(7)

Agricultural Meteorology, 27(1982) 49—58
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

PLANT RECOVERY FOLLOWING PROLONGED DROUGHT IN A SHORTGRASS STEPPE

O.E. SALA*, W.K. LAUENROTH and W.J. PARTON

Natural Resource Ecology Laboratory and Department of Range Science, Colorado State University, Fort Collins, CO 80523 (U.S.A.)

(Received January 29, 1982; revision accepted May 18, 1982)

ABSTRACT

Sala, O.E., Lauenroth, W.K. and Parton, W.J., 1982. Plant recovery following prolonged drought in a shortgrass steppe. Agric. Meteorol., 27: 49—58.

The recovery cycle of *Bouteloua gracilis* (H.B.K.) Griffiths after a 56-day drying cycle has been monitored to assess the effect of a prolonged drought upon the ability of different plant processes to respond to an increase in water availability. Leaf water potential before dawn and at noon recovered rapidly indicating that the previous drought had a minimal effect upon these variables. Leaf conductances during the first seven days of the cycle were considerably lower than the potential values estimated by a simple model, indicating that the prolonged drought had a profound effect on the behavior of stomata. Since leaf conductance represents the major control of photosynthesis during recovery cycles we suggested that the ecological significance of prolonged droughts and the after-effects lies in their impact upon carbon assimilation.

INTRODUCTION

Semiarid grasslands are water-controlled ecosystems in which biological activity is stimulated by scant and irregular pulses of precipitation (Noy-Meir, 1973). Available soil water is the major factor to which the variability in annual production of semi arid ecosystems can be attributed (Lauenroth, 1979). The availability of soil water influences primary production directly through plant water status and indirectly through its influence upon nutrient cycles.

In the semi arid shortgrass region, water entering the soil as a result of precipitation is lost to the atmosphere via evaporation or transpiration (Lauenroth and Sims, 1976). Deep drainage is a very rare phenomenon which has not occurred during the ten years we have been monitoring soil water dynamics. Our interests were focused on the factors which condition the partitioning of water between evaporation and transpiration.

The water status of plants and activity of water-controlled processes do not immediately respond to an increase in the water status of the soil. A

---

* On leave from Departamento de Ecologia, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, Buenos Aires, 1417, Argentia.

variable period of time elapses between a change in soil water status and an observed change in a plant process or plant variable status. This period of time is called the response time or time constant and is a measure of the inertia of a particular process (Orians, 1975; Westman, 1978).

A rainfall event wets the soil for a specific period of time. Processes with short time constants relative to the time the soil remains wet will exhibit long periods at or near the maximum activity level. Plant processes with long time constants will manifest shorter periods of time at an increased activity level according to the new status of the soil water. If the time constant is as long as the duration of the soil wetting, no response will be observed. The time constant of water-controlled processes is not fixed but is, at least partially, a function of the degree of water stress to which plants were previously subjected. The efficiency of utilization of a water input will decrease as the time constant of the process increases and therefore will depend on the water status of the plants before the rainfall event.

We designed an experiment in which we subjected the system to a prolonged drought and monitored the recovery cycle. By comparing the normal drying cycle with the recovery cycle, we attempted to assess the effect of prolonged drought upon the inertia of plant processes. Two key plant variables were chosen, leaf water potential and leaf conductance, and these were monitored throughout both cycles. Leaf water potential is related to photosynthesis, respiration, translocation, and transpiration. Leaf conductance is a major determinant of photosynthesis under water stress through its control of CO_2 uptake (Ludlow et al., 1980). Simultaneously it represents the major resistance in the transpiration pathway.

MATERIALS AND METHODS

The experiment was conducted at a shortgrass steppe site (latitude 40°48′N and longitude 104°45′W) located in north-central Colorado, approximately 61 km northeast of Fort Collins and 40 km south of Cheyenne. Mean annual precipitation is 311 mm, 70% of which occurs during the May to August growing season. Precipitation at this site is characterized by large annual variability and by a large proportion of small events which account for 47% of the total precipitation and 87% of the events. Mean monthly temperatures range from below 0° C in December and January to 22° C in July.

