daubenmire, 1958). Consequently, the following discourse is aimed only to provide an underpinning for experimental design, and an interpretation of water relations, productivity, and plant composition in terms of this experiment, rather than a literature review in the classical sense.

Water Relations

Water relations are probably the most direct interaction between plants and their environment: latent heat transfer is generally a large fraction of the energy budgets in a living green plant community, and plants have evolved control mechanisms for water relations. Water deficits are much more probable and important than water excesses, as a recent series of reviews on the ramifications of water deficits makes clear (Kozlowski, 1968, 1972). A review by Hsiao (1973) discussed plant responses to varying degrees of water deficits, but a recent critique of the literature on evapotranspiration (Stanhill, 1973) cautioned that many water-use data papers lack significance for either the physics, physiology, or ecology of water relations by severing water use from environmental influences.

Water relations of plants 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. This is primarily because most of these environmental parameters, commonly measured in ecological studies, are physically related, and 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 and wind speed the independent environmental variables, and stomatal diffusion resistance and leaf size the plant factors.

Water is absorbed by roots, but the rate of absorption is dependent upon temperature and water availability, and new root structures absorb water faster than older ones (Kramer, 1969), so the maintenance of root growth is important to continued efficient absorption of water from the soil. However, Lawlor (1973) reported that wheat roots grew progressively slower as water stress increased, and root growth stopped entirely at a water potential of -10 bars (see Kramer et al., 1966, for a discussion of soil water relations terminology). Lawlor also reported that plant water potential was not adversely affected if a portion of the plant's roots were in dry soil, so long as another substantial portion remained in relatively moist soil.

Translocation of photosynthates from source to sink is slowed by water stresses (Brown and Blaser, 1970). However, 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 has far-reaching consequences for stressed plants (Harper et al., 1970).

Productivity

Total production of a plant community is often closely related to the total amount of water available for its use, perhaps a log-log linear relation for climax communities (Rosenzweig, 1968). The productivity of many grass species depends upon both the amount and timing of precipitation during the growing season (Smoliak, 1956). However, production of biomass by a community bears almost the opposite relation to the environment in general as does water relations: Scott and Billings (1964), for example, found the productivity of a complex alpine community to be uncorrelated with environment except for "potential for soil movement", considered to be some measure of water status of the site. It is for this reason that most field studies of production by communities proceed as an observational, rather than an experimental, study.

Light relations rank with water relations as one of the fundamentals for plant production in communities. The literature devolving from considerations of community light relations is vast, and well reviewed by Anderson (1964). One of the generalizations used to compare communities in terms of production is the efficiency with which a community captures insolation as reduced carbon compounds in the plants. Efficiency is here defined as the energy content of plant tissues (net photosynthesis) per unit incoming energy (total insolation). Other definitions are discussed by 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) summarize many estimates of efficiency for several contrasting communities, mostly approximating 1% or less.

Experimental alteration of insolation in the field has been exploited recently. Gibbon et al. (1970) grew corn, kale and sugarbeet in two contrasting insolation climates (Britain and Italy), noting generally increased yields and decreased efficiencies in the higher insolation intensities of Italy. Corn was an exception; its efficiency increased with insolation, probably because it possesses the "C_4 pathway" as its principal photoreduction process. 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, again with increased yields and decreased efficiency as insolation decreased.

Plant Composition

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). General reviews of plant composition as a function of environment are apparently non-existent.

Of the several factors separated by proximate analysis (see the earlier section on Carbon Pathways), most effort has gone into studies of crude protein, because protein is an important aspect of forage value, and because nitrogen is typically limiting in grasslands. Crude protein content apparently was maximized in plants growing in warm, dry conditions under significant water stress (Gifford and Jensen, 1967; Campbell et al. 1969), but Hsiao (1973) summarizes several reports that water stress reduces protein content. Apparently the biochemical assays reviewed by Hsiao refer to true protein, rather than total nitrogen.

Crude protein content often enters into complex interrelations with environmental conditions, precluding very many simplistic generalizations. Chan and McKenzie (1972) reported that shading of corn introduced an interaction between yield and nitrogen uptake in both structural (leaf and stem) and reproductive (stover and ear) organs. Power (1971) reported that stress due to nitrogen deficiency was greatest where nitrogen availability was lowest, essentially independent of water relations. Water stresses were generally greatest at low nitrogen availability, emphasizing the importance of nitrogen availability and uptake.

Discussions concerning crude fat content of plants are relatively few. Crude fat content apparently contains both phenotypic and ecotypic dimensions and may be correlated with relatively dessicating environments. Newell (1968) found that sandy soils supported plants with higher crude fat content than did silty soils, whether the species had evolved on that soil texture or not. Furthermore, he found that ecotypes adapted to sandy substrates had a higher crude fat content than those adapted to silty soils.

Crude fiber content (essentially structural carbohydrates and lignins) may also be dependent on environment. Wilson and Ford (1971) found the concentration of structural carbohydrates to increase as temperature increased, but Gifford and Jensen (1967) reported crude fiber was minimized in compacted soil and dry conditions.

McIlroy (1967) reviewed many reports on plant carbohydrates, noting that celluloses increase regardless of environmental conditions as the plant matures, typically from 20% in juveniles to 30% in mature plants.

Soluble carbohydrates form the bulk of the nitrogen-free extract portion of the proximate analysis. McIlroy (1967) summarizes work indicating the concentration of soluble carbohydrates is highest at high light intensities and low temperatures, and lowest in low light intensities and high temperatures. Brown and Blaser (1970) found that water stress increased the concentration of soluble carbohydrates in stem bases, apparently due to lack of translocation.

III. METHODS AND MATERIALS

Ecology resembles Graeco-Roman wrestling: the opponent is slippery, and handholds are just plain scarce.

SITE DESCRIPTION

The experimental site was 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 south-eastern end of the Rattlesnake Hills, at 119°32' W, 46°26' N. The climate in this region is semi-arid and the natural vegetation probably is best described as shrub-steppe (Daubenmire, 1970). The lower elevations in this region 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 a 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; but the average precipitation during these three months is less than 3 cm, so evapotranspiration rapidly removes the stored water. Soils are essentially at permanent wilting throughout the profile after late May. Winter temperatures are cool, but the average maximum temperature in January is +2°C; severe cold spells (-20°C minima) are expected only every other year or so. Average maximum temperatures in the spring growing season range from about 10°C in early March to nearly 30°C in late May.

The experiment was performed on a small earth mound constructed from *in situ* materials (Figure 5). The mound is about two meters high and a hundred meters long, with a five meter wide horizontal surface on the top. The slopes face north and south and have an angle of 40 ± 1 degrees with horizontal. The slopes were seeded with *Bromus tectorum* shortly after the mound was constructed in autumn 1971.

ABIOTIC FLUXES

Radiant Fluxes

Insolation was measured with pyranographs (Belfort Instrument Co.), calibrated against an Eppley pyranometer at the Hanford Meteorological Station. Net radiation was measured with Dirmhirn design thermopile radiometers (Kahl Scientific Co.) situated 50 cm above and parallel to the sloping surfaces of the earth mound. 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, which were used with solar elevations (List, 1957) to compute hourly values of reflected shortwave flux.

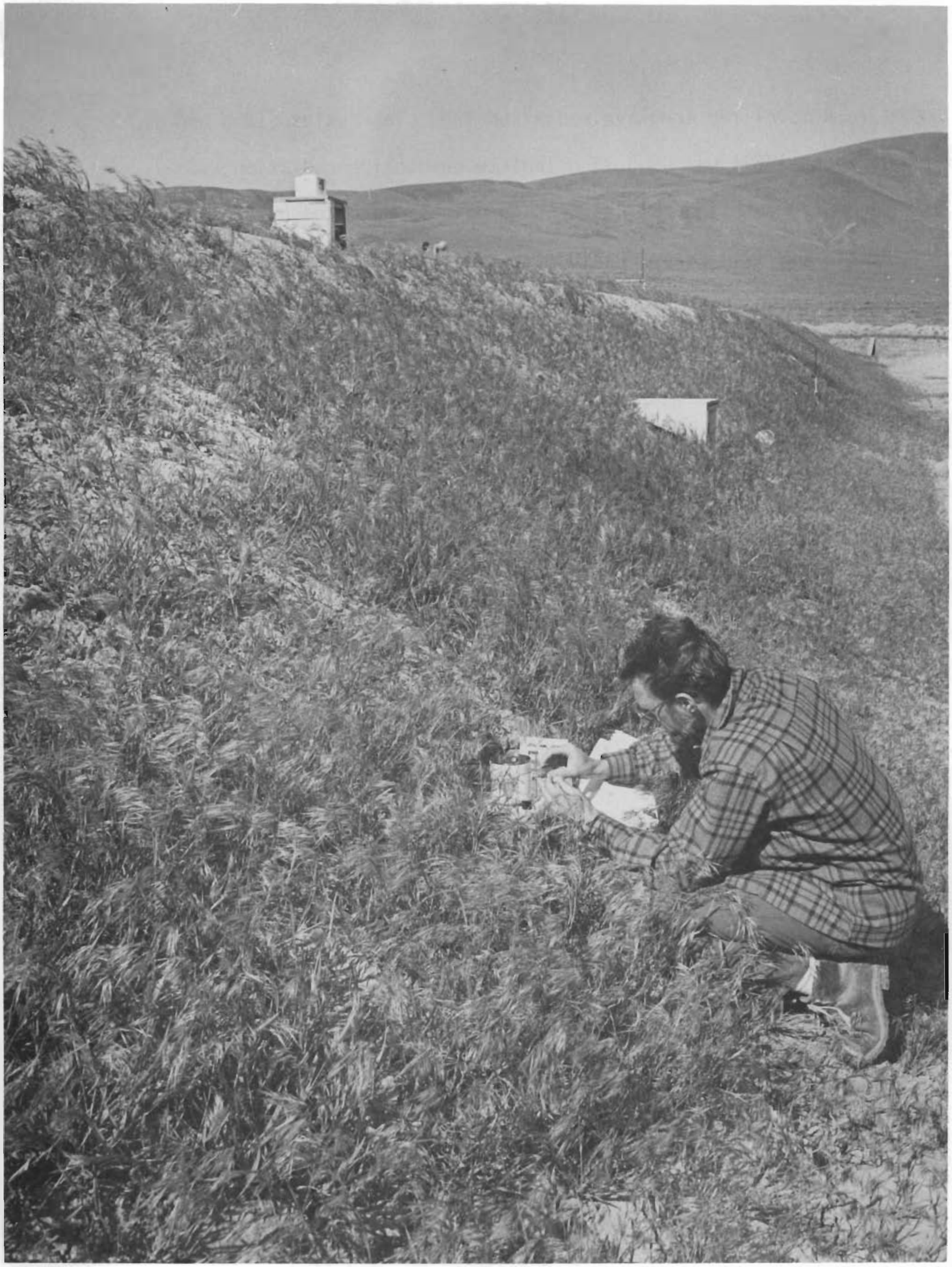


Figure 5. Experimental earth mound

A model for longwave radiation from clear skies (Idso and Jackson, 1969) was used to calculate downcoming radiation, augmented for cloud emission using values suggested by Morgan et al. (1971). Outgoing longwave radiation was calculated from the relation Iu = In - Id, (see equation 1), but the error involved must be large because no measured data were available. Surface temperatures were estimated from the Stephan-Boltzman equation assuming an emissivity of unity (Sellers, 1965).

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 using small lysimeters developed during the past three years (Hinds, 1973) from a Russian design (Konstantinov, 1963). The construction of the small lysimeters is shown in Figure 6. The lysimeters were constructed from five-inch (nominal) diameter PVC (polyvinyl chloride) irrigation pipe, with a plexiglass bottom riveted and glued in, and with a wire-in-surgical-tubing handle. The outer casing (sleeve) of the lysimeter installation was six-inch (nominal) diameter pipe, which fit snugly in a hole drilled by a seven-inch diameter 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

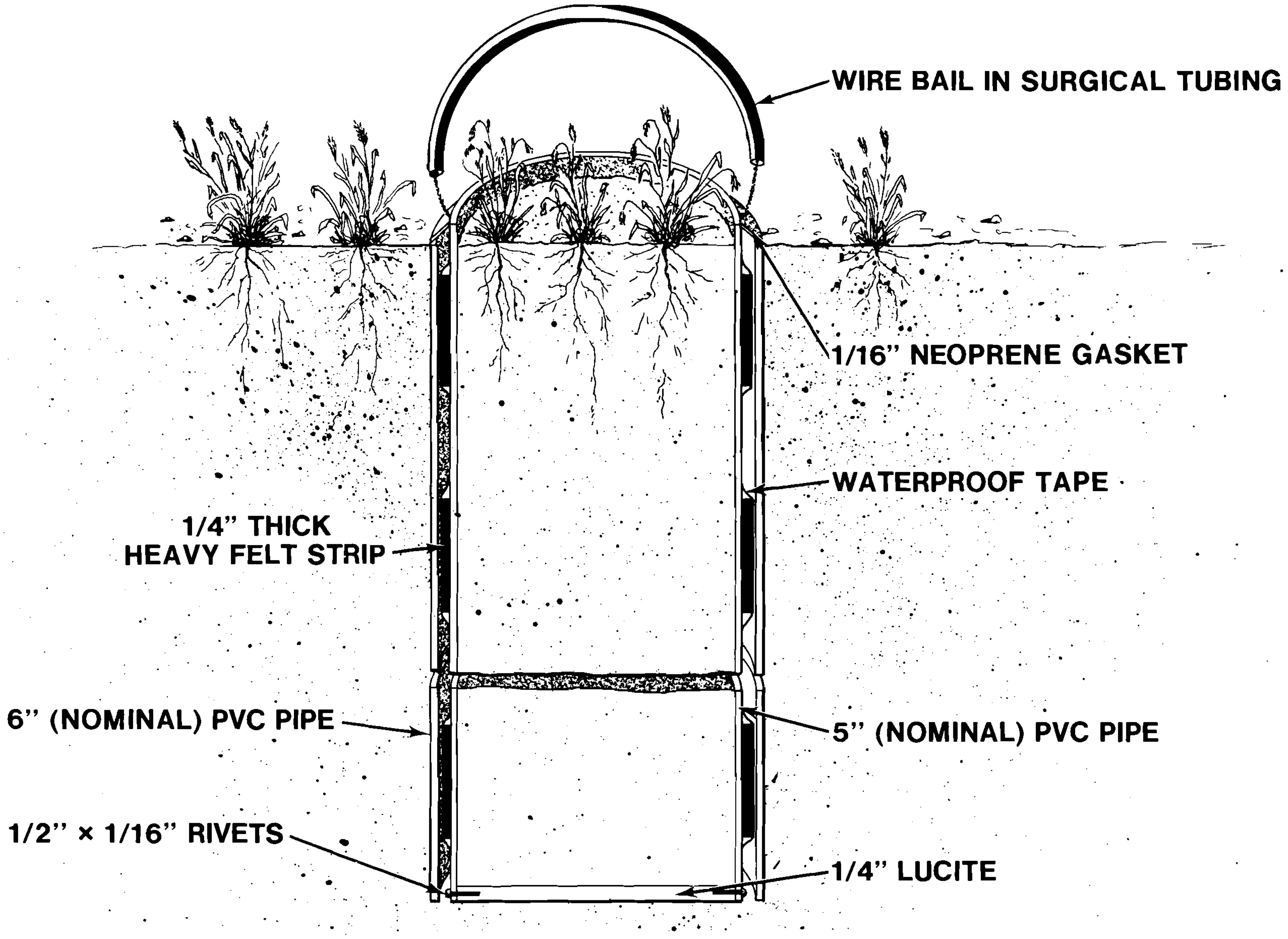


Figure 6. Details of the construction of the small lysimeters.

between the lysimeter and the sleeve, and four felt gaskets about 6 mm (1/4 inch) 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.

The plants to be used in the experiment were transplanted into the lysimeters. Randomly selected soil cores 20 cm deep from a uniform hillside sward of B. tectorum with a west-facing exposure were inserted into 17 partially filled lysimeters, thus preserving root structure, phenological advancement, and the surface mulch of dead plants developed over the past years in the hillside community. Evaporation from non-transpiring surfaces was estimated by plucking the green plants from the surface of four lysimeters. Transpiration was estimated as the difference between the evapotranspiration lysimeters, with green plants, and the evaporation lysimeters, without green plants.

Microclimatological Measurements

Air temperatures and humidities were measured with Belfort 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 Weather-Measure anemometers (starting speed ~ 1.5 m sec^{-1}) with the cups centered at 35 cm above the surface, about 20 cm above the maximum height of the grass. All continuous recordings were averaged over daytime and nighttime hours separately. Precipitation was measured with 6 small (5 cm diameter) rain gauges (3 each slope) buried in the soil with their openings 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.

BIOTIC FLUXES

Heat of Combustion

The heats of combustion ("calorie content") of the plant materials were determined using a Parr adiabatic 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 oxygen. Correction for NO_2 formation was performed, but not for SO_2.

Biomass Production

Standing crops of roots were estimated at the beginning of the experiment from randomly chosen cores from the community used for transplant cores. Two soil cores (0 to 10 cm, and 10 to 20 cm) for root sampling were removed for each sample to estimate initial root distribution (Appendix Table A8). The soil cores were washed with water spray, the root material floated and collected, then dried for 48 hours 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 collected, washed, dried, and ground as before.

