

Plant Water Relationships and Evapotranspiration

H.E. JENSEN

Royal Veterinary and Agricultural University, Thorvaldsensvej 40,
DK-1871 Frederiksberg C, Denmark

K.H. JENSEN & D. ROSBJERG

Institute of Hydrodynamics and Hydraulic Engineering, ISVA,
Technical University of Denmark, Building 115, DK-2800 Lyngby

ABSTRACT An introduction to transport of water through the soil-plant-atmosphere system is given with reference to recent review papers. The necessity for detailed studies of all involved physical processes is emphasized in order to achieve a more rigorous basis for the modelling of the evapotranspiration process. Some actual needs in research are highlighted.

1. INTRODUCTION

Usually methods for estimation of evapotranspiration are based on the concept of potential evapotranspiration with some corrections for limitations in the soil water availability. In the assessment of the potential evapotranspiration the atmosphere resistance may be taken into account, but quite often only correlation-based methods are used in which, for example, evaporation pan measurements are multiplied with empirical correction coefficients. In this way the physical and physiological behaviour of the plant communities is almost totally ignored resulting in models which are both site-specific and crop-specific.

Many researchers, however, have realized the necessity of a more process-oriented view in order to develop methods and models that can be used on a wider range of plant communities and reflect some of the dynamics involved in the evapotranspiration process. This implies detailed studies of individual processes such as root uptake of water, transport through the plant, diffusion of water vapour through the stomata openings and transport further up through the atmospheric boundary layer. All these interacting processes are governed by the incoming solar energy, but the energy transformations are so complicated that a net radiation term alone is far from being adequate in the quantification of evapotranspiration. In the well-known combination methods this has been accounted for, but there is still a definite need for detailed studies, among other things in order to assess the range of applicability of such methods.

A major problem for the further development of the theory of evapotranspiration is the need for experimental data which are difficult and very costly to obtain. However, the understanding that theoretical development and verification by field measurements are equally necessary is widely accepted, and large field

programs are now set up as a basis for progress in the theoretical comprehension of the processes. This is particularly needed when taking the heterogeneity of plant communities into consideration. Vertical (in forests) and horizontal heterogeneities play a much more significant role than previously anticipated.

Small scale studies of the behaviour of water transport in single plants or groups of plants should, however, still be carried out extensively. An adequate description of the complicated physical/biological processes in the soil-plant-atmosphere system is still a major challenge in hydrological research.

This paper should be regarded as a brief introduction to the subject. The concept of plant water relationships is briefly described, followed by a presentation of current measurement techniques. Then the soil-plant-atmosphere continuum approach is briefly described and continued in a description of the bulk evapotranspiration process and associated measurement techniques. The modelling of the actual evapotranspiration, in particular the physically based, has been broadly reviewed and the paper is concluded with some suggestions of primary fields of demand in research. The scope of the paper is limited to the transport of water and does not take the - also very important - aspects of transport of chemicals into account.

2. BASIC CONCEPTS OF PLANT WATER STATUS

Plant water status strongly influences plant growth through its influence on gas exchange and expansion of leaves and roots. Leaf water deficit results in stomatal closure limiting the CO₂ uptake, and net photosynthesis. Furthermore plant water deficit may negatively affect the process of photosynthesis itself. Plant water status and physiological consequences of crop water deficit have been reviewed recently by Turner (1986).

Plant water status may be described basically by two parameters viz. plant water content and energy status of the plant water. The water content is usually expressed as relative to that of full saturation, i.e. relative water content (RWC), while energy status of plant water usually is expressed as the total plant water potential (Ψ) or as a component of the total water potential.