Native vegetation of the Central Plains Experimental Range is dominated by blue grama [*Bouteloua gracilis* (H.B.K.) Griffiths] which accounts for 90% of above ground grass biomass and 30% of total above ground biomass (Lauenroth et al., 1978). Besides grasses, the perennial vegetation is made up of suffrutescent shrubs such as fringed sagewort (*Artemisia frigida* Willd.), forbs including scarlet globemallow [*Sphaeralcea coccinea* (Pursh) Rydb.], and succulents such as plains prickly pear (*Opuntia polyacantha* Haw.).

The experiment utilized a lysimeter containing a cylinder 3 m diameter x 1.5 m deep of the undisturbed steppe (Armijo et al., 1972). The lysimeter provided an accurate measurement of the water received and prevented lateral losses of water. The experimental system was subjected to a prolonged drying cycle which started early in the growing season with the soil profile completely wet and lasted 56 days. Following this, the area received a major rainfall event of 32 mm. Experimental conditions were obtained by eliminating natural rainfall. The lysimeter was covered with a canvas tarp supported by a portable structure 50 cm above the ground. Environmental conditions beneath the tarp were minimally modified because the area was covered and immediately uncovered after the rainfall occurred. Moreover, precipitation events in this region are mostly thunderstorms which occur in the late afternoon or early evening when the effect of covering the grassland was minimal.

Soil and plant water status were periodically monitored throughout the drying and recovery cycles. The data of the drying cycle have been previously published and are presented in this paper as a reference to compare the two cycles (Sala et al., 1981). (The leaf conductance values presented here are 2.23 times greater than the data presented by Sala et al., 1981, because of a correction for leaf width.) Plant water status was assessed by measuring leaf water potential and leaf conductance to water vapor. Both measurements were made exclusively on *B. gracilis.* Leaf water potential was measured using the pressure chamber technique (Scholander et al., 1965) at predawn and after noon between 1300 and 1400 h. Ten replications were used on each sample date maintaining the standard error below 7% of the mean.

Leaf conductance to water vapor was measured by means of a diffusion porometer (Kanemasu et al., 1969), the limitations of which were taken into account (Meidner, 1981). These data were collected simultaneously with the leaf water potential information for the same species, but only after noon. Leaf conductance variability was larger than leaf water potential variability, consequently the replication number was increased to 15 in an attempt to achieve similar standard errors.

We assessed soil water status by measuring soil water potential at different depths. We utilized thermocouple hygrometers (Spanner, 1951) placed at depths of 5, 15, 25, 40, and 60 cm. Six replications were installed at each level.

RESULTS

The 32-mm rainfall event on 8 August rapidly wet the soil profile to a depth of 15 cm (Fig. 1). Thereafter, water was lost to the atmosphere via evaporation and transpiration from the upper soil layer, slowly decreasing its soil water potential. The wetting front continued its movement downwards for 16 days. Deep soil layers at 40 and 60 cm did not exhibit a significant ($P > 0.05$) increase in soil water potential but the decreasing trend which was measured before 8 August ceased, suggesting that transpiration demand was being satisfied by the upper layers. These two constrasting processes,

