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ENERGY LEVELS OF WATER IN A COMMUNITY OF PLANTS AS INFLUENCED BY SOIL MOISTURE[1]

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Abstract. Free energy levels of plant water were measured during July and August in two communities of annual plants. One set of plants was irrigated, while the other grew on a silt loam soil that became increasingly drier. The different species of plants had widely varying levels of water potential on both the moist and dry soils. The more drought-tolerant plants on the dry soil had the lowest afternoon plant water potentials even though they had the most vigorous root systems (lamb's quarter, kochia, sugar beets, and sunflower). Some of the more drought-tolerant plants also had low water free energies when growing on moist soil. Most of the plants growing in the dry area gained enough water during the night to raise their water potentials above that of the soil surrounding the bulk of their roots.

INTRODUCTION

The influence of plant-water energy levels on critical plant processes has been reviewed in two monographs edited by Kozlowski (1968). Plant water potential is defined as the sum of the chemical and gravitational components of water potential in the plant. As a matter of convenience, the potential of pure water under 1-bar pressure may be taken as zero. If a solute is added to pure water, its vapor pressure and free energy, or potential, decreases. Raising the ambient pressure over the solution causes the vapor pressure to rise; therefore, the water potential of a solution may be conveniently defined as the negative of, or as minus, the number of bars of ambient pressure which would be required to isothermally raise the vapor pressure of the solution up to that of pure water. In general, the water potential in actively growing plants ranges between −5 and −30 bars, though under desert conditions potentials may drop to −80 bars; mangroves and other halophytes commonly grow at −30 to −60 bars (Scholander et al. 1965). Plant water potential decreases as the evaporative demand of the atmosphere increases, or as the soil water potential decreases. Soil water potential decreases as the soil dries or as the salinity of the soil solution increases. As the salinity rises, there is a corresponding increase of salt in most plants (Meiri and Poljakoff-Mayber 1969, Kirkham, Gardner, and Gerloff 1969). The increase in salt may injure some plants through specific ion effects as well as through reduction of plant water potential. In general, even if specific salt effects are excluded, decreases in plant water potential reduce growth.

Plant species differ widely in drought resistance. On nonsaline soil with a decreasing water content, some plants continue to grow slowly and mature, but others die. With respect to plant water potential, a plant may demonstrate drought resistance through two obvious mechanisms: (1) Plants that continue to grow on dry soil may have a more vigorous and competitive root system than the less hardy plants, and so have access to more soil water (Pavlychenko 1937). This may be coupled with morphological characteristics that reduce water loss from the leaves to the atmosphere, helping maintain relatively high water potentials. (2) On the other hand, the more drought-resistant plants may have a specially adapted physiology that allows them to continue growing at lower plant water potentials than the less drought-hardy species. In view of the lack of suitable data on plant water potential from field situations, a study was undertaken to gain information on the relative importance of these two possible drought-resistant mechanisms.

METHODS

The study was carried out in south-central Idaho during July and August 1969. The average high and low temperatures for these months is 33° and 12°C and 32 and 11°C, respectively. Average rainfall is 9.6 mm and 6.8 mm, respectively.

The plants were grown on Portneuf silt loam soil. This is a loess material with a carbonate- and silica-centered layer beginning at about 50 cm and extending to a depth of 65–80 cm. The cemented layer is permeable to water, but resistant to root growth; thus, the roots of most annuals are largely restricted to the upper 50 cm of soil.

Sugar beets (*Beta vulgaris*, L.) were planted in the experimental area early in April in 60-cm rows with a spacing of about 10 cm between plants. The soil was irrigated as required to establish the seedlings. All other plants that germinated from natural seed in the soil were allowed to grow. This included

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lamb's-quarter (*Chenopodium album* L.), sunflower (*Helianthus annuus* L.), wild lettuce (*Lactuca scariola* L.), nightshade (*Solanum nigrum* L.), kochia (*Kochia scoparia* L.), and wild oats (*Avena fatua* L.). In addition to the wild plants, red clover (*Trifolium pratense* L.) and pinto beans (*Phaseolus vulgaris* L.) emerged from seeds which were present from previous crops grown on the area.