Shoot standing crops were estimated 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 something of a problem. The fruiting body of cheatgrass is quite small, the caryopsis (grain) being about five millimeters long and less than a half millimeter in diameter. The concatenation of organs and tissues that is dispersed when mature includes the caryopsis and glumes; one glume (the lemma) possesses an awn about ten millimeters long. To estimate the weight and constitution of the "seed", the lemma and its awn were removed from the seed, but the palea was left attached to provide a physical support for the caryopsis during handling.

Seeds were separated from mature shoots before harvesting the shoots. The seeds were gathered separately from tall or dominant culms (stems), representing the dominant tillers in the stand, and small or suppressed culms, representing the suppressed tillers or individuals in the stand. 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 (seed head) in normal (nodding) position. The culms involved in each size category were counted and the seeds were weighed both as a total for each category, and in lots of 200 for seed weight estimates.

All biomass measurements refer to ash-free weights.

Proximate Analysis

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, Washington. Briefly, determination of crude protein involved boiling a subsample of the ground dry material in concentrated sulfuric acid to release the nitrogen as ammonia for subsequent analysis. Crude fat was determined by boiling another subsample in dry diethyl ether. A third subsample was boiled first in 1.25% sulfuric acid, then boiled in 1.25% sodium hydroxide, the residue being crude fiber. Ash content was determined by combustion of the crude fiber at 600°C. The nitrogen-free extract was determined by difference, that is, by subtracting the percentage for crude protein, crude fat, crude fiber, and ash from 100.

Soils

Two soils were used in this experiment: Esquatzel silt loam for the rooting medium in the bottom of the lysimeters; and Ritzville silt loam which was substrate for the stand of cheatgrass transplanted into the lysimeters (Hajek, 1968). Physical and chemical analyses of the two soils are summarized in Table 1. The Esquatzel soil had a relatively high pH, 8.1, and a relatively low nitrogen content, 11 parts per million, compared to the Ritzville soil of the hillside community used for transplants (pH of 6.9 and 34 ppm nitrogen).

Greenhouse Studies

The effects on seedling growth of differing soil fertility and characteristics of the soils used in the lysimeters was investigated by a factorial design with six replications. The treatments investigated were soil type (Esquatzel and Ritzville silt loams), and fertilization (control = no fertilization, 120 ppm N, 80 ppm P, 80 ppm K and the NPK fertilizations together). Fertilization was with $NaNO_3$ for nitrogen, NaH_2PO_4 for phosphorus, KCl for potassium, and NaCl in controls to maintain a comparable salt balance. Seeds were planted sixteen per pot (equivalent to 1600 m^{-2}), and thinned to eight per pot after germination. The pots were watered regularly and harvested for root and shoot biomass and mineral assays after nine weeks of growth.

MEASUREMENT DETAILS

Imprecisions and Statistics

In most cases, estimates of imprecision were based on standard errors (Snedecor and Cochran, 1967), whether from primordial measurements or from linear combinations of primary measurements. Statistical

TABLE 1

Soil Physical and Chemical Characteristics
for Esquatzel and Ritzville Silt Loams

Character	Unit	Esquatzel	Ritzville
Sand	%	27	31
Silt	%	71	47
Clay	%	2	22
pH	---	8.1	6.9
Organic Matter	%	1.6	1.8
NO_3 - Nitrogen	ppm	2	14
NH_4 - Nitrogen	ppm	9	20
Phosphorus	ppm	34	58
Potassium	ppm	900	1250
Calcium	meq $(100g)^{-1}$	13	8
Total Bases	meq $(100g)^{-1}$	18	14
Cation exchange capacity	meq $(100g)^{-1}$	16	17

tests of differences were performed on all measurements where such tests were appropriate. Table 2 segregates most of the quantities mentioned in the text into measured and inferred categories.

Geometric combinations of measurements (multiplication or division) skew the distribution of errors to a non-normal form so that tests of significance based on standard errors may be misleading (R. O. Gilbert, personal communication). Rough estimates of precision in these cases were made by adding and subtracting the standard errors 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 two to form an "estimated error" which gauges precision in the results but which is not appropriate for computing statistical tests such as the t test.

Most measurements involved replicated estimates of an average, such as lysimeter weights, biomass, or seed numbers, to which the above considerations apply. However, the measurements of radiation flux densities were different. Here, 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 experiment. Comparisons between north and south exposures required an estimate of error, 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, presumably

TABLE 2

Segregation of Major Quantities in the Experiment into Measured and Inferred Categories

	Entity	Measured	Inferred
Abiotic			
	Solar Radiation	X	
	Reflected Solar Radiation	X	
	Net Solar Radiation		X
	Atmospheric Radiation		X
	Terrestrial Radiation		X
	Net Radiation	X	
	Total Latent Heat Flux	X	
	Evaporative Heat Flux	X	
	Transpirational Heat Flux		X
	Sensible Heat Flux to Atmosphere		X
	Sensible Heat Flux to Soil		X
	Surface Temperatures		X
	Air Temperatures	X	
	Soil Temperatures	X	
	Vapor Pressure Deficits	X	
	Wind Speeds	X	
	Soil Water Deficits	X	
Biotic			
	Initial Root Biomass	X	
	Initial Shoot Biomass	X	
	Final Root Biomass	X	
	Final Shoot Biomass	X	
	Net Root Production		X
	Net Shoot Production		X
	Seed Production	X	
	Crude Protein	X	
	Crude Fat	X	
	Crude Fiber	X	
	Nitrogen-Free Extract		X
	Heats of Combustion	X	

a function of time. Consequently, a two-way random effects analysis of variance (without replication) was performed 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, 1967).

Potential Errors Due to Procedures

After transplanting the cores into the lysimeters, the lysimeters were weighed routinely on an 8-day sequence, with two exceptions: from 31 March 1972 to 17 April (18 days), and from 12 May to 15 May. The May period provided a more detailed measurement during the height of flowering activity; the first weeks in April probably allowed time for acclimation of the plants to their new environment (Mooney and West, 1964), if indeed acclimation was required. Weighing intervals approaching four days probably press the limits of accuracy for water budget techniques (Rouse and Wilson, 1971/1972).

Measurement of evaporation, as opposed to evapotranspiration, required the assumption that shading due to green shoots had no effect on evaporation, potentially allowing two sources of error: first, shading by the shoots reduces flux densities at the surface of the mulch layer, and second, evapotranspiration tends to dry the soil profile to a greater extent than evaporation. Consequently, this method placed an upper bound on evaporation, and a lower bound on transpiration. However, temperature profiles in the lysimeters were indistinguishable from field conditions (Hinds, 1973), and heat fluxes into the soil were very similar, so most of the incident radiation must have been absorbed by the mulch layer on both exposures, thus reducing the potential error in evaporation.

Harvest techniques for estimation of biomass have a few drawbacks, primarily in reference to multi-specific communities (Malone, 1968), where sequential harvests are required for estimation of peak standing crop of each species. Harvesting in the detail attempted here was a slow process, but errors in composition or biomass due to contrasting times of day at harvest were probably undetectable (Holt and Hilst, 1969; Jameson and Thomas, 1956).

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 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) ($1\ W\ m^{-2} = 0.00143\ cal\ cm^{-2}\ min^{-1}$). This change is awkward for this interdisciplinary study, because meteorological fluxes are now relatively familiar in terms of watts $meter^{-2}$, but biomass energy equivalents in terms of Joules are foreign to nearly all ecologists. I have chosen to stand in both yards, by using duplicate units for the abiotic fluxes, but restricting the biological measurements to the traditional units. This is undesirable in the sense that it reinforces resistance to the accepted SI system, but on the other hand, the point of a scientific paper is to communicate, and if ecologists do not (yet) have a gut-feeling for Joules (I don't), then communication in terms of Joules seems inappropriate. At this time.

IV. RESULTS AND DISCUSSION

Pointillism: a technique of certain French Impressionists, wherein a painting is developed by artfully placing many tiny dots on a large blank canvas.

MICROCLIMATE AND ABIOTIC ENERGY BUDGETS

Characteristics of the immediate environment in which plants grow have traditionally been termed the microclimate, that is, the climate of the (small) space surrounding the plants, as opposed to the regional climate in which the community or ecosystem exists. Broadbent (1951) proposed to differentiate between the microclimate the plants experience and the "ecoclimate" that instruments measure. This distinction is unprofitable, because a basic tenet of science is measurement: if one cannot measure something, it is to that extent unknowable.

Geiger (1965) used the term "ecoclimatology" to describe the climate near the ground, where plants and animals live, and pointed out early in his classic monograph (page 1) that radiation budgets were essential considerations; the smaller the habitat under investigation, the more essential is this point, because the atmosphere requires finite time and space intervals to adjust to changes in boundary conditions. The results of this experiment amply substantiate this expectation, in that contrasts between the north- and south-facing exposures were not obvious in terms of ordinary meteorological measurements. Figure 7 illustrates averages of air temperature, soil

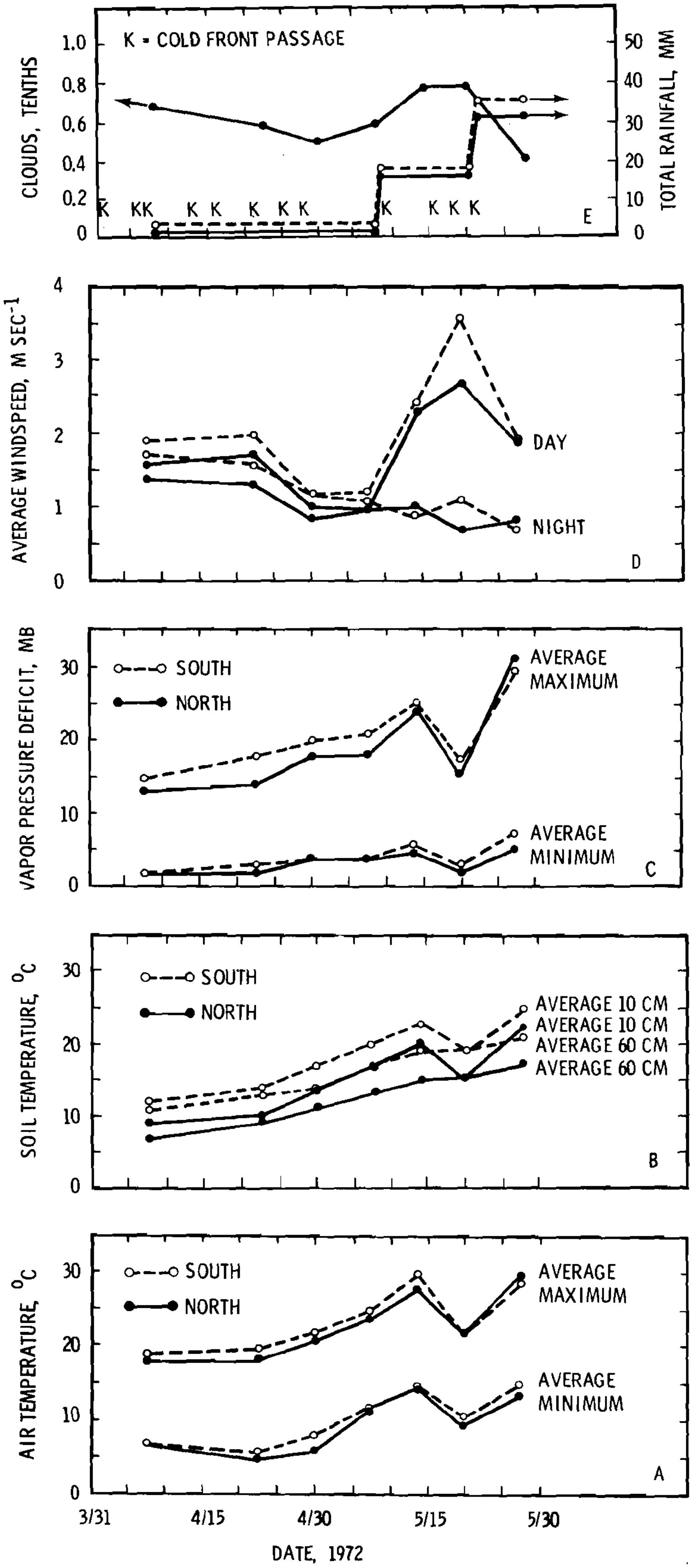


Figure 7. Average microclimatic conditions between weighings of the small lysimeters.

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 indicated time periods between weighings of the lysimeters) show that average air temperatures at 10 cm height rarely were so much as one degree Celsius apart, day or night, but soil temperatures on the south exposure were consistently two to four degrees Celsius warmer throughout the profile. 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. Night-time wind speeds showed a persistent tendency to decrease as the season progressed, probably due to 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 increased thereafter as vigorous frontal passages brought long-lived clouds. 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 (less than 0.4 sky cover), large vapor pressure deficits (exceeding 30 mb) and moderate winds (about 2 meters sec^{-1}), providing strong contrasts with the rather wet and cool conditions that prevailed during the preceeding weeks but still without provoking contrasts between the slope exposures. Average conditions throughout the experimental period are listed in Table 3, where the similarities between the two exposures are evident.

The small size of the experimental earth mound precluded formation of significant climatic modifications such as reported for ridges (Jackson, 1966) or mountains (Cantlon, 1955). However, the sloping surfaces made radically differing angles with incident solar radiation, creating differences in energy absorption that caused a whole cascade of energetic contrasts on the two slopes. This is illustrated in Figure 8, which shows the daily average angle of solar elevation with respect to the two slopes. Although the average elevation angle declined on the south exposure after about middle April, the average angle was about 35°, whereas on the north exposure the average angle was certainly less than 10°. This contrast was accentuated in the early part of April, because the sun could not shine on the north exposure until after 1100 hours.

Figure 9 shows the observed sequence of insolation on the two exposures (see Appendix Table A1), 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, just over half that on the south. Net radiation (Appendix Table A2) similarly was greater on the south, 260 cal cm^{-2} day^{-1} compared to about 150 cal cm^{-2} day^{-1} on the north. The difference between slopes had decreased substantially by mid-May. The reflected portion of incoming solar radiation was not greatly different on the two exposures, because the reflection coefficient increased with

TABLE 3

Average Climatological Conditions and Flux Densities on Contrasting North and South Exposures

	North	South
Daytime Temperature	21°C	22°C
Nightime Temperature	9°C	10°C
Soil Temperature (60cm)	11°C	15°C
Calculated Radiative Surface Temp.	31°C	40°C
Daytime Vapor Pressure Deficit	18 mb	20 mb
Nightime Vapor Pressure Deficit	5 mb	7 mb
Total Rainfall	3.3 cm	3.6 cm
Solar Radiation Flux Density	470 cal cm^{-2} day^{-1}	650 cal cm^{-2} day^{-1}
Net Radiation Flux Density	190	280
Transpiration Flux Density	66	70
Evaporation Flux Density	34	40
Sensible Flux Density to Atmosphere	90	160
Sensible Flux Density to Soil	4	4
Photosynthetic Flux Density	3	3

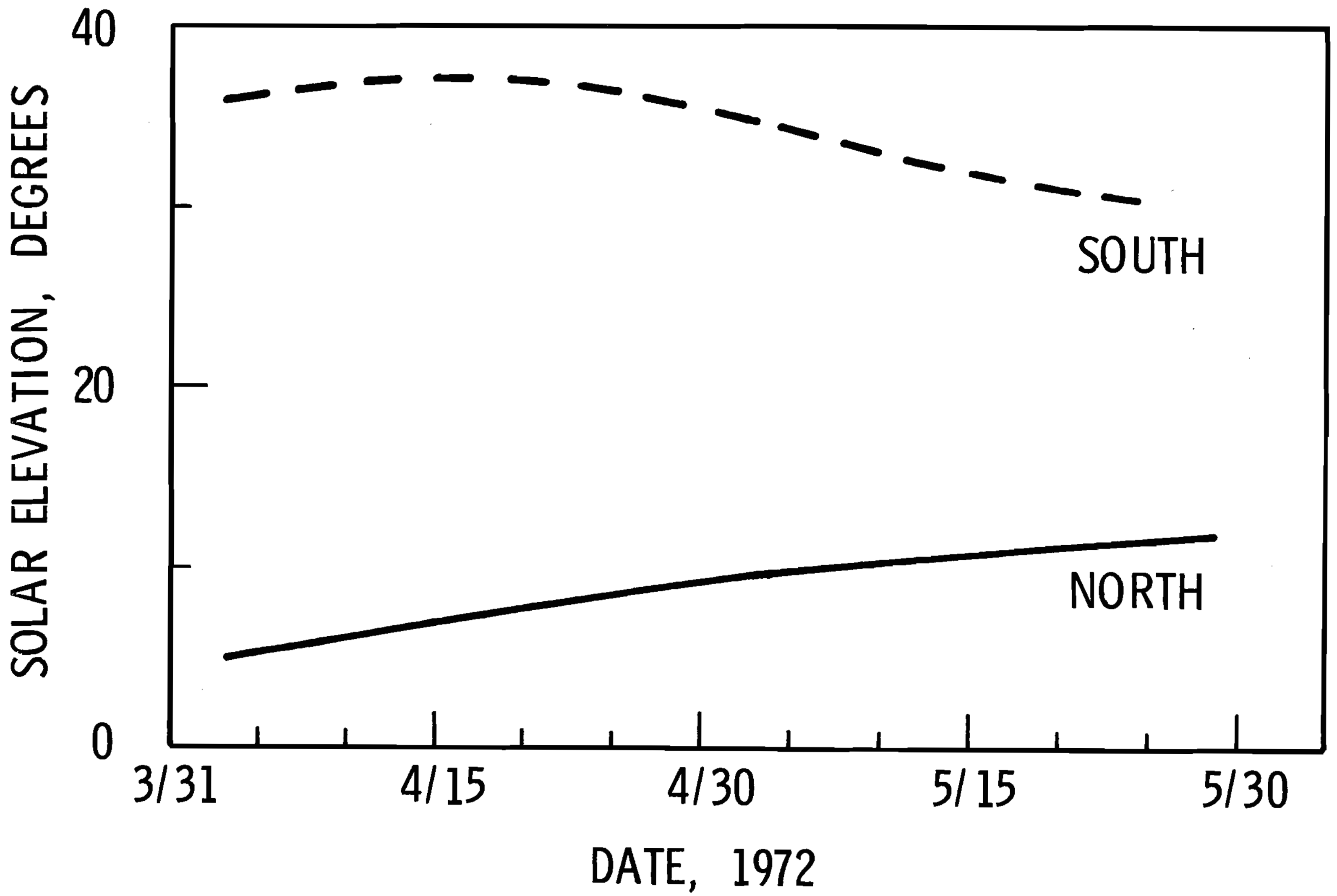


Figure 8. Average daily solar elevation angle with respect to 40° slopes, spring season.