The total plant water potential is defined as the difference between the chemical potential of plant water (μ_w) and that of pure free water (μ_w^o) (J mol⁻¹). By dividing the chemical potential by the partial molal volume of water, V_w (m³ mol⁻¹), the plant water potential can be expressed in terms of pressure, Eq. (1)

$$\Psi = \frac{\mu_w - \mu_w^o}{V_w} \quad (1)$$

An alternative expression relates the plant water potential to the ratio of the water vapour pressure in the system (p) to that of saturated water pressure (p_0), Eq. (2),

in which R is the gas constant $8.3143 \text{ J mol}^{-1} \text{ K}^{-1}$ and T is the absolute temperature (K).

$$\psi = \frac{RT}{V_w} \ln \frac{p}{p_0} \quad (2)$$

The total plant water potential can be divided into a number of potential components such as osmotic potential (ψ_π), turgor or pressure potential (ψ_p) and gravitational potential (ψ_g) referring to the various forces acting on the plant water. As the gravitational potential component is only 0.01 MPa m^{-1} , it can be neglected, except in the case of high trees. Hence Eq. (3) can be applied

$$\Psi = \psi_p + \psi_\pi \quad (3)$$

At equilibrium the total plant water potential is identical in all parts of the system, i.e. xylem, cell wall, cytoplasm, and vacuole. However, the potential components may be quite different in the various parts of the system. In the vacuole the total plant water potential arises largely from osmotic and turgor forces, whereas in the xylem and cell wall matric forces are dominant. The osmotic potential of the apoplastic water (water in xylem and cell wall) is usually high ($> -0.05 \text{ MPa}$). Plant cells (cytoplasm and vacuole) behave as osmometers due to the semipermeable plasma membrane and the total plant water potential in plant cells equilibrates within seconds. Typical cell sap from many plants has an osmotic potential of about -1 MPa .

Plant water relations are often described by the Höfler diagram in which the total plant water potential (ψ), the osmotic potential (ψ_π) and the turgor potential (ψ_p) are related to the relative water content (RWC) of the plant tissue, Fig. 1. At full turgidity $\psi = 0$ and $\psi_\pi = \psi_p$ and also at this point $\text{RWC} = 1$. When RWC decreases, the turgor potential (ψ_p) also decreases until the zero turgor point as a result of the elastic extension of the cell wall. Visible wilting is observed when the point of zero turgor is reached.

An important plant tissue characteristic determining the shape of the curves in Fig. 1 is the elasticity of the cell wall. If the cell wall is rigid, the total plant water potential as well as the potential components change relatively steeply for a given plant water loss. The rigidity of the cell wall may be described in terms of the bulk modulus of elasticity defined by Hellkvist et al. (1974), Eq. (4), in which V and V_0 are the actual and turgid volume of the plant cell, respectively

$$e = \frac{d\psi_p}{d\left(\frac{V}{V_0}\right)} \quad (4)$$

The total water potential is the driving force for the water movement through the soil-plant-atmosphere system. Furthermore the total plant water potential or the potential components may control the water movement through the plant by causing stomata closure and hence increase of stomata resistance against diffusion of water vapour.

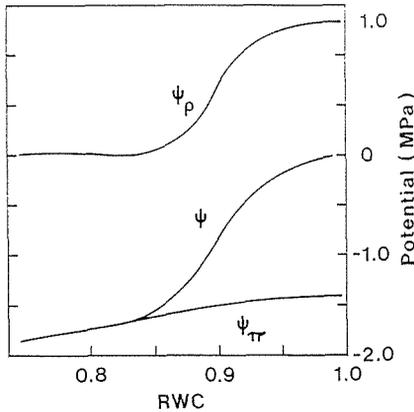


FIG. 1 Schematic Höfler diagram showing the relationships between total water potential (Ψ), turgor potential (Ψ_p), osmotic potential (Ψ_{π}) and relative water content (RWC) as plant tissue dehydrates from a fully turgid state.

3. MEASUREMENT OF PLANT WATER RELATIONSHIPS

The methodology applied for studying plant water relationships generally comprises measurement of both plant water content and total plant water potential and its components often associated with measurements of other plant responses to plant water deficit such as stomata openings, leaf resistance to gas diffusion, gas exchange, growth rate, etc. The subject has been reviewed recently e.g. by Bannister (1986) and Turner (1988).

A common approach for measuring relative water content of plants is based on measurement of fresh weight at the time of sampling, dry weight after drying at 80°C and turgid weight after floating leaves or leaf disks on water at the light compensation point for about 4 hours (Barrs and Weatherley, 1962). Recently also indirect methods have been made available such as application of beta radiation relating count rate to water content (Bannister, 1986) and leaf thickness measurement by using micrometers (Burquez, 1987).