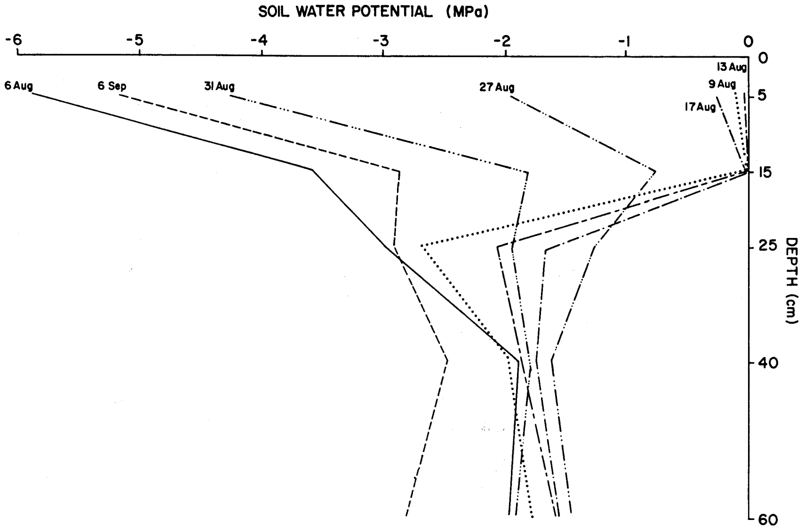

Fig. 1. Soil water potential as a function of depth throughout a recovery cycle.

drying of the soil from the top downwards and the wetting of it in the same direction from 15 cm, drove the system to a condition around 31 August in which the soil water potential was the same throughout the entire profile except in the 5 cm layer. Thereafter, the entire soil profile presented a decreasing water potential trend.

Predawn leaf water potential recovered rapidly following watering from − 1.8 to − 0.6 MPa (Fig. 2). After 18 days predawn leaf water potential began a decreasing trend which finalized when it reached a stable condition of − 2 MPa at the end of August. Leaf water potential at noon also recovered rapidly following watering. Values immediately following the rainfall event were characteristic of non-water deficit conditions (Fig. 2). Noon and predawn leaf water potentials began to decrease at the time the top soil layer exhibited a soil water potential of − 2 MPa. Both variables attained stable minima when the profile of soil water potential was similar to the one observed before watering. The maxima and minima of predawn and noon leaf water potential were similar to the ones observed during the first drying cycle.

The response of leaf conductance to watering was very slow (Fig. 3) when compared with the recovery of leaf water potential. Leaf conductances characteristic of non-stress were not observed until 7 days after rewatering. Leaf conductance decreased at the same time predawn and noon leaf water potential decreased and reached a stable condition at the end of August. However, this minimum value was significantly higher ($P \leqslant 0.05$) than the minimum attained at the end of the first drying cycle.

As a result of the 32-mm rainfall event, leaf water potential before dawn

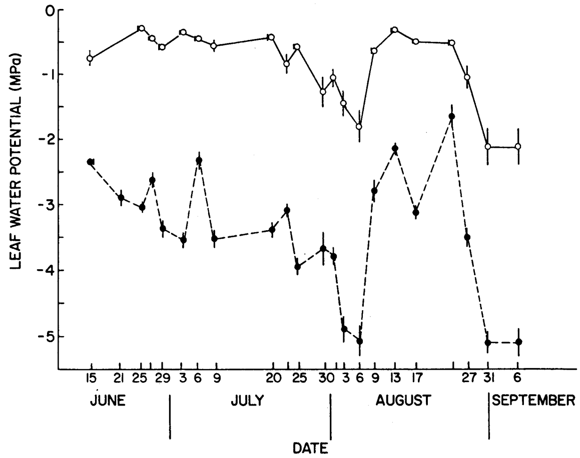

Fig. 2. Leaf water potential of *Bouteloua gracilis* throughout a drying and recovery cycle. The lower and upper lines represent values at noon and predawn, respectively. Each point represents the mean of 10 leaves and vertical bars represent ± 1 standard error.

and at noon remained at or near a maximum value for 18 days. In contrast, leaf conductance exhibited only 10 days at or near the maximum.

DISCUSSION

We previously developed models which predicted leaf water potential and leaf conductance using soil and plant variables (Sala et al., 1981). The models did not take into account the conditions to which the system had been previously subjected. Therefore, a good fit obtained using these models during the recovery cycle will indicate that the previous drought had no effect upon the status of the predicted plant variable. On the contrary, the magnitude of the deviation from the predicted response will be an indication of the effect of the previous drought upon the inertia of the process.