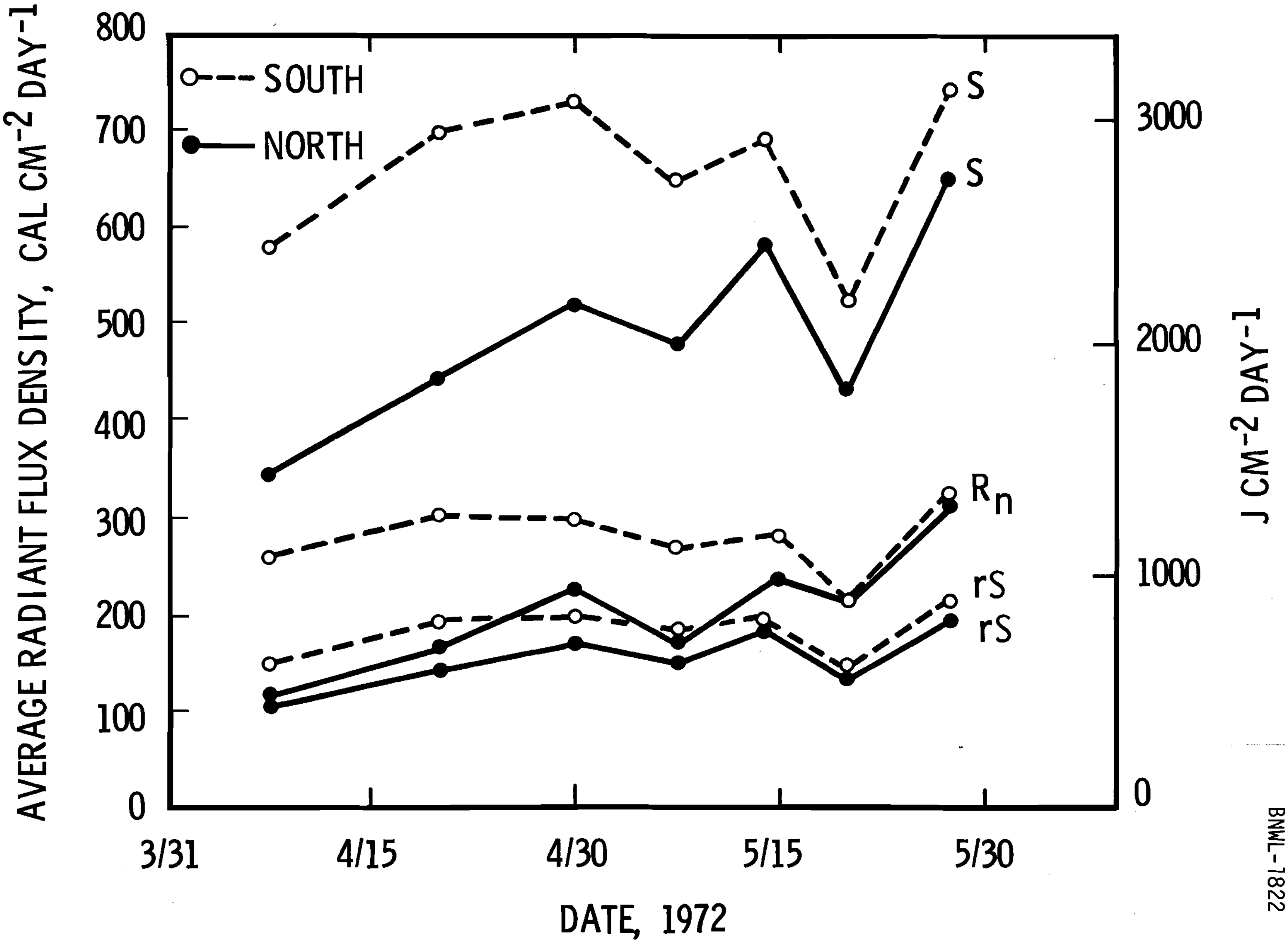


Figure 9. Average radiant flux densities on north- and south-facing slopes, Spring 1972.

declining solar elevation (Figure 2).

To provide a baseline for comparing the radiant fluxes, Table 4 lists the total incoming solar radiation on the two exposures for April and May and their corresponding deviations from reception measured on a horizontal surface. April was the month of strongest slope effect, causing about ± 20% or 25% deviation due to slope; May saw about ± 10% or 12% deviations. As a whole, the slope effect produced about equal enhancement on the south and diminishment on the north. This fact would not have been perceived by calculating direct beam reception on the slopes (as recommended by Garnier and Ohmora, 1968, for example), because the very significant effect of diffuse radiation would not then be considered. The significance of diffuse radiation was implicit in Figure 7, where it was shown that the daytime sky cover averaged over 60% throughout the spring, since overcast skies often have no direct beam component of insolation. Appendix Table A3 presents a detailed radiant energy budget.

Sensible heat fluxes are illustrated in Figure 10, 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....a good indication that almost all the insolation was intercepted by the cheatgrass community. Latent heat fluxes, given in detail in Appendix Tables A4 and A5 and summarized in Table A6, are illustrated in Figure 11, which shows that the rate of transpiration continued to increase on the north exposure long after it had declined on the south exposure.

TABLE 4

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%

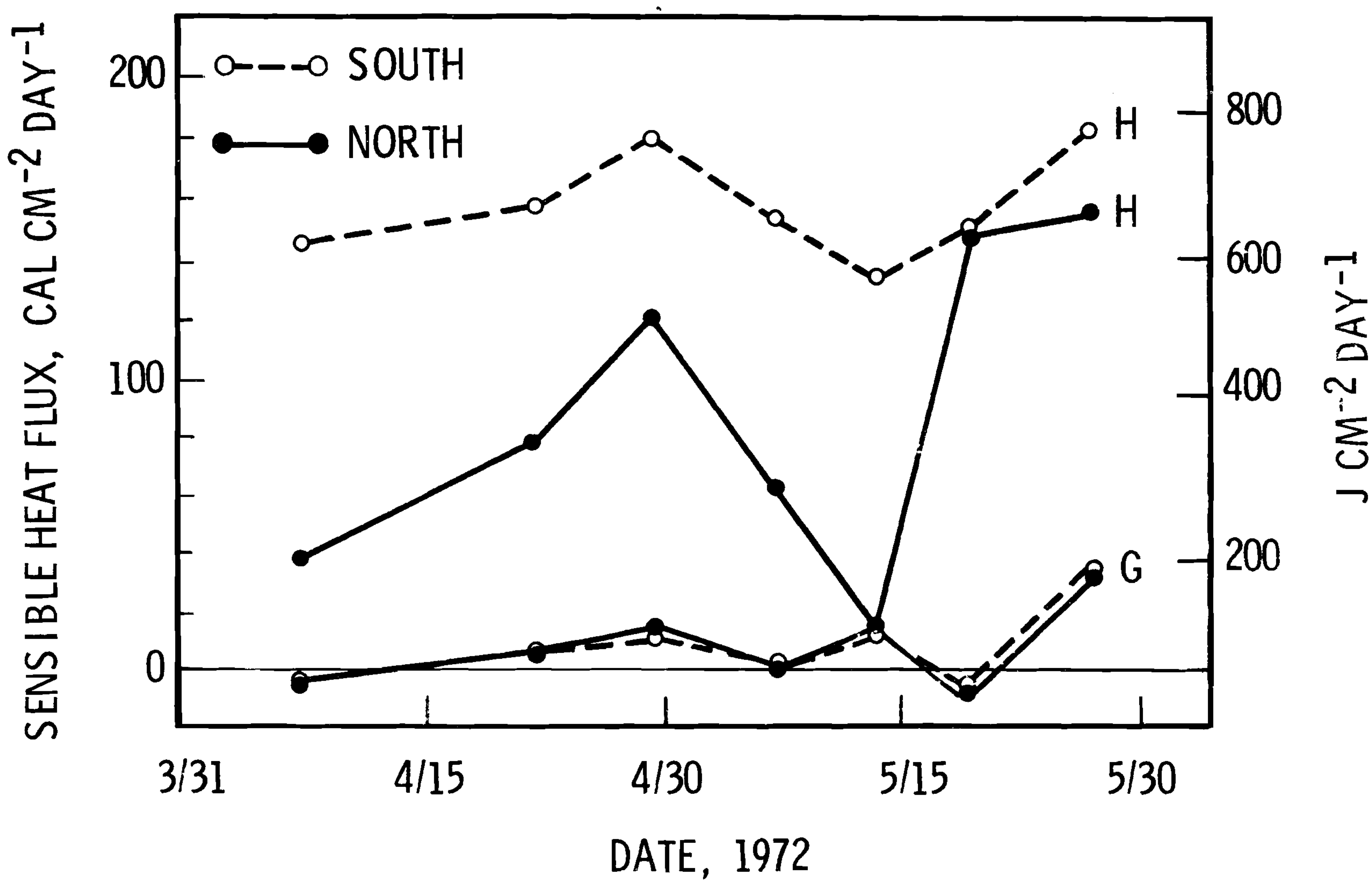


Figure 10. Average sensible heat fluxes on north- and south-facing slopes, Spring 1972.

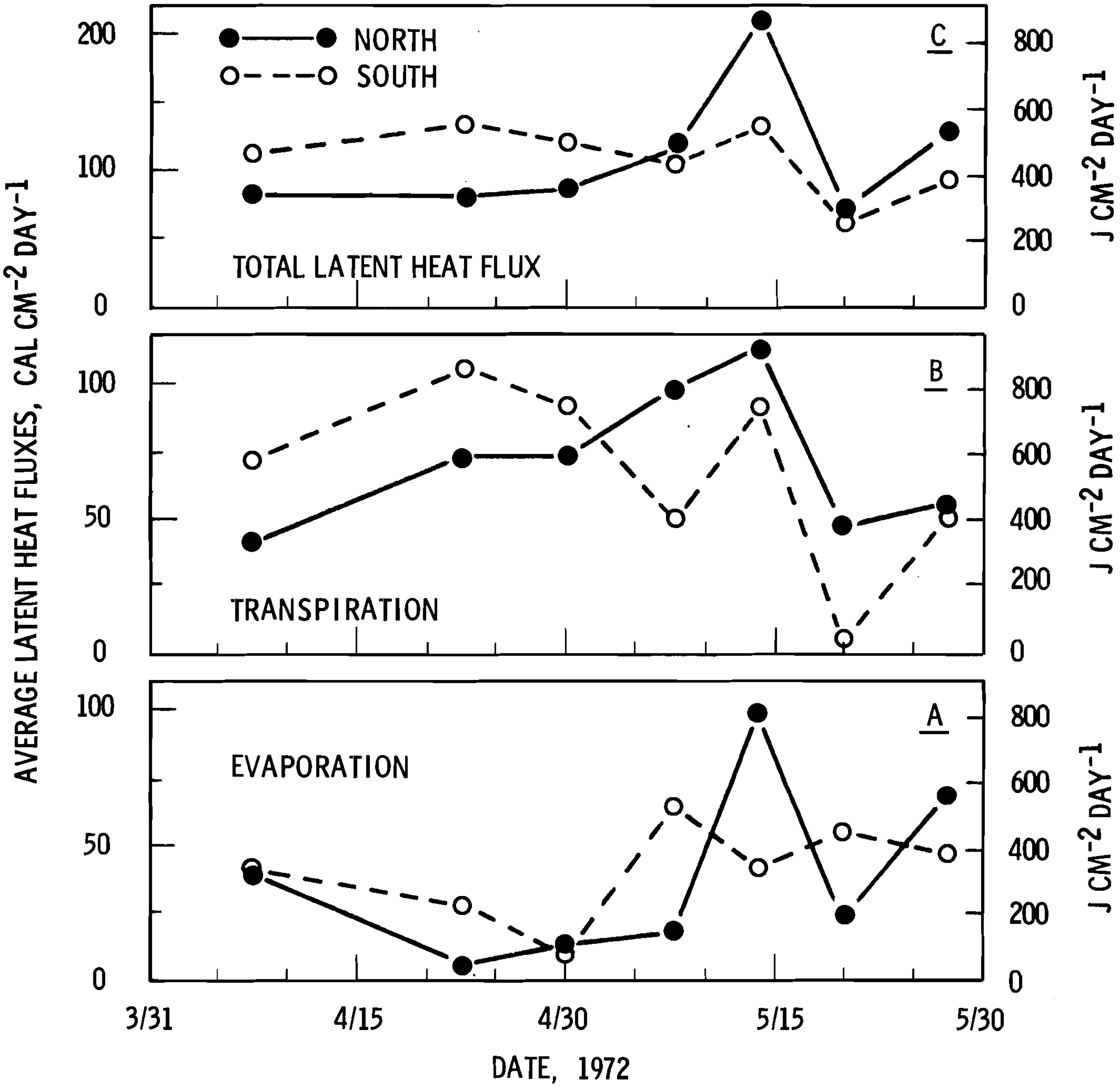


Figure 11. Average latent heat fluxes on north- and south-facing slopes, Spring 1972.

The total latent heat flux (evapotranspiration) remained much more nearly constant throughout the experiment on the south exposure than on the north.

Detailed comparisons of the various fluxes on the two exposures can be made from the energy budget data summarized in Table 5, which lists the seveeral fluxes and their corresponding standard errors of estimation. Most of the flux densities are very significantly different, as might be expected. However, transpiration totalled over the season was not significantly different, in spite of the preponderance of significant differences occurring throughout the season, because the direction of the differences varied from time to time (see Figure 11).