Measurement of total water potential has become routine either by use of thermocouple psychrometer or pressure chamber techniques both of which are commercially available.

The pressure chamber technique is much used to measure leaf water potential in the field due to its rapidity and reliability. The principle of the technique (Scholander et al., 1965) is that a leaf or branch is placed in the pressure chamber

with the cut end just protruding from the chamber through a rubber bung which seals the chamber. During the measurement the leaf is sealed in a bag to minimize evaporation. The pressure in the chamber is slowly increased by 10-30 kPa s⁻¹ to a pressure sufficient to balance the tension by which the water is held in the xylem and force the meniscus back to the cut surface, which easily can be recorded visually in a microscope. As the osmotic potential of the xylem sap is high (> -0.05 MPa), the negative balance pressure therefore approximately equals the total leaf water potential, and it is often used without correction for osmotic potential of the xylem sap.

The thermocouple psychrometer techniques are based on Eq. (2) and on the fact that the relative water vapour pressure of the plant water can be obtained after equilibration of the plant tissue in a small chamber. A detailed description of the use of the thermocouple psychrometer technique for measuring total plant water potential and its components is given by Slavik (1974). Calibration of thermocouple psychrometers has been investigated in detail by Savage et al. (1981).

The pressure volume method has widely been considered to be the most rigorous method and to provide the largest amount of information on the plant water status (Wilson et al., 1979; Livingston and de Jong, 1988). By this technique a leaf or shoot is rehydrated with the cut end in pure water in a humidified box, so that the total plant water potential (ψ) becomes close to zero. At this stage a series of water potential determinations is performed, most often by the pressure chamber technique, during stepwise dehydration of the leaf. The decrease of volume of the plant tissue is calculated from the decrease of water content. The results are presented as the inverse of water potential ($1/\psi$) as a function of relative water content (RWC), Fig. 2. Below the RWC value of zero turgor ($\psi_p = 0$) the relation ($1/\psi$) = f(RWC) appears to be linear indicating that ψ_{π} RWC = constant. By extrapolation of the relationship to RWC = 1 the value of ψ_{π} at full turgor can be derived. Furthermore, from the extrapolated regression curve of $1/\psi_{\pi}$ on RWC in the turgid region values of ψ_p can be obtained as ψ subtracted the extrapolated values of ψ_{π} . Thus the relationship between ψ_p and RWC can be established from which the bulk modulus of elasticity (ϵ) of the plant tissue can be calculated, Eq. (4).

Different approaches for calculating plant tissue parameters from pressure volume curves have been outlined and discussed recently by e.g. Stadelmann (1984), Kikuta and Richter (1986), Bannister (1986) and Andersen et al. (1991). The advantage of the pressure volume method is that apoplastic water does not interfere in the determination of the osmotic potential and that the elasticity of the plant tissue can be quantified.

The epidermis of leaves creating the boundary between leaf interior and the atmosphere is covered by a relatively impermeable cuticle except at stomata openings through which gases (CO₂ and water vapour) mainly exchange between leaf interior and the atmosphere. When water deficits develop in the plant leaves, the turgor pressure regulated stomata cells partly close stomata resulting in a corresponding reduction in transpiration and CO₂ uptake.

Stomatal conductance and resistance to diffusion of gas can be calculated from measurements of water vapour loss in leaf chambers under laboratory conditions