On June 22 the area was irrigated and divided in half, leaving two plots, each about 20 m on a side. One plot was then irrigated throughout the summer to maintain adequate soil moisture. The other plot was not irrigated again until August 18, when it was subdivided and one-half was watered. The remaining half of the dry area received no irrigation after June 22, and there was no significant rainfall during the study period.

The leaf water potential of a number of the plants growing on the wet and dry areas was measured periodically between June 27 and September 4. The potentials were measured twice during those days, in the morning between daylight and sunrise and in the early part of the afternoon. The height of representative plants from each species was also measured. Water potentials of composite samples of soil from depths of 0–15, 15–30, and 30–45 cm were interpolated from a moisture-desorption curve obtained with pressure-plate apparatus and a solution-vapor-equilibrium technique. The soil was completely covered with a plant canopy by July 1, which gave a uniform drying of the soil in the nonirrigated area. By July 24 soil moisture varied less than 3% with depth on a dry weight basis. Notes were made throughout the season on the appearance of the various species of plants. Seeds were also harvested and tested for viability.

The water potentials of the plants were measured with a portable freezing point meter (Cary and Fisher 1969, Wiebe et al. 1971). The gravitational component was neglected. The potential measurements were made in the field and completed within 4 min of plant sampling. Duplicate samples were generally reproducible within 2 bars, though in some cases variations of 5 bars were observed when taking random samples of different plants of the same species. Previous comparisons between the freezing point method and vapor pressure psychrometer suggested that, on the average, results will compare within 3 bars though differences may become greater at very low water potentials. In general, the data reported in this study have a confidence interval of ± 5 bars.