So, although standard climatological measurements failed to indicate strong differences between the exposures, the radiation and sensible heat budgets were very different. An insight into the relation between sensible and radiant fluxes can be obtained after calculating the long-wave radiation balance from equation 1 (Appendix Table A7). Given net short-wave radiation and net all-wave radiation, net long wave radiation is by definition the difference. The long-wave radiation fluxes estimated thusly are illustrated in Figure 12, along with the corresponding estimated surface temperatures. The surface temperatures on the south exposure apparently averaged about 40°C, compared to about 30°C on the north exposure. The difference between this radiative temperature and the measured air temperature is termed the "temperature excess"; it is due to atmospheric resistance to heat

TABLE 5

Average Energy Budgets 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	11900 ± 400
	South	260 ±10	301 ±11	302 ±15	275 ±13	286 ±12	212 ±12	326 ±12	277 ± 7	17200 ± 400
Evaporation	North	39 ±10	5 ± 3	12 ± 4	17 ± 3	99 ±29	23 ±17	68 ± 5	34 ± 2	2060 ± 100
	South	40 ± 4	27 ± 7	9 ± 3	64 ± 4	41 ±11	55 ±12	46 ±25	40 ± 2	2460 ± 100
Transpiration	North	42 ± 6	74 ± 4	74 ± 6	99 ± 5	113 ±15	48 ± 8	57 ± 6	66 ± 3	3980 ± 160
	South	72 ± 6	106 ± 6	91 ± 5	50 ± 8	92 ±12	6 ± 7	51 ±15	70 ± 4	4260 ± 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	5000 ± 850
	South	153 ±12	164 ±13	190 ±18	161 ±18	140 ±13	160 ±13	194 ±13	163 ±14	9600 ± 880

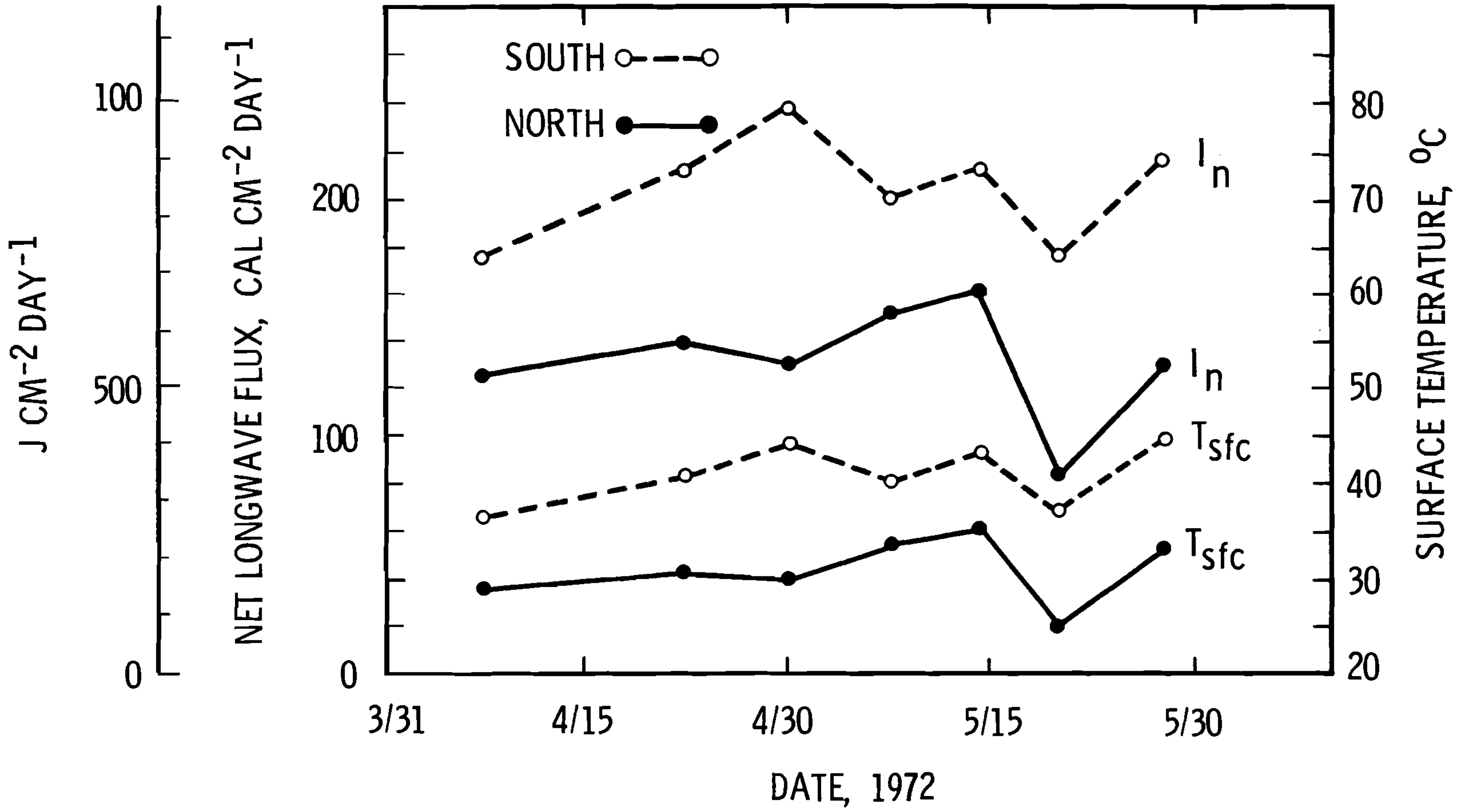


Figure 12. Average (calculated) longwave fluxes and radiative surface temperatures on north- and south-facing slopes, Spring, 1972.

transfer near surfaces. The excesses estimated here are about 18°C on the south exposure, and about 8°C on the north, which are comparable to excesses reported from more reliable data. Robinson (1957) reported excesses approaching 20°C, and Monteith and Szeicz (1961) note that excesses of 10°C or more can be expected even over swards with no water stresses. Grass communities faced with a water deficit can be expected to have a higher radiative temperature because of the lack of transpirational cooling (Gates, 1966; Glover, 1972). Therefore, it appears that the microscale climatic perturbations on these small mounds were concentrated into the radiation budgets, inducing much higher surface temperatures on the south exposure. The high surface temperatures in turn enhanced heat transfer to the atmosphere, leading to the high sensible heat fluxes noted in Figure 10.

WATER RELATIONS

It may be no accident that the only significant flux in the energy budget (Table 5) that did not differ between exposures was the one under some direct influence of biotic activity--transpiration. There was a general consistency in water usage on the two exposures, exemplified in Figure 13, which shows the cumulative total of transpired water as a function of soil water deficit. The straight line indicates the relationship before the rains in May (Figure 7E), showing that both exposures behaved almost identically in removal of soil water. The slope of the straight line in Figure 13 is essentially unity, indicating

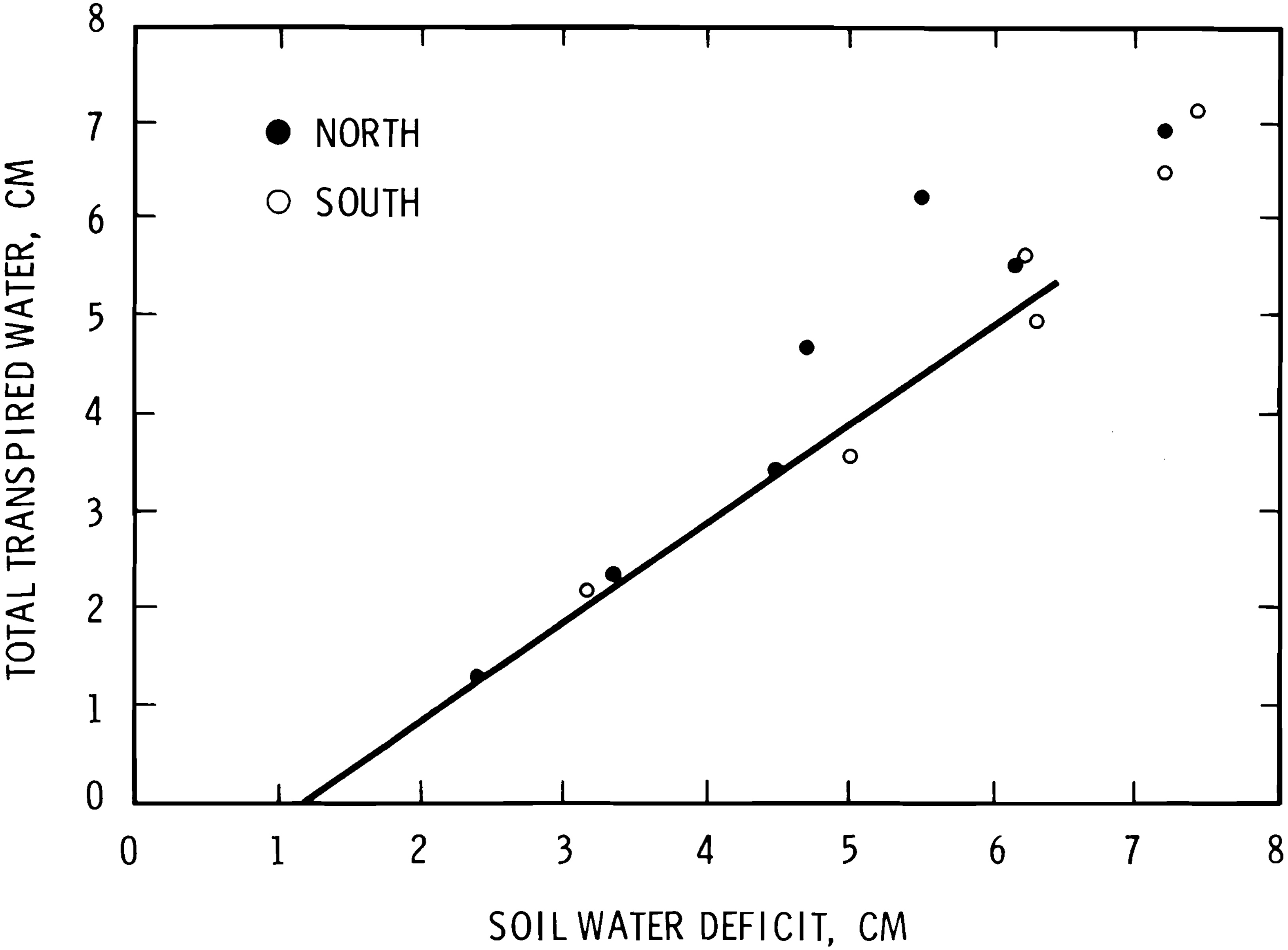


Figure 13. Cumulative total of transpired water on north- and south-facing slopes, against soil water deficit. The several points above the line followed substantial rains

that all soil water removed from the profile went to transpiration. This observation raises a swarm of questions for a physiologist, especially in terms of the distribution of roots with time and depth, and the relative water contents of the root-inhabited soil layers. However, to an ecologist, the straight line is the answer, not the question: water in the profile was transpired, rather than evaporated, on both exposures. After the rainfall in May, the two exposures behaved differently, due to a wet surface that allowed evaporative flux to compete with transpiration. The post-rainfall observations lie approximately on a line with slope of unity, even so.

A direct comparison of evaporation and transpiration is shown in Figure 14. The south exposure started with the same evaporative flux as the north, but as the season progressed, the evaporation from the south exposure increasingly exceeded that from the north exposure. Transpiration was quite the opposite: the south exposure started out at a higher rate, but later in the season, the transpiration rate from the south exposure dwindled so that the final tally was identical on both exposures.

The reason for the rather abrupt change in transpiration rate on the south exposure was not difficult to determine. Figure 15 is a composite of three data plots showing the temporal coincidence on both exposures of (1) change of rate of transpiration with (2) change fraction of available energy used in transpiration and with (3) depletion of soil water content to ~ 7.5 cm^3 cm^{-2}. This soil water content corresponds to an average water potential throughout the profile

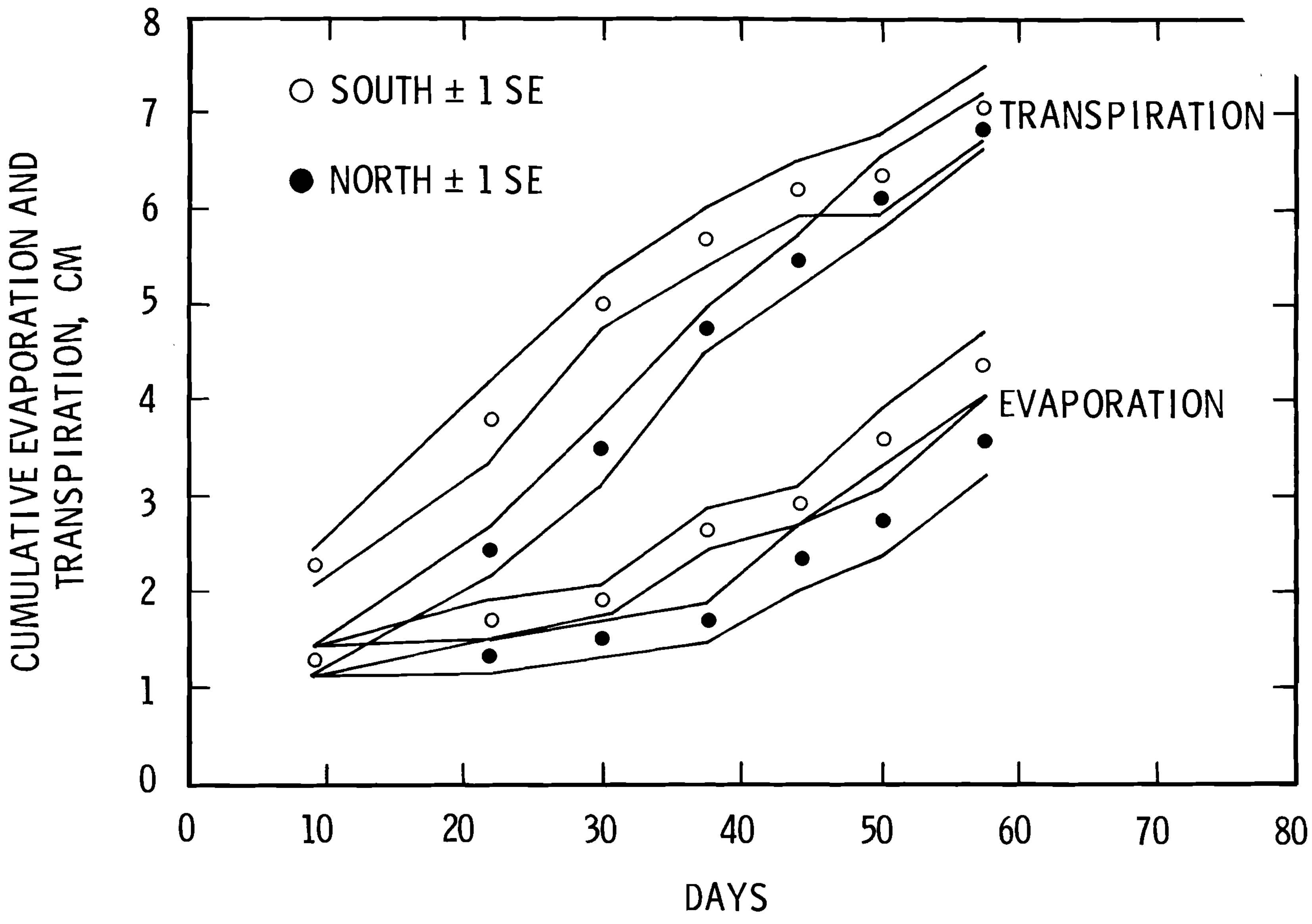


Figure 14. Cumulative evaporation and transpiration on north- and south-facing slopes as a function of time.

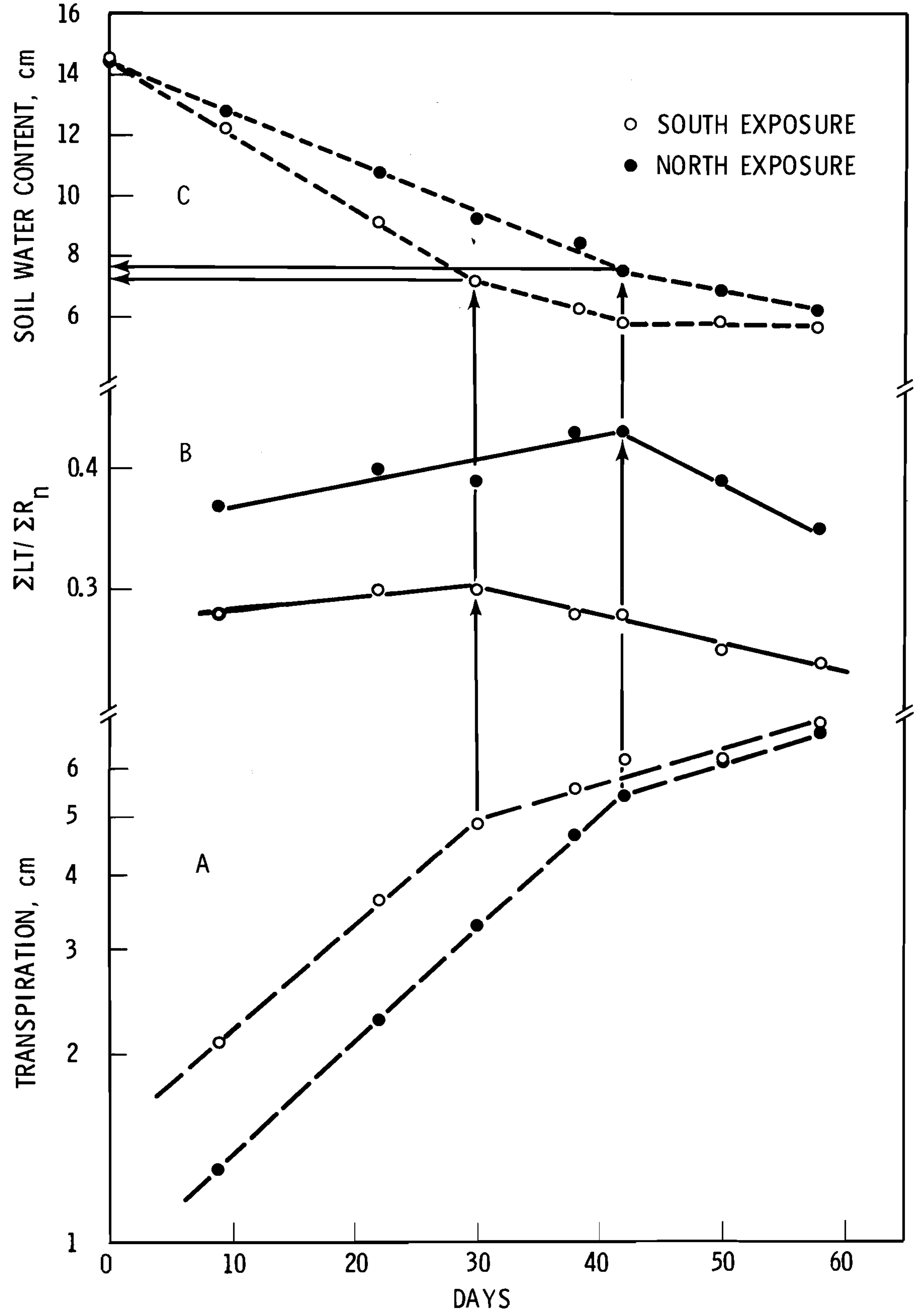


Figure 15. Cumulative transpiration (log scale), fraction of available energy used in transpiration, and soil water content in the profile (60 cm deep), as a function of time.

approaching -14 bars; a soil water content of about 9 cm corresponds to an average soil water potential of about -10 bars, just about the point that Lawlor (1973) found wheat roots to cease growth entirely. Soil water available for transpiration was initially removed at rates corresponding to the energy available, and resistance to water movement was primarily in the plants and atmosphere. However, after the average water potential of the profile decreased below about -14 bars, an additional resistance was injected into the water pathway, namely a soil hydraulic resistance, that reduced transpiration immediately. Ritchie et al. (1972) described similar results for corn and cotton, but with LET/R_n $\sim$ 1.0. It will be shown in the next section that root biomass was much less on the south exposure than on the north, perhaps due to this shortening of the growing season for the roots.