One of the models predicted predawn leaf water potential (Ψl_{PD}) as a linear function of soil water potential of the wettest soil layer (Ψ_s)

$$\Psi l_{\mathrm{PD}} = -0.45 + 0.84\,\Psi_s$$

This model, when it was applied to the recovery cycle data, very closely predicted predawn leaf water potential (Fig. 4(a)) indicating minimal effect of the previous drought upon the behavior of this variable.

Noon leaf water potential (Ψl_{N}) was predicted as a function of effective soil water potential (Ψ_{E}) (Van Bavel and Ahmed, 1976) which is a soil water potential weighed by the root biomass of different soil layers

$$\Psi l_{\mathrm{N}} = -3.07 - 0.48\,\Psi_{\mathrm{E}} - 0.22\,\Psi_{\mathrm{E}}^2$$

This model predicted very closely the course of noon leaf water potential during the early stages of the recovery cycle (Fig. 4(b)) indicating that the

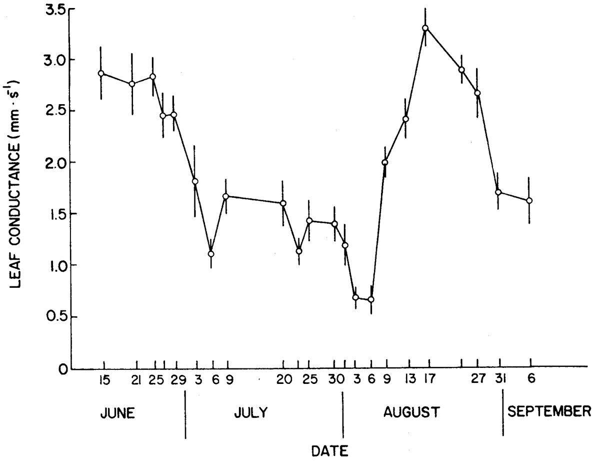

Fig. 3. Leaf conductance of *Bouteloua gracilis* throughout a drying and recovery cycle. Each point represents the mean of 15 leaves and vertical bars represent ± 1 standard error.

previous drought had a minimal effect upon the behavior of noon leaf water potential and it did not alter its response time.

Leaf conductance (g_l) was predicted as a function of leaf water potential at noon

If $\Psi l_N > -3$ MPa $\quad g_l = 2.77$ mm s^{-1}

If $-4.2 \leqslant \Psi l_N \leqslant -3$ MPa $\quad g_l = 8.04 + 1.76\,\Psi l_N$

If $\Psi l_N < -4.2$ MPa $\quad g_l = 0.66$ mm s^{-1}

The observed leaf conductance during the first 7 days of the recovery cycle were considerably lower than the predictions of the model (Fig 4(c)). This deviation during the first stages of the recovery cycle suggested that the prolonged drought to which these plants were subjected had a profound effect upon stomatal behavior. The increase in the response time of leaf conductance as a result of prolonged drought is called 'after-effect' (Davies et al., 1981).

This model predicted leaf conductance at noon utilizing only noon leaf water potential and it did not consider any of the other environmental factors such as ambient humidity, leaf temperature, carbon dioxide concentration and radiation which are known to have a major influence upon stomatal conductance (Hall et al., 1976). Having previously obtained a good fit with this model (Sala et al., 1981), the lack of fit observed during the first stages of the recovery cycle was attributed to the after-effect of the prolonged drought because the other environmental factors had remained constant at noon during the portion of the growing season explored.