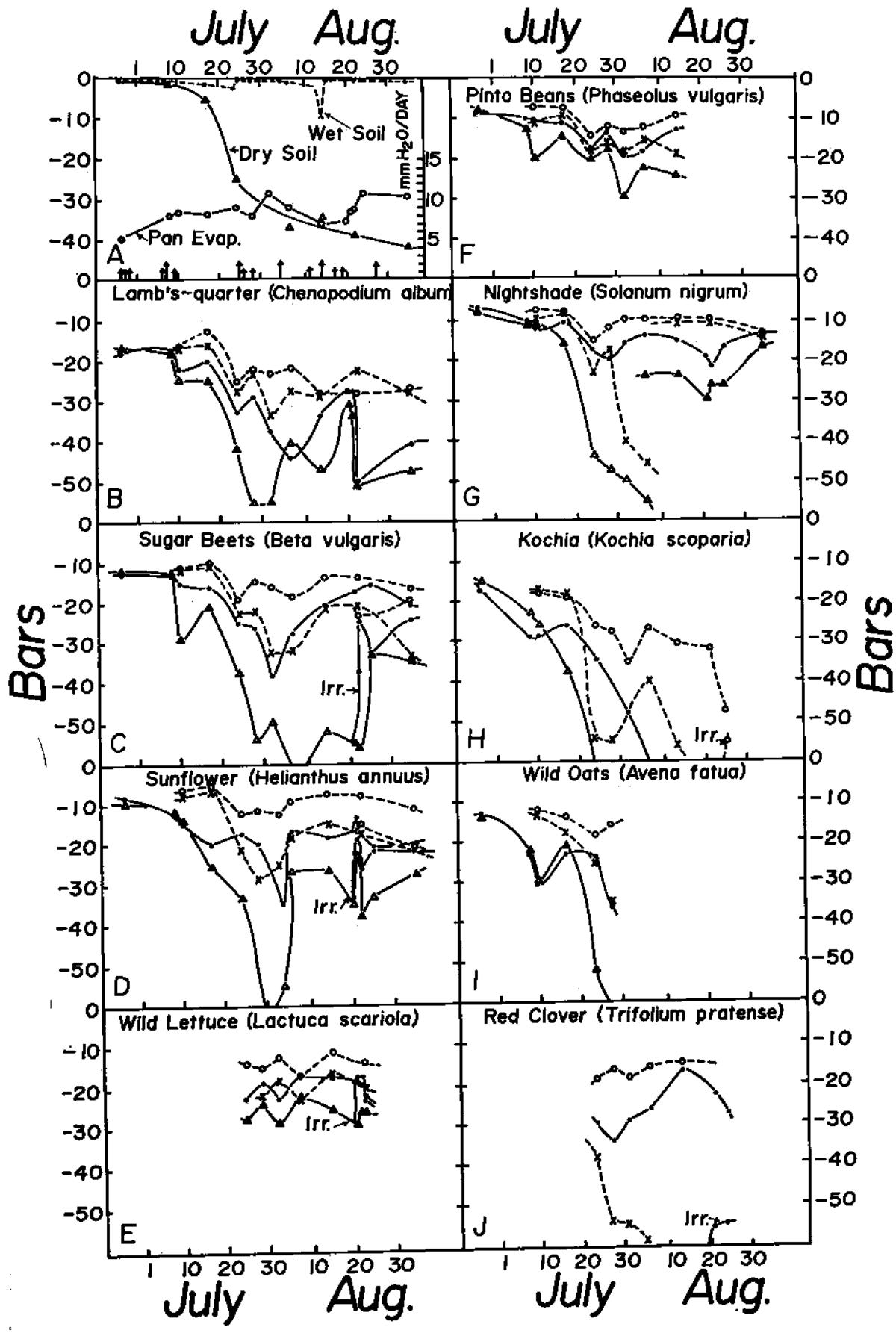
Results and Discussion

The average soil moisture potentials for the wet and dry plots are shown in Fig. 1A, along with a plot of the Weather Bureau pan evaporation, which gives a qualitative measure of the evaporative demand of the atmosphere. The tall arrows in Fig. 1A indicate irrigation dates on the wet plot, and the short arrows represent traces of rainfall.

By July 10 the lamb's quarter was beginning to show the effect of decreasing soil water potential (Fig. 1B). The low potential shown during the afternoons at the end of July corresponds to a high evaporative demand of the atmosphere. The lamb's-quarter plants studied at the first of the season reached their maximum height by July 8 when vegetative growth ceased and seed set began. On August 1 younger plants were chosen for observation. These plants, which were just starting to flower, produced new vegetative growth until September 1, even on the dry plot. At the time of changeover on August 1, the water potential in the mature plants was not measurably different from the water potential in the younger growing plants. By July 24 the leaves of the lamb's-quarter on the dry plot were beginning to show a loss of turgor during the afternoon, though otherwise the plants appeared healthy. The plants on the wet and dry plots had surprisingly similar water potential after the early part of August and both produced viable seed. Irrigation on August 18 had little effect on the lamb's-quarter on the dry plots, since its potential was already similar to the wet plot plants. The plants in the dry area were able to absorb enough water during the night to raise their potential above that of the soil in which the bulk of their roots were growing. This probably resulted from the diurnal temperature changes that caused dew condensation on both the tops and roots of the plants (Stone 1958, Cary 1966, Stark and Love 1969), though a few small roots may have been able to penetrate the cemented layer and reach areas with higher water potentials.

The high evaporative demand of the atmosphere near the end of July caused a severe decrease in plant water potential in sugar beets (Fig. 1C). On July 24 beets on the dry plot were showing noticeable loss of turgor during the afternoon, followed by overnight recovery. By July 28 the dry beets were completely wilted by each midday, and the older leaves were beginning to die. On August 1 turgor was lost by midmorning, though most of the younger leaves still recovered at night. A significant increase in plant water potential in the dry beets was evident 3 days after irrigation when the leaves had regained turgor and stopped wilting during the afternoon. However, the water potentials remained lower than those in the wet check plot until the end of the study. A few of the youngest leaves on the dry plots continued to regain turgor every night, though by September most of the large leaves were dead and the small leaves became completely flaccid soon after sunrise.

The moisture potential changes in sunflower (Fig. 1D) were similar to those in beets, though in general


July
Aug.
Bars
Wet Soil
Dry Soil
Pan Evap.
mm H2O/DAY
Pinto Beans (Phaseolus vulgaris)
Lamb's-quarter (Chenopodium album)
Nightshade (Solanum nigrum)
Sugar Beets (Beta vulgaris)
Kochia (Kochia scoparia)
Sunflower (Helianthus annuus)
Wild Oats (Avena fatua)
Wild Lettuce (Lactuca scariola)
Red Clover (Trifolium pratense)
Irr.
A
B
C
D
E
F
G
H
I
J

the potentials were not quite as low. Near the end of July, afternoon potentials decreased, but there was a general increase later in the summer. The increase on the dry area probably resulted from less leaf surface area following a gradual drying of the older leaves. The sunflowers were forming flower buds by July 17 on both wet and dry plots. Vegetative growth had stopped on the dry plots by July 24, and by July 28 the plants were beginning to lose turgor during the afternoon; yet on August 6 flower buds were still forming and opening on both plots. By August 22 many of the larger leaves of the plants on the dry plot were dry, though smaller living leaves were still present at each node.