PRODUCTION AND ENERGY FIXATION

Ordinarily, a significant aspect of slope effects is the alteration of phenological progressions on contrasting exposures (Jackson, 1966; Cantlon, 1953). Cheatgrass is especially plastic in this respect, and observations on other earth mounds have indicated as much as a month difference in phenological milestones of cheatgrass on north and south slopes (Rickard et al., 1971). Direct comparisons between north and south slopes in this experiment require the plants to be at the same phenological stage, and this was the case, as shown in Table 6. Although plants on the south

TABLE 6

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 March	31 March
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 May 31--	
Green Culms, %	16 ± 2.0	12 ± 2.0
Red Culms, %	21 ± 2.0	20 ± 1.6
Dead Culms, %	63 ±	68 ± 3.6

slope began flowering a day or two sooner (11 May, compared to 12 May on the north) and at a slightly faster rate (four days, compared to six 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 by two factors: 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. This might indicate that seedling environment is critical for determining phenological progression later in the season, as postulated by Rickard et al. (1971).

The biomass of the cheatgrass at the beginning of the experiment (31 March) and at the end of the experiment (31 May) is tabulated in Table 7, and in detail in Appendix Tables A8 through A13. The final standing crop (above- and below-ground) was not significantly different on the two exposures, 608 gm m^{-2} on the north and 564 gm m^{-2} on the south. Neither was the springtime production of stem and leaves: 214 gm m^{-2} on the north and 228 gm m^{-2} on the south. However, the springtime production of roots and seeds were significantly higher on the north exposure, 121 compared to 94 gm m^{-2} for roots and 119 compared to 88 gm m^{-2} for seeds. Still, total springtime production was only marginally different, 454 compared to 410 gm m^{-2}, perhaps partly because the standard errors of this estimation were inflated by repeated additions (of plant parts) and subtractions (initial from final biomasses).

The standing crop of leafy tissues provides the photosynthetic activity supporting the growth of the rest of the plant. An indication

TABLE 7

Biomass Production (gm m^{-2} ashfree) of *Bromus tectorum* Grown in Small Lysimeters on North- and South-Facing Slopes Between 31 March and 31 May, 1972*
(n is sample size)

Plant Part	Exposure	31 March	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^{-4}		10^{-4}
Total	North	154 ± 11	--	608 ± 37	13	454 ± 54
	South	154 ± 11	--	564 ± 31	13	410 ± 48
	p			.2		.1

---

* Numbers following ± are standard errors, p is probability of the difference occurring by chance.

of the relative efficacy of leaf activity on the two exposures may be the amount of nonphotosynthetic tissues added and supported during the season. Table 8 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 greater. However, in terms of springtime growth of leafy tissues (shoots), roots and seeds, a constant ratio resulted: .56 on the north, and .40 on the south, for both root/shoot and seed/shoot ratios. This indicates that each gram of spring-grown shoot tissue from the north supported the growth of 1.12 gm of nonproductive tissues, as opposed to 0.8 gm by the south shoots, a very important 40% increase ([1.12-.8]/.8 = 40%) more 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 9 (and detailed in Appendix Tables A10 through A13), but it differed significantly between plant parts, and, for both roots and shoots, decreased with maturity. The heats of combustion in Table 9 are somewhat lower than expected from literature values for grasses in general; Hunt (1966) suggested 4.9 kcal gm^{-1} ashfree as an appropriate average for grasses, substantially higher than the 4.36 kcal gm^{-1} noted for mature shoots in Table 9. Possibly, Hunt was referring to relatively young, green tissues, but his suggestion is still higher than the 4.66 kcal gm^{-1} I found for immature cheatgrass shoots. Other workers have reported higher values for cheatgrass than I

TABLE 8

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)

	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

---

* Numbers following ± are estimated error (see "Imprecision and Statistics" in Methods Section).

TABLE 9

Heats of Combustion (kcal gm^{-1} ashfree) of Bromus tectorum Grown in Small Lysimeters on North- and South-Facing Slopes*

Date	Plant Part	Exposure	Sample Size	Heat of Combustion
31 March	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

---

* Numbers following ± are standard errors.

found here, particularly for seeds. R. K. Schreiber (personal communication) determined heats of combustion of cheatgrass seeds from a different site on the Hanford Reservation to be about 4.7 kcal gm^{-1}.

The photosynthetic efficiency determined for the two exposures is summarized in Table 10. The overall efficiency was calculated on the basis of total incoming solar radiation, and ashfree biomass production, resulting in an efficiency of 0.67% on the north and 0.43% on the south. It should be kept in mind that this efficiency is based on (1) approximately equal biomass production on the two exposures (Table 7); (2) equal heats of combustion (Table 9) and (3) unequal solar fluxes (Table 5). The efficiency calculated here is therefore not the same thing as the "efficacy" of leafy biomass in supporting other tissues discussed earlier, because the term "efficacy" was derived from consideration of partitioning, or allocation, of biomass, whereas the efficiency calculated in Table 9 was derived from production and energy availability.

The efficiencies determined in Table 10 are somewhat lower than corresponding efficiencies reported in other climates or for other species. Botkin and Malone (1968) summarize results from divers climates and communities, mostly reporting efficiencies under one percent for aboveground production alone. However, gross efficiencies from (nonagricultural) monospecific communities are usually lower than 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.

TABLE 10

Net (ashfree) Photosynthetic Efficiency of Bromus tectorum Grown in Small Lysimeters on North- and South-Facing Slopes*
(sample size = 13)

	Exposure	Root	Shoot	Seed	Total
Net Production	North	120 ± 11	214 ± 21	119 ± 6.6	453 ± 32
gm m^{-2}	South	93 ± 8	228 ± 19	88 ± 6.9	409 ± 24
	p	.009	.50	.0001	.1
Heat of Combustion	North	4.09 ± .083	4.36 ± .026	4.22± .023	---
kCal gm^{-1}	South	4.08 ± .072	4.38 ± .010	4.23± .056	---
	p	.009	.50	.0001	.1
Photosynthetic Energy	North	491 ± 46	933 ± 91	502 ± 28	1926 ± 106
Fixation, kCal m^{-2}	South	379 ± 33	999 ± 83	372 ± 29	1750 ± 94
	p	.009	.4	.0001	.09
Incident Shortwave	North	---	---	---	29.0 ± 0.60
Radiation, kCal cm^{-2}	South	---	---	---	40.5 ± 0.60
Net Photosynthetic	North	0.17 ± .02	0.32 ± .04	0.17 ± .01	0.67 ± .05
Efficiency, %**	South	0.093 ± .009	0.24 ± .02	0.093 ± .009	0.43 ± .03

---

* Numbers following ± are standard errors; p is probability of the difference occurring by chance.

** Numbers following ± are estimated error (see "Imprecision and Statistics" in Methods Section).

CARBON PATHWAYS

The distribution of photosynthetically fixed carbon in cheatgrass plants between various endpoints in roots and shoots at the beginning of the experiment is listed in Table 11 (and tabled in detail in Appendix Tables A8 and A9). The analysis shown in Table 11 is quite comparable to that of many other immature grasses: high in crude protein, low in crude fiber (National Academy of Sciences, 1968; McIlroy, 1967). The analysis of root, shoot and seed biomass at the end of the experiment is shown in Table 12 (in detail in Appendix Tables A10 through A15). 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. For root material, 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 immature cheatgrass (Table 11), the mature grass (Table 12) had much less crude protein content, and much more crude fiber content. Rapid nitrogen uptake by juvenile plants is such a fundamental aspect of plant physiology that 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

TABLE 11

Proximate Analysis (% ashfree) of Immature *Bromus tectorum* Plants, 31 March 1972

Plant Part	Sample Size	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

TABLE 12

Proximate Analysis (% ashfree) of Mature Bromus tectorum Grown in Small Lysimeters on North- and South-Facing Slopes, Spring 1972*

Plant Part	Exposure	Sample Size	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

---

* Numbers following ± are standard errors; p is the probability of the difference occurring by chance.

providing the strength required to support heavy seed panicles on very slender columns.

A relationship between heat of combustion and crude fat content for mature cheatgrass is shown in Figure 16. This relation is rather more marked than noted in other studies (c.f. Johnson and Robel, 1968), possibly because Figure 16 refers to different tissues within a single species, rather than similar tissues in differing species. The slope of the regression line in Figure 16, 0.087 kcal gm^{-1} (% crude $fat)^{-1}$, implies a heat of combustion of the fats of about 8.7 kcal gm^{-1}, quite comparable to typical values ($\sim$ 9 kcal gm^{-1}) for fatty substances (Morowitz, 1968). However, even for cheatgrass, the relationship in Figure 16 is not universal, because the immature shoots had a heat of combustion of 4.66 kcal gm^{-1} and a crude fat content of 2.9%, well above the regression line (immature roots fell right on the line). This is due to the high protein content of the immature shoots compared to the mature tissues; the mature tissues all had about the same crude protein content (about 10%), so the major contributor of varying heat of combustion was crude fat.

A detailed analysis of the relative importance of the various carbon pathways for springtime aboveground growth of cheatgrass is provided in Table 13. The pathway types are identified according to proximate analysis, so there is potentially a significant overlap in some of the biochemicals involved. This is particularly true for the division of carbohydrates into "celluloses" (crude fiber) and "starches" (nitrogen-free extract), because of failings of the

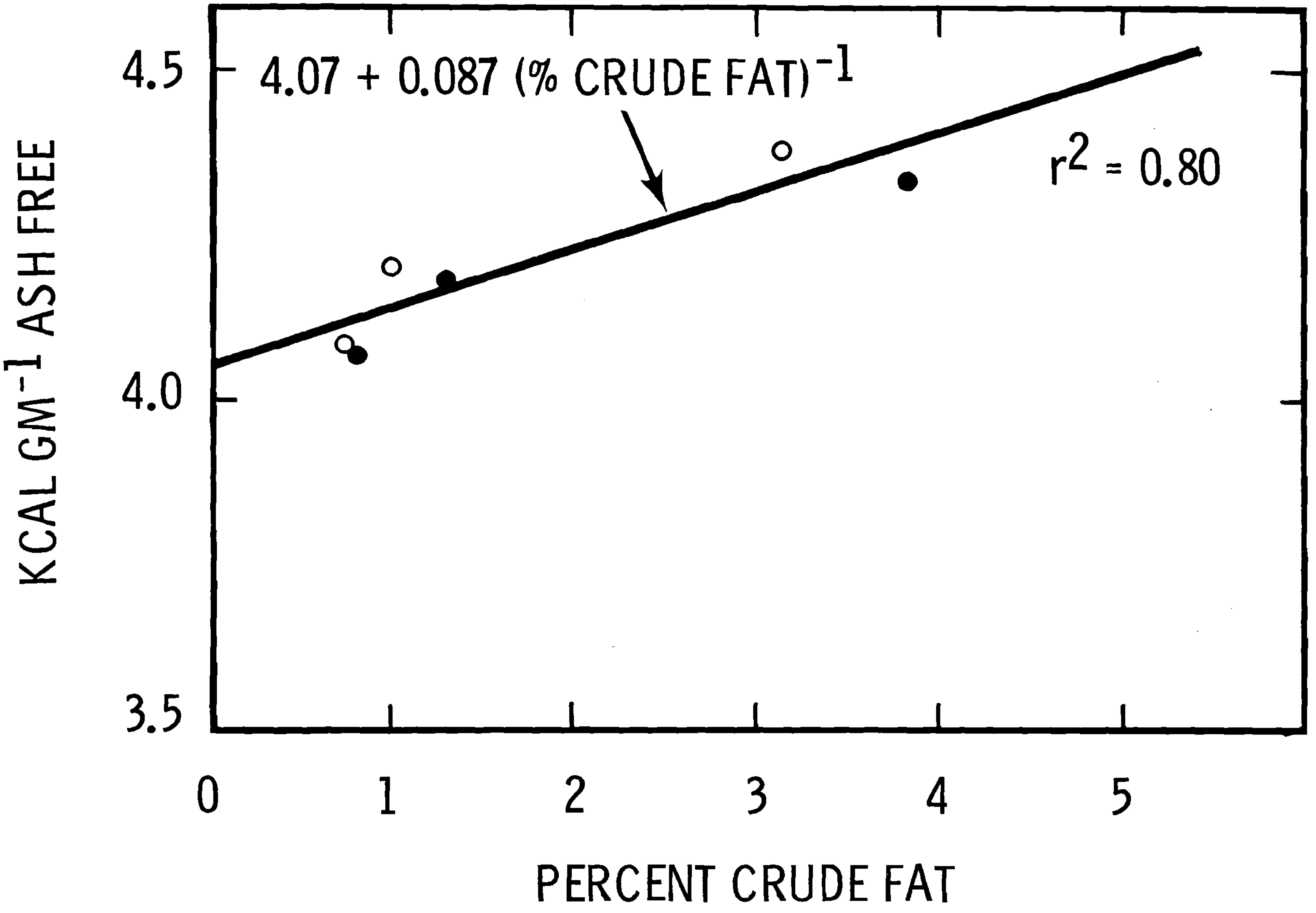


Figure 16. Heat of combustion of tissues from mature *Bromus tectorum* as a function of crude fat content.

TABLE 13

Allocation of Assimilation Among Four Carbon Pathways in Springtime Production of *Bromus tectorum* Grown in Small Lysimeters on North- and South-Facing Slopes*

		Root		Shoot		Seed		Total	
	Exposure	gm m^{-2}	%	gm m^{-2}	%	gm m^{-2}	%	gm m^{-2}	%
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	
Crude Fat	North	.8 ± .2	1	8 ± 2	4	1.6± .3	1	10 ± 2	2
	South	.7 ± .2	1	8 ± 2	4	.9± .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

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* Numbers following ± are estimated errors (see "Imprecision and Statistics" in Methods Section).

proximate analysis technique (Van Soest, 1967). Nonetheless, useful ecological insights devolve from Table 13.

The negative production of crude protein in shoot material 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, but statistical testing of the numbers was precluded because true standard errors do not exist for these calculations. Production of crude fats, crude fibers, 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 seed material in all categories. Seed material from the north exposure totaled to a higher biomass, but with similar percent composition, reflecting the higher total biomass noted earlier.

Comparison of mature with immature cheatgrass shows that phenological alteration of carbon pathways was very similar on the two exposures. The crude protein pathways were not strongly represented during spring growth, being about an order of magnitude less important during the spring than in 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, rather more marked than noted by McIlroy (1967) for grasses in general. Table 13 thus shows that for cheatgrass, at least, phenologically induced changes in carbon pathways were largely decoupled from most environmental rigors or abundances, and the phenological plasticity for which cheatgrass is noted must have been accompanied by a very sturdy homeostatic physiology of growth and development.

Mineral Uptake From the Lysimeter Soils

Figure 17 shows visual differences between cheatgrass growth observed in the greenhouse studies. Visual evidence of some nitrogen deficiency was clear in control specimens in both soil types, as well as with fertilization with P or K alone. The Esquatzel soil is noticeably poorer in nitrate (2 ppm) and total nitrogen (11 ppm) than the Ritzville, (14 ppm and 34 ppm, respectively) but the reaction to nitrogen was visually more pronounced in the Ritzville soil. The full NPK fertilization created the visual impression of close similarity between both soils (see also Table 1), perhaps indicating ample supply of other nutrients, in spite of a notable difference between pH of the soils (Esquatzel, 8.1; Ritzville, 6.9). Table 14 provides some numerical verification of the visual evidence: nitrogen content was almost identical between the soils, and nitrogen content was almost the same in control, P only and K only treatments. Phosphorus and potassium contents tended to be greater in the Ritzville soil when nitrogen or potassium were added, but other comparisons between nutrients and fertilizations were of no consequence. Roots were substantially less responsive to fertilization in all treatments.