The models underestimated leaf conductance and overestimated noon leaf water potential during the later stages of the recovery cycle (Fig. 4(b), (c)). We hypothesize that the higher conductances observed at the end of the

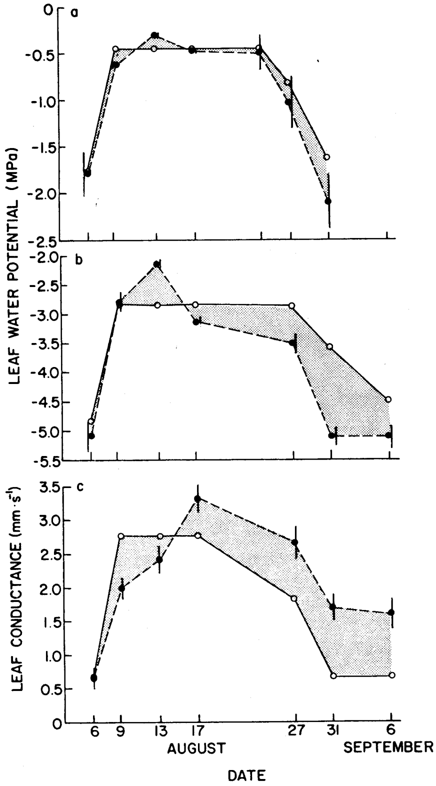

Fig. 4. (a) Leaf water potential before dawn; (b) leaf water potential at noon; and (c) leaf conductance at noon throughout a recovery cycle. Observed (●— — —●) and predicted (○———○) by a model. Vertical bars represent ± 1 standard error.

cycle are the result of changes in the average age of leaves and changes in phenology which occur rapidly at the end of the growing season. Syvertsen et al. (1981) found that old leaves of orange trees were capable of maintaining open stomata at lower leaf water potentials than young leaves. On the other hand, Ludlow and Wilson (1971) observed a decrease in stomatal conductance with age. The studies of Frank (1981) in *Agropyron intermedium* [(Link) Halac], *Agropyron desertorum* [(Fisch. ex Link) Schult] and *Phalaris arundinacea* (L.) suggested a minimal effect of leaf age on stomatal behavior. It can be concluded that the overestimation of noon leaf water potentials is a result of the higher leaf conductance observed. The model predicted leaf water potential using only water potential of the soil and assumed a fixed relationship between leaf conductance and leaf water status. A distortion of this relationship resulted in an increase of the transpiration rate for a given condition of soil water availability and finally a decrease in the water status of the plant.

Fereres et al. (1979) in a field experiment subjected orange trees [*Citrus sinensis* (L.) Osbeck] to severe water stress inducing predawn leaf water potentials of − 6.6 MPa. After irrigation they observed that leaf water potential reached normal values in shorter periods of time than leaf conductance. Furthermore, leaf conductance of trees under the most severe stress did not fully recover in 2 months. Levy and Krikun (1980) working with *Citrus jambhiri* Lush found after a mild water stress an immediate response in leaf water potential, but leaf conductance required 5 days to attain normal values. Ludlow et al. (1980) also found for a C_4 grass that leaf water potential recovered to the control level after 24 h while leaf conductance needed 48 h to attain a comparable level. All these experiments provided support for Bengston et al.'s (1977) statement that the extent of the after-effect of a drought period varies with the degree of water stress experienced.

We found that when the soil profile was very dry, small rainfall events frequently wet only the upper layer which very rapidly dried out. Under these conditions *B. gracilis* was subjected to very rapid and severe drying cycles. Although these plants attained leaf water potentials before rewatering, even lower than those presented here, they showed a smaller after-effect (Sala and Lauenroth, 1982). Therefore, we suggest that the extent of the after-effect depends not only on the degree of water stress experienced, which can be measured as soil or plant water potential, but also upon the length of the dry period. Schulze et al. (1980) reported that net photosynthesis of wild and cultivated plants in the Negev Desert was a function not only of water stress, estimated as leaf water potential before dawn, but also of the duration of water stress experienced by the plants.

Usually in the laboratory under controlled conditions and using relatively small pots, we can only simulate short drying cycles. Prolonged droughts occur when plants are able to explore the entire soil profile. In this case lower soil layers maintain a minimum supply of water for a long period of time which sustains plants although they may be subjected to severe stress. Under these conditions, roots in the upper layers in particular, will be subjected to very low water potentials for long periods of time.