The water potential for wild lettuce is shown in Fig. 1E. Of all the plants that were still actively growing on the dry plot on August 18, the wild lettuce showed the fastest and most complete recovery in plant water potential upon irrigation. On July 28 plants on the dry plots looked healthy and were blooming, as well as beginning to produce their first seeds. By August 1 the plants on the dry plots had smaller and lighter colored leaves, though some flower buds were still opening. These new flowers were marked, and seed from them harvested at maturity. Germination of these seeds was equal to those produced by the wild lettuce on the wet plot. Flower buds continued to open on the dry plants as late as August 14, but by September 4 the plants were fully matured and beginning to dry rapidly.

As pinto beans are not renowned for their drought hardiness, it was surprising that plants survived on the dry plot until the middle of August and produced viable seeds. After the middle of July the beans on the dry plot maintained a higher water potential, even during the middle of the afternoon, than the bulk of the soil in which they were growing (Fig. 1F). Dew was occasionally noted on the bean leaves before sunrise and must have been an important source of moisture. Shading from other plants in the canopy helped them maintain the relatively high water potentials during the day. First blooms began appearing on the beans on July 17. On July 28 the beans on the dry plot had very dark green leaves, indicating water stress. By July 24 the dry beans had completed their vegetative growth, and by August 1 some of the leaves were beginning to dry. The beans on the dry plot were mature by August 22.

The plant water potential for nightshade is shown in Fig. 1G. The plants on both plots began blooming about July 15, and by July 24 there was some fruit on the plants in both plots, though the plants in the dry plot were beginning to appear droughty. On July 28 nightshade on the dry plot was becoming badly wilted and infested with spider mites (*Tetranychus*). Spider infestation was not a problem on the wet plot. By August 1 the nightshade on the dry plot was continually wilted even before sunrise and appeared near death. It is known that disease may have a significant effect on plant water potential (Kozlowski 1968). On August 6 several nightshade plants were found on the dry plot that had apparently escaped spider infestation. These were then used for measurements, and the difference in water potential is obvious in Fig. 1G. By August 22 some of the leaves were wilting during midafternoon, and some were remaining turgid. The breaking point appeared to be around −25 bars. On September 4 a few buds on the dry nightshade plants were still opening into flowers. Seed harvested from the dry plot plants on this date were as viable as those from the wet plot. There were no healthy nightshade plants on the half of the dry plot that was irrigated, so no comparisons in change in water potential could be made.

The water potential measurements made on the kochia plants are shown in Fig. 1H. This plant was unique in that the potentials became very low and remained so, even on the irrigated plot. The kochia plant has a fibrous spreading root system, but it does not remove as much soil moisture as other competitive plants, such as cocklebur (*Xanthium pennsylvanicum* L.) and Russian thistle (*Salsola kali* L.) (Davis, Wiese, and Pafford 1965). The kochia began to flower about the middle of July and was producing large quantities of pollen by July 24. At this time plant leaves on the dry plot were beginning to show some browning on their tips, and all plants on both areas had completed their vegetative growth. By August 1 the kochia leaves on the dry plot appeared lighter colored and showed some leaf margin burn. On August 22 the kochia on the dry plots were mature and produced viable seed. These plants did show a response to irrigation, as their potentials rose back into the meter range.

Water potential in wild oats is shown in Fig. 1I. These plants were well headed out on both areas on July 17 and had completed their vegetative growth. By August 1 most of the leaves were turning brown and the seeds were being shed. The seeds from the plants on the dry area were 95% viable.