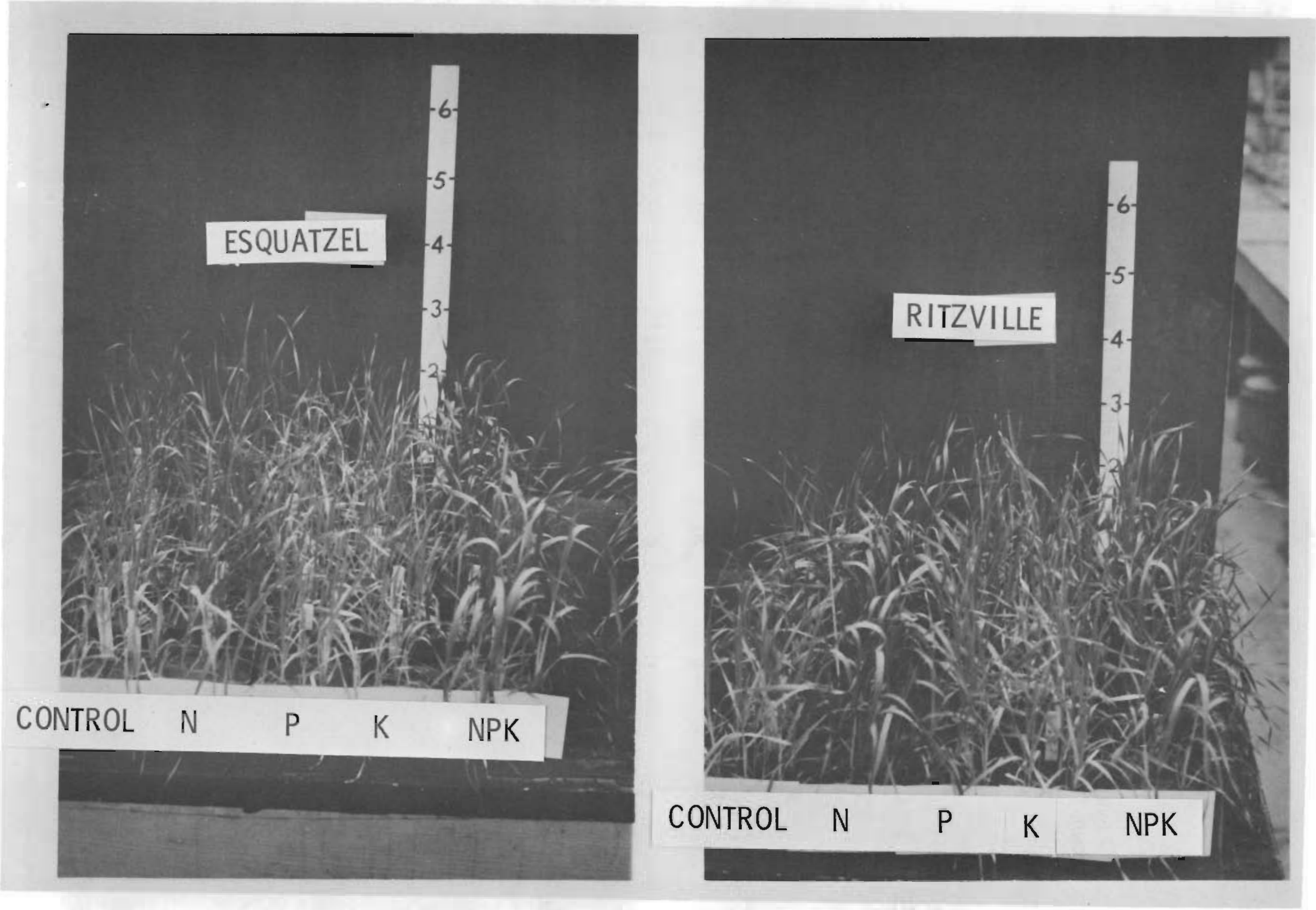

Figure 17. Comparison of growth of Bromus tectorum seedling on native and fertilized soils used in the small lysimeters.

TABLE 14

Average Nutrient Content (% ashfree) of Bromus tectorum Grown in Fertilized Esquatzel (E) and Ritzville (R) Silt Loams, Greenhouse Trials (Sample Size = 6)

Plant Part	Nutrient	Soil Type	Nutrient Added: N	P	K	NPK	None
Root	N	E	1.8	1.4	1.4	1.9	1.4
		R	1.8	1.2	1.4	1.6	1.4
	P	E	.16	.36	.16	.42	.20
		R	.26	.27	.22	.32	.18
	K	E	.16	.14	.16	.10	.20
		R	.20	.18	.18	.20	.17
	Ca	E	1.4	.70	1.1	.50	1.2
		R	1.1	1.2	1.0	1.2	1.1
Shoot	N	E	4.4	1.7	1.9	4.0	2.2
		R	4.3	1.8	1.8	3.0	2.0
	P	E	.22	.53	.15	.60	.32
		R	.68	.80	.57	.82	.57
	K	K	6.0	3.7	2.6	6.0	6.1
		R	6.8	5.5	5.1	6.8	5.1
	Ca	E	.45	1.0	.55	1.1	.53
		R	.45	.75	.40	.45	.35

Biomass production is summarized in Table 15, showing that root biomass responded significantly to fertilization only in the Ritzville soil, and only to P and K additions. However, shoot biomass increased significantly in the Ritzville soil for all treatments, whereas the Esquatzel soil yielded a significant reaction only to the total (NPK) treatment. The Esquatzel soil did not respond to nitrogen alone, as noted in the visual impressions, in spite of the relatively low nitrogen content of the soil.

The nutrient content of the shoots of the mature field-grown plants at the end of the experiment is summarized in Table 16. The nitrogen content was substantially less in the mature plants than in the greenhouse plants, which reflected the rapid nitrogen uptake known for juvenile plants (Langer, 1957). Phosphorus content was suppressed by about 20% in the mature plants, and potassium content was strongly reduced to about one-fifth in the mature plants, compared to the control treatment in the greenhouse. Calcium contents were higher in the field grown plants. However, the differences between greenhouse (juvenile) and mature plants are biologically less significant than the differentiation between the mature plants on the north- and south-facing exposures: all nutrient contents were (statistically) very significantly higher on the south (warm, dry) exposure.

The greenhouse trials indicated a slight but noticeable difference between soils insofar as reaction to fertilization was concerned, with the Esquatzel soil (used in the bottom 40 cm of the lysimeters) somewhat less responsive (less fertile?) than the

TABLE 15

Average Root and Shoot Biomass (gm m^{-2} ashfree) of *Bromus tectorum* Grown in Fertilized Esquatzel and Ritzville Silt Loams, Greenhouse Trials (n = 6)

Plant Part	Soil	Nutrient Added				
		N	P	K	NPK	None
Root ($D_{.05}$ = 17)*	Esquatzel	13	28	22	21	20
	Ritzville	23	57	60	33	31
Shoot ($D_{.05}$ = 12)*	Esquatzel	46	43	30	87	38
	Ritzville	85	57	50	83	40

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* $D_{.05}$ = Studentized least significant difference at $p < .05$ (Snedecor and Cochran, 1967, p. 272ff).

Table 16

Nutrient Content (% ashfree) of Bromus tectorum Shoots Grown in Small Lysimeters on North- and South-Facing Slopes*
(Sample Size = 13)

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}

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* Numbers following ± are standard errors, p is the probability of the difference occurring by chance.

Ritzville soil in which the transplanted grass was rooted. The greenhouse trials indicated no difference between soils in control treatments. Therefore, the uniform differentiation between slopes in nutrient content noted in the mature plants was a response to environmental conditions, rather than soil conditions or root distribution in the two soil layers.

REPRODUCTION

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 that "safe sites" for germination will be occupied by viable seeds. The response of cheatgrass to environmental conditions insofar as production of reproductive organs was concerned forms an important part of the natural history of this grass. Table 17 summarizes Appendix Tables A16 through A21, some pertinent data regarding seed production and numbers from the north and south exposures.

The seeds from dominant tillers, that is, large and vigorous culms with thoroughly filled seed panicles standing well above the general mass of leaves, were gathered separately from seeds from the relatively suppressed culms. The dividing line between dominant and suppressed culms was rather arbitrarily set at panicles exceeding 8 cm from flag leaf to top of the (nodding) panicle. The number of culms fitting this category was much higher on the north, 640 m^{-2} compared to 480 m^{-2} on the south, but the much more numerous suppressed

TABLE 17

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)

Tiller Size	Exposure	Sample Size	No. Culms	Seeds Culms^{-1}	Weight Seed^{-1}	No. Seeds	Total Seed Biomass
			m^{-2}		mg	1000's m^{-2}	gm m^{-2}
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	2600 ± 250	10 ± .7	1.98 ± .06	25 ± 2.4	49 ± 4
	South	8	2900 ± 120	7 ± .8	1.89 ± .10	20 ± 2.6	39 ± 7
	p		.12	.0007	.28	.06	.08
All	North	13	3300 ± 220	---	2.22 ± .05	54 ± 3.4	119 ± 7
	South	13	3400 ± 120	---	2.07 ± .05	43 ± 3.1	88 ± 7
	p		.56		.006	.002	.0001

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* Numbers following ± are standard errors, p is the probability of the difference occurring by chance.

culms were about as numerous on both exposures (2600 m^{-2} on the north and 2900 m^{-2} on the south). The preponderance of the suppressed culms led to no significant difference in total density of culms on both exposures, about 3300 m^{-2} on both. This density was toward the high side of the densities studied by Hulbert (1955).

The number of seeds per dominant culm was about the same on both exposures (45 on the north, 43 on the south) but the number of seeds per suppressed culm was significantly higher on the north, 10, compared to 7 on the south. Seed weights were uniformly larger from the north exposure, and larger from the dominant culms, decreasing in the order 2.48 mg (dominant, north), 2.32 mg (dominant, south), 1.98 mg (suppressed, north), and 1.89 mg (suppressed, south). (An analysis of variance 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 culms, and as a total, 54000 m^{-2} on the north, compared to 43000 m^{-2} on the south. The total seed biomass from dominant culms was significantly higher from the north exposure (70 gm m^{-2} compared to 50 gm m^{-2} from the south), but the difference in biomass of seeds from the suppressed culms, like the number of suppressed culms, did not attain significance. Total seed biomass was highly significantly different, 119 gm m^{-2} from the north compared to 88 gm m^{-2} from the south.

The picture described here was one of very successful reproduction on the north exposure compared to a noticeably less robust effort on the south. However, there is more to reproductive success than mere numbers. Table 18 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 identical. This probably was an important compensation. Lowe and Ries (1973) found that seedling survival in wheat was directly correlated with the amount, not the concentration, of nitrogen in wheat seeds; the same may well be true for cheatgrass, which resembles wheat both taxonomically and phenologically.

Crude fat, crude fiber, and nitrogen-free extract in the average seeds 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 the starches in the endosperm; it appears the north exposure seeds have about 8% more inventory to supply the seedling during the early stages of germination and growth. The relative importance of this excess (compared with seeds from the south exposure) in comparison with identical crude protein content (noted above) is unknown at this time.

Germination success in soil of the seeds from the various culms, from tests with 15 replications of 16 seeds each, showed the seeds to be highly viable, $\sim$ 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., 1972) and were amply demonstrated in this

TABLE 18

Average Composition of Seeds From *Bromus tectorum* grown in Small Lysimeters on North- and South-Facing Slopes*

Exposure	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract	Average Seed Weight
	mg	mg	mg	mg	mg
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

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* Numbers following ± are estimated errors (see "Imprecision and Statistics" in Methods Section).

experiment. Homeostatic relations between seeds from the two slopes apparently decreased in the following order: viability (very strong) > composition (strong) > weight (moderate) > numbers (none noticeable).

V. CONCLUSIONS

A successful cookie jar is not full of crumbs.

Temperatures and humidities on the contrasting north- and south-facing exposures were much more similar than the rates and disposition of energy fluxes on the two slopes. Average daytime temperatures and vapor pressure deficits were quite similar, as was total rainfall and wind speeds, perhaps leading to a conclusion that little difference redounded from slope exposure. However, this would be untrue, for the energy-rich south exposure had specific modes of energy transfer exaggerated in comparison with the north exposure (Figure 18), the most important of which was sensible heat transfer to the atmosphere from the warmed leaves. Plants growing on the south exposure had about a third again as much energy impinge upon them as net radiation; of this excess, about 80% went into heating the atmosphere, and about 20% into evaporation from soil surfaces. The surface temperatures of the south exposure plants were strongly elevated compared to the north exposure, providing the gradient for such a substantial increase in sensible heat transfer.

Water apparently played a passive role in the energy budgets of the cheatgrass; so long as the water remained readily available (more than 11% by weight), 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% or 11%, the rate of transpiration decreased to about a third of the freely transpiring rate observed

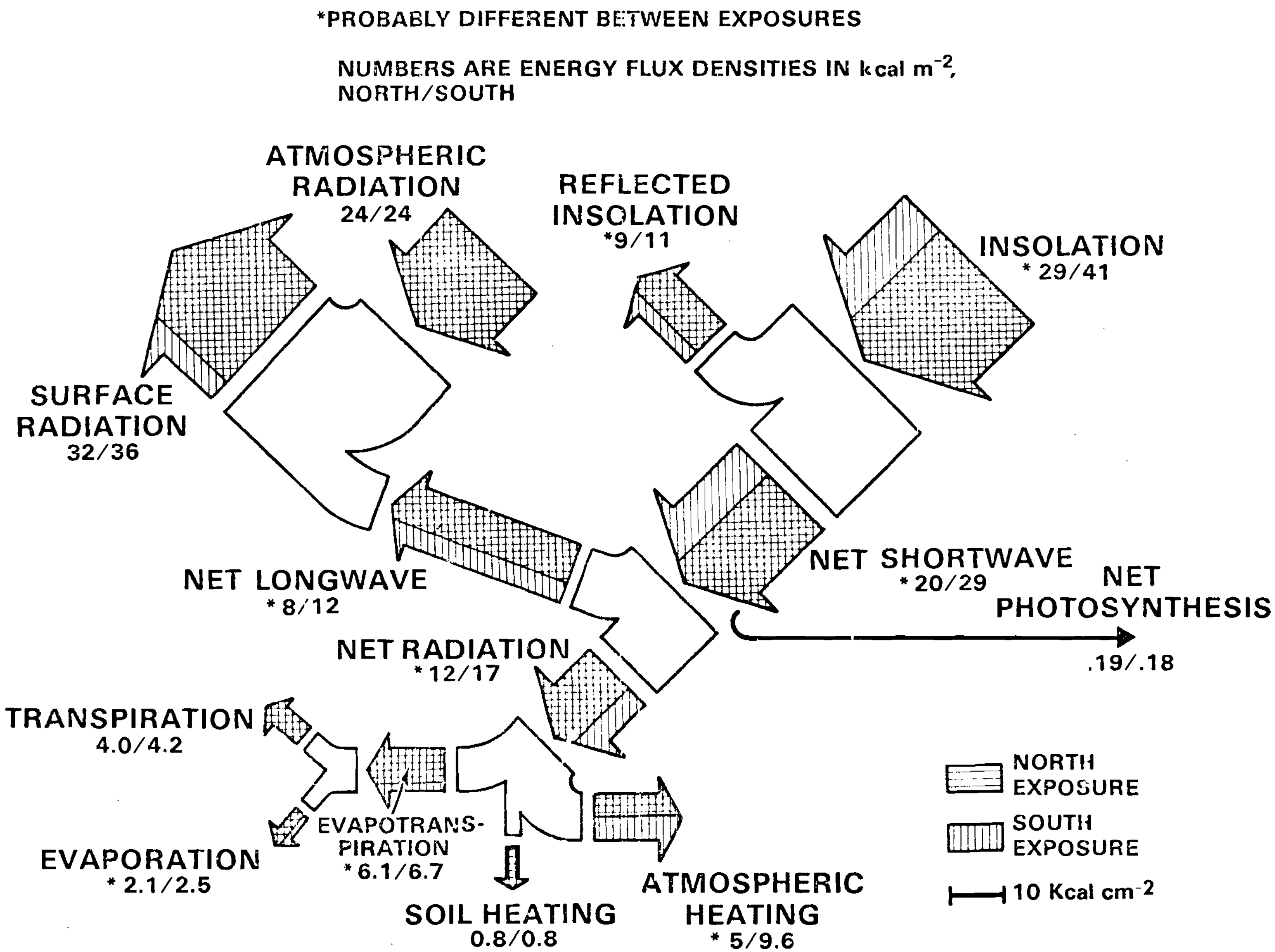


Figure 18. Flow sheet of energy in the environment on north- and south-facing slopes, Spring 1972.

earlier, probably due to an increase in rhizosphere resistance rather than atmospheric or surface resistance. The 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 50% longer growing season with little stress. The decrease in rate of water use occurred about 10 days before flowering on the south exposure, but after initiation of flowering on the north, apparently a timing that was peculiarly difficult for the south exposure plants.