The physiological mechanism of the after-effect has not been described for *B. gracilis*. However, there is abundant evidence in the literature suggesting a negative feedback for drought on stomatal behavior via endogenous regulators (Davies et al., 1981). This negative feedback occurs via accumulation of abscisic acid (McMichael and Hanny, 1977) or a redistribution within the leaves (Loveys, 1977).

The initiation of new leaves upon rewatering and the time lag in their attaining a functional state (Leopold and Kriedemann, 1975) may explain a portion of the delay in the recovery of stomatal conductance. Field observations convinced us that the largest portion of the response could be attributed to leaves which survived the drought.

The response time of leaf water potential before dawn and at noon appeared not to be affected by the prolonged drought. On the contrary, the response time of leaf conductance or its closely-related stomatal conductance

(Jarvis, 1981) increased as a result of the prolonged drought. Stomatal resistance exerts a greater influence on the recovery of photosynthesis than the intracellular resistance since it is usually larger and recovers more slowly (Boyer, 1971, 1976; Bielorai and Hopmans, 1975; Ludlow et al., 1980). We suggest that the ecological significance of prolonged droughts and the aftereffects lies in their impact upon the carbon assimilation process. Prolonged droughts should then decrease the water use efficiency. Furthermore, we suggest that the total activity of processes associated with carbon gains and losses in an ecosystem depends not only upon total annual precipitation but also upon the frequency distribution of different event sizes and the temporal pattern of occurrence during the growing season.

ACKNOWLEDGMENTS

We would like to thank Dr. J. K. Detling for his very hepful suggestions. This work was supported by USDA-SEA Science and Education Grant No. 58-9 AHZ-8-332 and Consejo Nacional de Investigaciones Científicas y Técnicas, República Argentina.

REFERENCES

Armijo, J.D., Twitchell, G.A., Burman, R.D. and Nunn, J.R., 1972. A large, undisturbed weighing lysimeter for grassland studies. Trans. Am. Soc. Agric. Eng., 15: 827—830.

Bengston, C., Falk, S.O. and Larsson, S., 1977. The after-effect of water stress on transpiration rate and changes in abscisic acid content of young wheat plants. Physiol. Plant., 41: 149—154.

Bielorai, M. and Hopmans, P.A.M., 1975. Recovery of leaf water potential, transpiration and photosynthesis of cotton during irrigation cycles. Agron. J., 67: 629—632.

Boyer, J.S., 1971. Recovery of photosynthesis in sunflower after a period of low leaf water potential. Plant Physiol., 47: 816—820.

Boyer, J.S., 1976. Photosynthesis at low water potentials. Philos. Trans. R. Soc. London, Ser. B, 273: 501—512.

Davies, W.J., Wilson, J.A., Sharp, R.E. and Osonubi, O., 1981. Control of stomatal behaviour in water-stressed plants. In: P.G. Jarvis and T.A. Mansfield (Editors), Stomatal Physiology. Society for Experimental Biology, Seminar Series 8. Cambridge University Press, London, pp. 163—185.

Fereres, E., Cruz-Romero, G., Hoffman, G.J. and Rawlins, S.L., 1979. Recovery of orange trees following severe water stress. J. Appl. Ecol., 16: 833—842.

Frank, A.B., 1981. Effect of leaf age and position on photosynthesis and stomatal conductance of forage grasses. Agron. J., 73: 70—74.

Hall, A.E., Schulze, E.-D. and Lange, O.L., 1976. Current perspectives of steady-state stomatal responses to environment. In: O.L. Lange, L. Kappen and E.-D. Schulze (Editors), Ecological Studies, Vol. 19. Water and Plant Life. Springer-Verlag, New York, pp. 169—188.