Potential measurements on red clover are shown in Fig. 1J. When measurements were initiated on July 24, the plants on both plots appeared normal even during the afternoon. By August 4 the clover leaves on the dry plots were beginning to lose turgor in the afternoon, though plants on both plots were

FIG. 1. Changes in soil and plant water potentials in nine species of plants over the time interval of the experiment. Open circles, average values for early morning measurements on the irrigated plots; closed circles, afternoon measurements on the irrigated plots; crosses, early morning measurements on the dry plots; triangles, afternoon measurements on the dry plots.

still actively blooming. Visual signs of drought stress began to increase on the dry area, and by August 21 only a few green leaves remained, which were continually wilted. Although the plants on the dry plot experienced extremely low water potentials, they produced seed equally as viable as those on the wet plot and demonstrated a slight recovery in water potential after irrigation on August 18.

In addition to the observations reported in the preceding discussion, the plants on the dry plot were ranked in order of increasing severity of drought symptoms during the afternoon of August 1. This ranking was: lamb's-quarter < wild lettuce < clover = sunflower < kochia < beets < beans < spider-infested nightshade. This visual ranking would not correspond to a ranking of afternoon water potentials in the various plants.

At the conclusion of the study, pits were dug in the dry plot and root systems of representative plants were washed out with a stream of water. Though many of the fine roots were broken during the washing process, there was no evidence of any root penetration through the cemented layer at 50 cm. Other observations on similar sites have shown a few roots of perennials penetrating the cemented layer. The penetration probably occurs when root growth on top of the layer is vigorous before appreciable drying begins. Since the hard layer is permeable to water, soil water flows upward from the subsoil in response to drying of the surface 50 cm. However, the hydraulic conductivity becomes very small at −30 bars soil water potential, thus upward movement from the subsoil must have been very small in the dry plot after July 20. Upward thermal pumping of subsoil water should have also been very small at the 50-cm depth.

Kochia had the most fibrous and spreading root system, followed closely by lamb's-quarter. Wild lettuce and sunflower also had vigorous root systems, but they were not quite as fibrous and spreading. Red clover had the next largest root system, which tended to be spreading in the 10- to 20-cm layer. The wild oats had a similar root system, but not as deep, with most spreading in the upper 15 cm of soil. Next in vigor were the beets, with a taproot about 40 cm long supporting a few fine lateral roots. Nightshade had a fairly vigorous root system, but not as good as that of red clover, and it tended to be nearer the surface. Beans had the scantest and least developed roots.

Conclusions

In this study the most drought-tolerant plants had the largest, most fibrous, and most penetrating root systems; however, they did not maintain the highest water potentials during the middle of the day. Their low water potentials suggest that they continued to exchange water vapor, oxygen, and CO_2 with the surrounding air during most of the day, and their metabolism must be such that they continue to grow with very low water potentials. Plants in this category included lamb's-quarter, kochia, sugar beets, and sunflower. Kochia and lamb's-quarter were particularly interesting, for in spite of their excellent root systems they maintained relatively low water potentials even on the moist soil. Sugar beets and sunflower tended to have higher water potentials when soil moisture was available. Apparently the more drought-tolerant plants utilize both a very competitive root system and a physiology that allows them to grow with low cell-water potentials.

Plants with the smaller and less competitive root systems did not develop the very low water potentials on the dry soil with the exception of nightshade, which was infested by spiders. The higher plant water potentials on the dry soil suggest that the beans, the healthy nightshade, and probably the wild lettuce stopped exchanging CO_2, oxygen, and water vapor rather early during the day. This helped them to maintain water potentials at a higher level than the water potential of the bulk of the soil in which they were growing. Red clover appeared to be an intermediate plant, preferring to grow at moderately high water potentials on moist soil, yet when experiencing low water potentials in the drought conditions able to survive to some extent.

With the exception of red clover, all the plants studied in the dry area were able to raise during the night the free energy of their water above that of the soil encompassing the bulk and possibly all of the plant roots. Diurnal cooling, which can condense water on both the aerial and root parts of plants, is believed to be an important factor in this nighttime response in very dry soils.

The water potential patterns of different species of plants growing together under natural environmental conditions may be very different. Nevertheless, the results presented here show some overall similarities to the observations made on a variety of other plants by Gračanin et al. (1970), Hickman (1970), and Strain (1970), who have conducted somewhat similar field studies.

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