Biomass production of shoot material (leaves and stems) was not very different on the two exposures, in spite of the apparent differences in growing season, but both root and seed production were greater on the north exposure (Figure 19). If, as Lawlor (1973) reported for wheat, cheatgrass roots slowed or ceased their growth in soils dried to about 11% (∿ -10 bars), 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 could have allowed formation of a greater number of fertile florets during flowering. The rate of water use was more restrictive than the total amount, 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. Consequently, each gram of shoot tissue on the north supported 1.12 grams of non-productive tissues (roots and seeds), but only 0.8 gm on the south

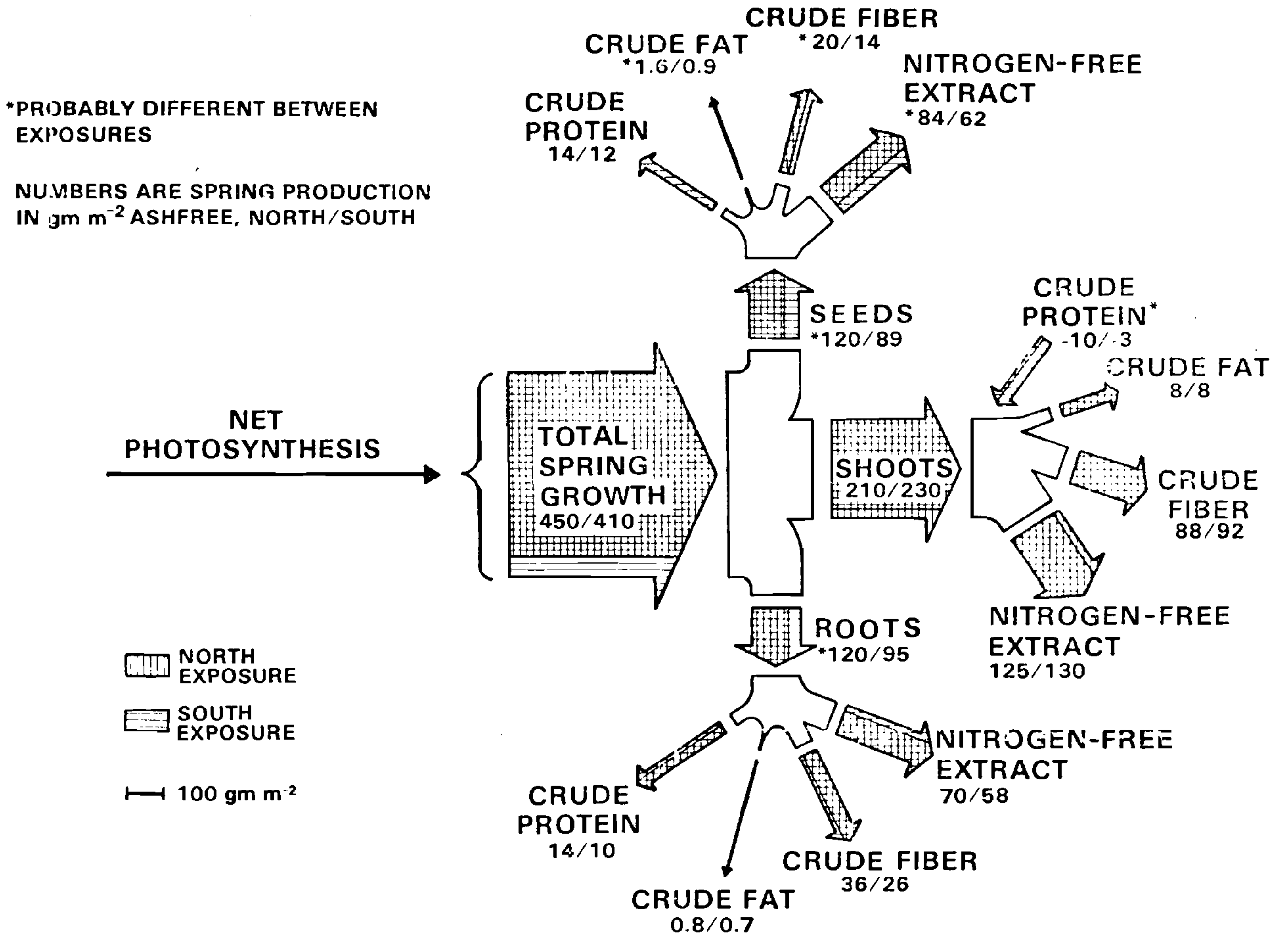


Figure 19. Fate of assimilated carbon during the spring growth phase of Bromus tectorum, on north- and south-facing slopes, Spring 1972.

exposure, a difference of 40%. However, the gross 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, 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 (∿ 1/3) than on the south (∿ 1/10). The fraction of mass allocated to crude fiber increased from about 18% in juvenile plants to about 40% 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 (gm m^{-2}) on the two exposures was significantly different, greater on the north, but the fractionation (%) between crude protein, fat, fiber and NFE differed only for protein. However, seed production was very different on the two exposures, being greater on the north for biomass, numbers, production of crude protein, fat, fiber, and NFE, and percent crude fat, fiber, and NFE. However, the protein content of the average seed from the two exposures was the same, potentially a significant compensation for viability (Lowe and Ries, 1973), although the average weight of the seeds from the south exposure were significantly smaller (∿ 10%).

Mineral uptake was also significantly different between exposures: the content (%) of N, P, K, and Ca were all smaller from shoots on the north exposure. Greenhouse studies showed this difference was probably not due to different patterns of uptake from the two soil layers used in the small lysimeters, but rather, due to environmental conditions and plant responses. The specific environmental variable(s) responsible were unidentifiable in this experiment. Nitrogen, phosphorus, potassium, and calcium were all about 20% greater (as percent of shoot biomass) on the south exposure.

How, then, to sum up the experiment? Two general conclusions seem appropriate. First, ecologists must be aware of the very important differences between climates considered with, and considered without, energy fluxes. On a microscale, temperatures and humidities can (and will) be similar, but the disposition of energy can (and will) differ. Alterations in energy relations imply considerable ecological importance, exemplified here by radical shifts in sensible and radiant heat fluxes. Second, water relations on a time scale of days are not the same as those on scales of seconds, at least to the extent that fleeting and reversible changes in resistance to water movement through leaves eventually mean little when averaged over a canopy and over day-to-day weather conditions.

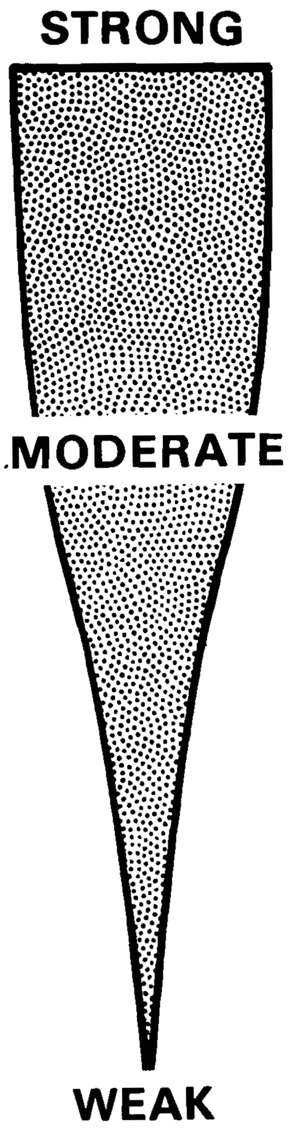
Now, more intimate notes relating only to cheatgrass. The time available for growth, being determined by the conditions for growth, poses the question, what would it profit a sward if it grew rapidly, but briefly? In this experiment, nothing. The imputed rapid growth rate for grass on the south exposure (deduced from rapid transpiration) ultimately led to fewer, smaller seeds, a sorry trade-off for an annual with colonizer traits.

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

Development was decoupled from the environment far more than was production for these juvenile plants with identical seedling histories; in this experiment, the decoupling was almost total, in that the progression to maturity proceeded apace on both exposures to nearly identical carbon distributions 60 days after beginning, water and temperature stresses to the contrary.

Homeostasis was variably evident in several aspects of the cheatgrass stand (Figure 20): greatest for seed viability and composition, and for leafy production; less for routing of the various biochemicals measured here; and least for seed numbers and mineral uptake.

Finally, more than half of the 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 seedling survival, compared with seedlings from the masses of the suppressed stems. This is indeed an adaptive trait for a colonizing annual.



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

Figure 20. Degrees of homeostasis observed in Bromus tectorum growing on north- and south-facing slopes, in terms of deviation from averages of the two exposures.

This experiment presented an unusually detailed accounting of the dissimilar fates of energy and carbon in a simple community. In a general sense, the study also illustrated the range of ecological insights made available by including even relatively crude energy relations (other than photoperiodism) in autecological or general ecological investigations. Perhaps the most valuable aspect of the experiment lies in specifying the range of invariance to be found in several ecologically pertinent attributes of this grass. Studies of communities dominated by this grass may now realistically take account of two important considerations for trophic dynamics in contrasting conditions: differences in biomass production on the one hand, and similarities in composition on the other.

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TABLE A1

Daily Totals of Incident Shortwave Radiation (cal cm^{-2}) on North- and South-Facing Slopes, Spring 1972

Day	North	South
3/31	276	700
4/1	328	537
4/2	311	611
4/3	380	759
4/4	276	566
4/5	137	226
4/6	363	685
4/7	346	714
4/8	311	655
4/9	398	552
4/10	380	552
4/11	363	359
4/12	293	463
4/13	433	714
4/14	380	552
4/15	311	478
5/16	502	744
5/17	433	596
Avg	346	581
4/18	467	759
4/19	467	700
4/20	259	581
4/21	485	729
4/22	467	818
4/23	485	729
4/24	554	774
4/25	363	537
Avg	443	703
4/26	502	759
4/27	572	803
4/28	554	729
4/29	470	655
4/30	519	788
5/1	538	700
5/2	519	729
5/3	572	803
Avg	531	746
5/4	519	774
5/5	572	818
5/6	538	700
5/7	606	611
5/8	172	256
5/9	380	600
5/10	572	803
5/11	538	744
Avg	487	663
5/12	606	818
5/13	659	759
5/14	641	700
5/15	450	537
Avg	589	704
5/16	398	448
5/17	189	226
5/18	659	700
5/19	624	774
5/20	502	522
5/21	67	93
5/22	589	729
5/23	450	788
Avg	435	535
5/24	276	611
5/25	693	788
5/26	728	818
5/27	728	803
5/28	711	788
5/29	728	818
5/30	728	729
5/31	659	700
Avg	656	757

TABLE A2

Daily Totals of Net (All-Wave) Radiation (cal cm^{-2})
on North- and South-Facing Slopes, Spring 1972

Day	North	South
3/31	109	254
4/1	102	243
4/2	69	272
4/3	104	293
4/4	93	290
4/5	72	130
4/6	104	352
4/7	116	274
4/8	79	297
4/9	127	309
4/10	112	264
4/11	130	235
4/12	103	224
4/13	141	341
4/14	154	186
4/15	101	152
4/16	182	358
4/17	152	251
Avg	114	260
4/18	161	326
4/19	164	300
4/20	154	244
4/21	157	313
4/22	153	354
4/23	189	313
4/24	166	334
4/25	157	224
Avg	163	301
4/26	196	326
4/27	254	347
4/28	229	313
4/29	167	160
4/30	194	347
5/1	244	244
5/2	244	332
5/3	310	347
Avg	227	302
5/4	196	365
5/5	195	309
5/6	186	292
5/7	147	225
5/8	78	72
5/9	127	214
5/10	240	383
5/11	262	336
Avg	179	275
5/12	270	355
5/13	251	295
5/14	246	295
5/15	197	199
Avg	241	286
5/16	188	155
5/17	102	40
5/18	271	299
5/19	275	302
5/20	233	179
5/21	83	14
5/22	292	313
5/23	301	390
Avg	218	212
5/24	264	195
5/25	321	355
5/26	332	345
5/27	332	344
5/28	322	338
5/29	332	354
5/30	340	313
5/31	345	365
Avg	324	326

TABLE A3

Summary of Average Radiation Fluxes (cal cm^{-2} day^{-1}) Over North- and South-Facing Slopes, Spring 1972*

		Dates								
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
Insolation	North	346	443	531	487	589	435	656	468	29000
		±19	±15	±10	±22	±24	±27	±25	±10	± 600
	South	581	703	746	663	704	535	757	653	40500
		±19	±15	±10	±22	±24	±27	±25	±10	± 600
Reflection	North	108	142	170	152	183	135	203	147	9100
		±19	±15	±10	±22	±24	±27	±25	±10	± 600
	South	148	190	202	185	197	149	214	177	11000
		±19	±15	±10	±22	±24	±27	±25	±10	± 600
Net Shortwave	North	238	301	361	335	406	300	453	322	19700
		±27	±21	±14	±31	±34	±38	±35	±14	± 850
	South	433	513	544	478	507	386	543	477	29100
		±27	±21	±14	±31	±34	±38	±35	±14	± 850
Net Radiation	North	114	163	227	179	241	218	324	192	11900
		±10	±11	±15	±13	±12	±12	±12	± 7	± 400
	South	260	301	302	275	286	212	326	277	17200
		±10	±11	±15	±13	±12	±12	±12	± 7	± 400

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* Numbers following are ± are standard errors.

TABLE A4

Evaporation and Evapotranspiration Measurements (mm day^{-1}), From Lysimeters With and Without _Bromus tectorum_ Plants, on a North-Facing Slope, Spring 1972

Lysimeter	DATES							
	3-31 4-17	4-18 4-26	4-27 5-3	5-4 5-11	5-12 5-15	5-16 5-23	5-24 5-31	Total
Bromus								
N - 1	1.01	0.58	0.54	1.27	2.17	1.20	2.75	76.6
2	1.43	1.49	1.88	1.92	4.20	1.38	1.81	109.0
3	1.23	1.05	1.16	2.14	4.28	1.63	2.32	104.4
4	0.87	1.09	0.94	2.03	3.91	1.49	2.57	95.4
5	1.26	1.12	1.59	2.28	4.06	0.83	2.25	102.2
6	1.72	1.63	1.85	1.78	2.90	1.23	1.85	107.6
7	1.55	1.59	1.92	2.28	3.41	0.83	1.81	107.4
8	1.18	1.12	1.41	2.36	4.42	1.09	2.43	105.0
9	1.59	1.59	1.59	2.03	3.33	0.94	1.63	102.6
10	1.18	1.45	2.07	2.50	4.06	1.20	1.99	110.0
11	1.50	1.23	1.56	2.03	3.62	1.20	2.32	106.7
12	1.86	1.63	1.67	1.74	3.33	0.98	1.99	109.0
13	1.65	1.27	1.41	1.70	3.62	1.81	2.07	108.6
Average	1.39	1.36	1.47	1.99	3.63	1.22	2.14	103.4
± Std. Error	±.081	±.064	±.12	±.091	±.17	±.083	±.092	± 2.5
Mulch Only								
NM - 1	0.65	0.18	0.11	0.33	1.09	0.18	1.16	31.1
2	0.39	0.04	0.18	0.18	2.68	0.04	1.30	31.3
3	0.97	0.04	0.33	0.36	1.30	0.98	1.01	43.4
Average	0.67	0.087	0.21	0.29	1.69	0.40	1.16	35.3
± Std. Error	±.17	±.47	±.065	±.056	±.50	±.29	±.084	± 4.1

TABLE A5

Evaporation and Evapotranspiration Measurements (mm day^{-1}), From Lysimeters With and Without Bromus tectorum Plants, on a South-Facing Slope, Spring 1972

	Dates							
Lysimeter	3-31 4-17	4-18 4-26	4-27 5-3	5-4 5-11	5-12 5-15	5-16 5-23	5-24 5-31	Total mm
Bromus								
S - 1	1.98	2.25	2.14	1.59	2.68	0.98	2.57	120.6
2	1.99	2.97	1.88	2.36	1.01	1.12	1.99	159.2
3	1.23	2.32	1.70	1.41	2.03	0.72	2.11	95.1
4	1.69	2.14	2.28	1.78	2.97	1.01	1.66	111.6
5	2.32	2.64	1.56	2.17	1.38	0.72	1.70	115.3
6	1.98	2.39	1.27	1.78	2.25	0.62	2.48	111.0
7	1.21	1.41	1.88	2.86	4.06	1.67	2.11	116.3
8	1.52	1.63	1.85	3.22	2.75	1.45	1.61	114.9
9	2.03	2.57	1.70	1.88	1.74	1.01	1.28	109.0
10	1.76	2.36	2.17	2.21	2.32	0.94	1.99	116.6
11	2.52	2.28	1.23	1.52	1.74	1.16	1.74	113.2
12	2.22	2.36	1.52	1.30	2.25	0.83	1.70	108.4
13	2.54	2.21	1.20	1.34	2.17	1.20	1.82	114.0
Average	1.92	2.27	1.72	1.96	2.26	1.03	1.90	115.8
± Std. Error	±.12	±.11	±.099	±.16	±.21	±.082	±.099	± 4.0
Mulch Only								
SM - 1	0.73	0.72	0.22	1.05	0.58	0.36	2.19	51.0
2	0.68	0.29	0.29	0.98	0.51	1.38	-0.17	35.8
3	0.49	0.25	0.11	1.12	0.43	0.94	1.08	38.0
4	0.85	0.58	0.04	1.27	1.23	1.05	0.50	47.0
Average	0.69	0.46	0.16	1.10	0.69	0.93	0.90	43.0
± Std. Error	±.075	±.11	±.056	±.062	±.18	±.21	±.50	± 3.6

TABLE A6

Summary of Average Water Fluxes (mm day^{-1}) for Bromus tectorum Grown in Small Lysimeters on North- and South-Facing Slopes, Spring 1972*

Treatment	Sample Size	Exposure	3-31 4-17	4-18 4-26	4-27 5-3	5-4 5-11	5-12 5-15	5-16 5-23	5-24 5-31	Season Average	mm Total
Bromus	13	North	1.39 ±.08	1.36 ±.06	1.47 ±.12	1.99 ±.09	3.63 ±.17	1.22 ±.08	2.14 ±.09	1.72 ± .04	105.0 ± 2.4
	13	South	1.92 ±.12	2.27 ±.11	1.72 ±.10	1.96 ±.16	2.26 ±.21	1.03 ±.08	1.90 ±.10	1.90 ± .07	115.8 ± 4.0
		p	2×10^{-5}	10^{-6}	.03	.8	10^{-6}	10.2	.02	.003	.0006
Mulch	3	North	0.67 ±.17	0.09 ±.05	0.21 ±.06	0.29 ±.06	1.69 ±.50	0.40 ±.29	1.16 ±.08	0.58 ± .07	35.3 ± 4.1
		South	0.69 ±.08	0.46 ±.11	0.16 ±.06	1.10 ±.06	0.69 ±.18	0.93 ±.21	0.90 ±.50	0.70 ± .06	43.0 ± 3.6
		p	.9	.005	.4	10^{-5}	.03	.007	.40	.1	.09
Transpiration		North	0.72 ±.10	1.27 ±.06	1.26 ±.11	1.70 ±.08	1.94 ±.26	0.82 ±.24	0.98 ±.09	1.12 ± .05	68.1 ± 2.8
		South	1.23 ±.11	1.81 ±.11	1.56 ±.09	0.86 ±.14	1.57 ±.20	0.10 ±.12	1.00 ±.26	1.19 ± .06	72.8 ± 3.9
		p	5×10^{-5}	10^{-6}	.006	10^{-6}	.1	.0005	.9	.2	.2

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* Numbers following ± are standard errors; p is the probablity of the difference occurring by chance.