Jarvis, P.G., 1981. Stomatal conductance, gaseous exchange and transpiration. In: J. Grace, E.D. Ford and P.G. Jarvis (Editors), Plants and Their Atmospheric Environment. Blackwell Scientific, Oxford, pp. 175—204.

Kanemasu, E.T., Thurtell, G.A. and Tanner, C.B., 1969. Design, calibration and use of stomatal diffusion porometer. Plant Physiol., 44: 881—885.

Lauenroth, W.K., 1979. Grassland primary production: North American grasslands in perspective. In: N.R. French (Editor), Perspectives in Grassland Ecology, Springer-Verlag, New York, pp. 3—24.

Lauenroth, W.K. and Sims, P.L., 1976. Evapotranspiration from a shortgrass prairie subjected to water and nitrogen treatments. Water Resour. Res., 12: 437—442.

Lauenroth, W.K., Dodd, J.L. and Sims, P.L., 1978. The effects of water and nitrogen induced stresses on plant community structure in a semiarid grassland. Oecologia (Berlin), 36: 211—222.

Leopold, A.C. and Kriedemann, P.E., 1975. Plant Growth and Development. McGraw-Hill, New York, p. 545.

Levy, Y. and Krikun, J., 1980. Effect of vesicular-arbuscular mycorrhiza on *Citrus jambhiri* water relations. New Phytol., 85: 25—31.

Loveys, B.R., 1977. The intracellular location of abscisic acid in stressed and non-stressed leaf tissue. Physiol. Plant., 40: 6—10.

Ludlow, M.M. and Wilson, G.L., 1971. Photosynthesis of tropical plants. III. Leaf age. Aust. J. Biol. Sci., 24: 1077—1087.

Ludlow, M.M., Ng, T.T. and Ford, C.W., 1980. Recovery after water stress of leaf gas exchange in *Panicum maximum* var. *trichoglume*. Aust. J. Plant Physiol., 7: 299—313.

McMichael, B.L. and Hanny, B.W., 1977. Endogenous levels of abscisic acid in water-stressed cotton leaves. Agron. J., 69: 979—982.

Meidner, H., 1981. Measurements of stomatal aperture and responses to stimuli. In: P.G. Jarvis and T.A. Mansfield (Editors), Stomatal Physiology. Society for Experimental Biology, Seminar Series 8. Cambridge University Press, London, pp. 25—49.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Ann. Rev. Ecol. Syst., 4: 25—52.

Orians, G.H., 1975. Diversity, stability and maturity in natural ecosystems. In: W.H. Van Dobben and R.H. Lowe-McConnell (Editors), Unifying Concepts in Ecology. Junk, The Hague, pp. 139—150.

Sala, O.E. and Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semiarid regions. Oecologia (Berlin), 53: 301—304.

Sala, O.E., Lauenroth, W.K., Parton, W.J. and Trlica, M.J., 1981. Water status of soil and vegetation in a shortgrass steppe. Oecologia (Berlin), 48: 327—331.

Scholander, P.F., Hammel, H.T., Bradstreet, E.D. and Hemmingsen, E. A., 1965. Sap pressure in vascular plants. Science, 148: 339—346.

Schulze, E.-D., Hall, A.E., Lange, O.L., Evenari, M., Kappen, L. and Buschbom, V., 1980. Longterm effects of drought on wild and cultivated plants in the Negev Desert. Oecologia (Berlin), 45: 11—18.

Spanner, D.C., 1951. The Peltier effect and its use in the measurement of suction pressure. J. Exp. Bot., 2: 195—198.

Syvertsen, J.P., Smith, M.L. and Allen, J.C., 1981. Growth rate and water relations of citrus leaf flushes. Ann. Bot., 47: 97—105.

Van Bavel, C.H.M. and Ahmed, J., 1976. Dynamic simulation of water depletion in the root zone. Ecol. Model., 2: 189—212.

Westman, W.E., 1978. Measuring the inertia and resilience of ecosystems. BioScience, 28(11): 705—710.