TABLE A7

Summary of Calculated Average Longwave Radiation Fluxes (cal cm^{-2} day^{-1}) and Surface Temperatures (°C) on North- and South-Facing Slopes, Spring 1972*

		Dates								
Flux	Exposure	3-31 4-17	4-18 4-26	4-27 5-3	5-4 5-11	5-12 5-15	5-16 5-23	5-24 5-31	Season Average	Total
Net Longwave	North	124 ±29	138 ±24	134 ±21	156 ±34	165 ±36	82 ±40	129 ±37	129 ±16	7900 ± 950
	South	173 ±29	212 ±24	242 ±21	203 ±34	221 ±36	174 ±40	217 ±37	200 ±16	12200 ± 950
Longwave Downward	North	383 ±40	383 ±40	383 ±40	389 ±40	394 ±40	401 ±40	404 ±40	390 ±40	23800 ±2400
	South	383 ±40	383 ±40	383 ±40	389 ±40	394 ±40	401 ±40	404 ±40	390 ±40	23800 ±2400
Longwave Outward	North	507 ±50	521 ±45	517 ±45	545 ±55	559 ±55	483 ±55	533 ±55	519 ±43	31600 ±3400
	South	556 ±50	595 ±45	625 ±45	592 ±55	615 ±55	575 ±55	621 ±55	590 ±43	36000 ±3400
Surface Temperature	North	29 ± 6	31 ± 6	30 ± 6	34 ± 6	36 ± 6	25 ± 6	33 ± 6	31 ± 6	--
	South	36 ± 6	41 ± 6	45 ± 6	41 ± 6	44 ± 6	37 ± 6	45 ± 6	40 ± 6	--

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* Numbers following ± are estimated errors (see "Imprecision and Statistics" in Methods Section).

TABLE A8

Standing Crop, Distribution with Depth, Heat of Combustion and Proximate Analysis of Immature Roots from a *Bromus tectorum* Community Used for Core Transplants to Small Lysimeters, 31 March 1972 (Ashfree)

Standing Crop			Heat of combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
gm m^{-2}	1st 10 cm	2nd 10 cm	kCal gm^{-1}	%	%	%	%
23	97	3					
8	86	14					
26	100	0	4.30	10.9	.83	19.7	68.6
31	78	22					
17	90	10					
30	85	15					
5	90	10	4.33	11.6	1.35	23.3	63.7
12	92	8					
6	89	11					
19	80	20					
17	--	--	4.32	10.8	1.38	23.4	64.4
19	--	--					
21	--	--					
16	--	--					
20	--	--	4.35	12.5	1.46	21.1	64.8
27	--	--					
Average 18	89	11	4.32	11.4	1.26	21.9	65.4
Std. Error ± 2.0	± 2	± 2	±.02	± .39	± .14	± .90	±1.10

TABLE A9

Standing Crop, Heat of Combustion, and Proximate Analysis of Immature Shoots from a *Bromus tectorum* Community Used for Core Transplants to Small Lysimeters, 31 March 1972 (Ashfree)

Standing Crop gm m^{-2}	Heat of Combustion kCal gm^{-1}	Crude Protein %	Crude Fat %	Crude Fiber %	Nitrogen-Free Extract %
187					
148	4.99	22.0	3.3	16.9	67.8
128					
190	4.61	26.4	2.7	18.9	52.1
115					
121	4.62	25.5	3.3	19.7	51.4
151					
174	4.66	28.6	3.1	18.2	50.1
137					
90					
53					
161	4.51	20.6	2.4	19.8	57.2
145					
120	4.54	21.1	2.8	16.9	59.2
117					
Average 136	4.66	24.0	2.93	18.4	56.3
Std. Error ±9.3	±.071	±1.33	±.15	± .53	±2.72

TABLE A10

Standing Crop, Heat of Combustion, and Proximate Analysis of the Mature *Bromus tectorum* Roots From Small Lysimeters on a North-Facing Slope, 31 May 1972

Lysimeter	Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
	gm m^{-2}	kCal gm^{-1}	%	%	%	%
North - 1	67	4.25				
2	150	3.87	11.7	.5	28.7	59.1
3	121	3.77				
4	187	4.36				
5	88	3.73	11.1	3.4*	32.2	53.4
6	112	4.00				
7	154	3.90				
8	116	4.02	9.8	.9	26.7	62.6
9	148	3.89				
10	198	4.80	10.9	.7	24.7	63.7
11	192	4.31				
12	131	4.00	12.8	.9	30.7	55.6
13	143	4.33				
Average	139	4.09	11.3	.75	28.6	58.9
± Std. Error	±11	±.083	±.49	±.10	±1.3	±2.0

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* Rejected at P < .001 by an outlier rule (Snedecor and Cochran, 1967, p. 322).

TABLE A11

Standing Crop, Heat of Combustion, and Proximate Analysis of the Mature *Bromus tectorum* Roots From Small Lysimeters on a South-Facing Slope, 31 May 1972

Lysimeter	Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
	gm m^{-2}	kCal gm^{-1}	%	%	%	%
South - 1	117	3.65				
2	91	4.17				
3	134	4.04	9.8	1.0	25.6	63.5
4	89	4.02				
5	136	4.05				
6	108	4.12				
7	104	4.00	10.9	0.5	23.4	65.3
8	96	4.02				
9	174	4.61				
10	111	3.60				
11	126	4.23	10.4	0.8	29.8	58.9
12	66	4.17				
13	99	4.30				
Average	112	4.08	10.4	0.77	26.3	62.6
± Std. Error	± 7.5	±.072	± .32	±.15	± 1.88	±1.9

TABLE A12

Standing Crop, Heat of Combustion, and Proximate Analysis of Mature *Bromus tectorum* Shoots From Small Lysimeters on a North-Facing Slope, 31 May 1972

Lysimeter	Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
	gm m^{-2}	kCal gm^{-2}	%	%	%	%
North - 1	275	4.53	10.65	5.42	29.1	54.8
2	518	4.36	5.39	3.47	31.4	59.7
3	321	4.40	6.94	3.98	31.0	58.0
4	391	4.54	6.78	6.60	30.2	56.4
5	300	4.36	7.38	3.10	31.7	57.8
6	331	4.35	7.04	2.95	32.6	57.4
7	374	4.33	6.44	2.71	35.5	55.4
8	321	4.32	5.35	2.82	34.6	57.3
9	336	4.42	5.32	4.72	33.2	56.7
10	441	4.24	5.57	1.28	16.1*	77.1*
11	280	4.32	6.12	2.65	31.9	59.3
12	330	4.26	6.21	1.32	16.1*	76.4
13	337	4.26	6.48	1.37	15.2*	77.0*
Average	350	4.36	6.59	3.26	32.1	57.3
± Std. Error	±19	±.026	±.39	±.44	±.61	±.49

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* Rejected at p < .001 by an outlier rule (Snedecor & Cochran, 1967, p. 322).

TABLE A13

Standing Crop, Heat of Combustion, and Proximate Analysis of Mature *Bromus tectorum* Shoots From Small Lysimeters on a South-Facing Slope, 31 May 1972

Lysimeter	Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
	$gm\ m^{-2}$	$kCal\ gm^{-1}$	%	%	%	%
South - 1	379	4.33	9.39	1.94	14.7*	73.9*
2	397	4.34	7.85	2.43	34.0	55.8
3	284	4.39	8.21	3.45	31.2	57.2
4	295	4.35	7.83	2.77	31.4	58.0
5	378	4.44	15.01*	2.68	30.3	51.9
6	330	4.40	8.13	3.66	24.8	63.4
7	378	4.38	8.45	3.01	33.0	55.6
8	318	4.37	7.84	3.07	34.9	54.2
9	445	4.37	7.83	3.16	32.6	56.4
10	376	4.44	9.14	4.08	41.5	45.3
11	428	4.38	8.36	3.12	30.0	58.6
12	437	4.36	8.63	2.70	30.2	58.5
13	286	4.35	8.04	2.66	30.2	59.1
Average	364	4.38	8.31	2.98	32.0	56.2
± Std. Error	±16	±.010	±.15	±.15	±1.1	±1.3

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* Rejected at $p < .001$ by outlier rule (Snedecor & Cochran, 1967, p. 322).

TABLE A14

Standing Crop, Heat of Combustion, and Proximate Analysis of *Bromus tectorum* Seeds From Small Lysimeters on a North-Facing Slope, 31 May 1972

Lysimeter		Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
		gm m^{-2}	kCal gm^{-1}	%	%	%	%
North -	2	57	4.10	12.4	1.3	16.9	69.3
	2	138	4.15				
	3	117	4.45				
	4	135	4.20	11.4	2.0	17.9	68.7
	5	99	4.22				
	6	103	4.24				
	7	140	4.27	11.8	1.0	14.7	72.5
	8	131	4.24				
	9	144	4.19				
	10	136	4.17	12.1	1.2	18.3	68.4
	11	118	4.22				
	12	122	4.24	10.9	1.0	16.1	72.1
	13	104	4.17				
Average		119	4.22	11.7	1.3	16.8	70.2
± Std. Error		±6.6	±.023	±.26	±.18	±.65	±.87

TABLE A15

Standing Crop, Heat of Combustion, and Proximate Analysis of *Bromus tectorum* Seeds From Small Lysimeters on a South-Facing Slope, 31 May 1972

Lysimeter	Standing Crop	Heat of Combustion	Crude Protein	Crude Fat	Crude Fiber	Nitrogen-Free Extract
	$gm\ m^{-2}$	$kCal\ gm^{-1}$	%	%	%	%
South - 1	51	4.84				
2	114	4.29				
3	52	3.98	13.2	1.2	16.3	69.3
4	82	4.11				
5	94	4.18				
6	81	4.23				
7	137	4.18	13.3	1.0	15.8	69.9
8	101	4.17				
9	100	4.23				
10	99	4.22				
11	73	4.19	12.7	0.9	14.9	71.5
12	100	4.24				
13	59	4.09				
Average	88	4.23	13.1	1.0	15.7	70.2
± Std. Error	± 6.9	±.056	± .19	±.088	± .41	± .66

TABLE A16

Seed Numbers and Weights From Dominant Culms* of <u>Bromus tectorum</u> in Small Lysimeters on a North-Facing Slope

Dominant Culms

Lysimeter	No. Culms m^{-2}	Seeds $Culm^{-1}$	Wt. $Seed^{-1}$ mg	No. Seeds 1000's m^{-2}	Total Seed Wt. gm m^{-2}
North - 1	352	32	2.69	11.2	30.0
- 2	704	55	1.93	38.9	75.1
- 3	496	47	2.37	23.1	54.8
- 4	792	46	2.55	36.8	93.9
- 5	744	38	2.26	28.5	64.4
- 6	300	45	2.62	13.4	35.2
- 7	600	59	2.44	35.6	86.9
- 8	768	37	2.60	28.3	73.6
- 9	632	56	2.46	35.4	87.1
- 10	1048	49	2.27	51.1	115.9
- 11	448	44	2.83	19.8	56.1
- 12	864	46	2.32	39.4	91.5
- 13	563	32	2.71	18.0	48.8
Average	639	45	2.48	29.2	70.3
Std. Error	±59	±2.4	±.067	±3.2	±6.9

---

* Dominant culms were defined to be those standing at least 8 cm above their flag leaf.

TABLE A17

Seed Numbers and Weights from Suppressed Culms* <u>Bromus</u> <u>tectorum</u> in Small Lysimeters on a North-Facing Slope

Lysimeter	No. Culms m^{-2}	Seeds $Culm^{-1}$	Wt. $Seed^{-1}$ mg	No. Seeds 1000's m^{-2}	Total Seed Wt. gm m^{-2}
North - 1	1550	7.0	2.47	10.8	26.7
- 2	2260	14.8	1.89	33.2	62.8
- 3	3330	9.2	2.03	30.7	62.4
- 4	2130	8.3	2.32	17.7	41.0
- 5	1860	10.3	1.82	19.1	34.7
- 6	3140	10.9	1.98	34.2	67.7
- 7	3180	9.2	1.80	29.4	52.9
- 8	2120	14.4	1.88	30.5	57.4
- 9	3330	8.0	2.14	26.7	57.2
- 10	1140	10.4	1.72	11.8	20.6
- 11	4120	8.3	1.81	34.2	61.9
- 12	2060	8.2	1.88	17.0	31.9
- 13	3780	7.6	1.94	28.6	55.5
Average	2620	9.7	1.98	24.9	48.7
Std. Error	±250	±.68	±.060	±2.4	±4.3

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* Suppressed culms were defined to be those standing less than 8 cm above their flag leaf.

TABLE A18

Seed Numbers and Weights From all Culms of *Bromus tectorum* in Small Lysimeters on a North-Facing Slope

Lysimeter	No. Culms m^{-2}	Wt. Seed^{-1} mg	No. Seeds 1000's mg^{-2}	Total Seed Wt. gm m^{-2}
North - 1	1900	2.58	22.0	56.7
- 2	2960	1.91	72.1	138.0
- 3	3830	2.17	53.8	117.0
- 4	2920	2.48	54.5	135.0
- 5	2600	2.08	47.6	99.0
- 6	3440	2.16	47.6	103.0
- 7	3780	2.15	65.0	140.0
- 8	2890	2.23	58.8	131.0
- 9	3960	2.32	62.1	144.0
-10	2190	2.16	62.9	136.0
-11	4570	2.19	54.0	118.0
-12	2920	2.16	56.4	122.0
-13	4340	2.23	46.6	104.0
Average	3250	2.22	54.1	119.0
Std. Error	±225	±.047	±3.4	±6.6

TABLE A19

Seed Numbers and Weights From Dominant Culms* of *Bromus tectorum* in Small Lysimeters on a South-Facing Slope

Lysimeter	No. Culms m^{-2}	Seeds $Culm^{-1}$	Wt. $Seed^{-1}$ mg	No. Seeds 1000's m^{-2}	Total Seed Wt. gm m^{-2}
South - 1	264	--	--	--	--
- 2	768	--	--	--	--
- 3	384	26	2.66	10.0	26.6
- 4	568	37	2.50	21.0	52.6
- 5	568	53	1.98	30.0	59.4
- 6	216	--	--	--	--
- 7	616	37	2.50	22.5	56.3
- 8	696	35	2.57	24.6	63.1
- 9	704	51	1.94	35.7	69.2
- 10	464	--	--	--	--
- 11	384	--	--	--	--
- 12	400	--	--	--	--
- 13	192	60	2.10	11.5	24.2
Average	479	43	2.32	22.2	50.2
Std. Error	±53	±4.6	±.11	±3.5	±6.7

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* Suppressed culms were defined to be those standing less than 8 cm above their flag leaf.

TABLE A20

Seed Numbers and Weights From Suppressed Culms* of
Bromus tectorum in Small Lysimeters on a South-Facing Slope

Lysimeter	No. Culms m^{-2}	Seeds $Culm^{-1}$	Wt. $Seed^{-1}$ mg	No. Seeds 1000's mg^{-2}	Total Seed Wt. gm m^{-2}
South - 1	2540	--	--	--	--
- 2	2700	--	--	--	--
- 3	3160	3.8	2.08	12.0	25.0
- 4	2410	6.8	1.82	16.5	30.0
- 5	2470	7.7	1.80	19.1	34.4
- 6	2390	--	--	--	--
- 7	3390	10.0	2.36	34.0	80.2
- 8	2700	8.3	1.71	22.4	38.3
- 9	2800	6.8	1.60	19.1	30.6
- 10	2710	--	--	--	--
- 11	3010	--	--	--	--
- 12	3400	--	--	--	--
- 13	3800	4.8	1.89	18.4	34.7
Average	2880	6.9	1.89	20.2	39.0
Std. Error	±120	±.79	±.096	±2.6	±7.0

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* Suppressed culms were defined to be those standing less than 8 cm above their flag leaf.

TABLE A21

Seed Numbers and Weights From all Culms of *Bromus tectorum* in Small Lysimeters on a South-Facing Slope

Lysimeter	No. Culms m^{-2}	Wt. $Seed^{-1}$ mg	No. Seeds 1000's mg^{-2}	Total Seed Wt. gm m^{-2}
South - 1	2800	1.85	27.6	51.1
- 2	3470	2.18	52.3	114.0
- 3	3540	2.33	22.0	51.6
- 4	2980	2.20	37.5	82.6
- 5	3040	1.91	49.1	93.8
- 6	2610	1.94	41.6	80.8
- 7	4000	2.41	56.5	136.0
- 8	3400	2.15	47.0	101.0
- 9	3500	1.82	54.8	99.8
-10	3170	2.19	47.4	99.1
-11	3390	1.96	37.4	73.3
-12	3800	1.97	50.8	100.0
-13	3990	1.97	29.9	58.9
Average	3330	2.07	42.6	87.8
Std. Error	±120	±.052	±3.1	±6.9

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