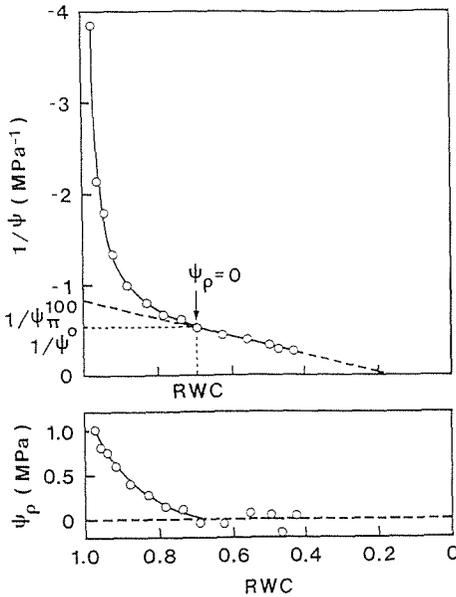


FIG. 2 A pressure volume curve illustrating the inverse of total water potential (ψ) and turgor potential (ψ_p) as a function of relative water content (RWC). The osmotic potential at full turgid weight (ψ_{π}^{100}) is derived from extrapolation of the linear portion of the $1/\psi$ versus RWC curve. The inverse water potential ($1/\psi^0$) and RWC at zero turgor ($\psi_p = 0$) are also indicated.

(Sestak et al., 1971). For field conditions a portable technique is required, and most work on stomatal resistance is now carried out with portable diffusive porometers based on an electronic moisture-sensor system. Theory, calibration, and application of porometers are described in detail elsewhere (Schulze et al., 1982; Jones, 1983; Beadle et al., 1985; Bannister, 1986).

Sap flow in trees can be estimated by means of the so-called heat pulse velocity techniques (Marshall, 1958; Swanson and Whitfield, 1981). The sap flow velocity is measured as the transport velocity of an artificially created heat pulse by means of implanted sensors. Although some time-lag between sap flow and transpiration may occur, the measured sap flow is considered to be a good approximation to the actual transpiration of the tree.

4. THE SOIL-PLANT-ATMOSPHERE CONTINUUM CONCEPT

The rate of transpiration depends not only on stomatal openings and atmospheric factors affecting the evaporation but also on the rate of water absorption which in turn depends on the rate at which water can move from the soil to the root surface. Thus water movement through the soil, plant, and atmosphere can be treated

as a series of interrelated interdependent processes. An expression similar to Ohm's law for electricity was formulated by Van den Honnert (1948) for steady state water movement through the soil, plant, and atmosphere, Eq. (5)

$$Q = \frac{\psi_s - \psi_r}{R_s} = \frac{\psi_r - \psi_l}{R_p} = \frac{\psi_l - \psi_a}{R_a} \quad (5)$$

in which Q is the water flow, ψ_s , ψ_r , ψ_l and ψ_a , are the total water potential of bulk soil at the root surface, of the evaporating surfaces of the leaf, and of the bulk air, respectively. The R_s , R_p , and R_a are the resistances of the soil, plant, and the water vapour pathway, respectively. It is noted that R_p includes stomata resistance as well as an aerodynamic resistance. Actually the stomata resistance depends on stomatal openings while the aerodynamic resistance depends on vapour pressure deficit and air movement. Thus, it is preferable to use vapour pressure or vapour concentration rather than water potential in dealing with movement of water in the vapour stage.

The consideration of the pathway of water movement in soil, plant and atmosphere as a continuum, frequently referred to as the soil-plant-atmosphere continuum, has certainly led to considerable improvement in the understanding of physical processes involved in water flow and transpiration. It provides a useful concept of describing water movement through the system because factors affecting the water movement can be described in terms of their effects on either the driving forces or the resistances against water movement. The control of stomatal closure under water stress by decrease of turgor pressure of stomatal cells caused by decrease of water potential in the leaves is well recognized as the crucial resistance regulating water vapour flux out of the plant.

Although all intermediate values of water potential along the pathway of water movement (soil-root-xylem-leaves-atmosphere) are not well established, the general shape of the potential drop through the system given in Fig. 3 is probably realistic showing an essential potential drop at the soil root interface and at the transition to the atmosphere.

However, it should be realized that Eq.(5), like most generalizations, is an oversimplification. The condition of steady state movement seldom exists in plants, although water movement may be treated as a sequence of quasi-steady states. Furthermore, uncritical adoption of this analogy may lead to confusion rather than enlightenment, which is particularly true where there is a change in phase, as in the case of a substomatal cavity, where transport of solutes is involved or where the transport of water is nonlinear with respect to the change in water potentials (Turner, 1986).

5. POTENTIAL AND ACTUAL EVAPOTRANSPIRATION

As mentioned above the process of evapotranspiration is very difficult to predict because it is controlled by a number of interacting meteorological, biological,

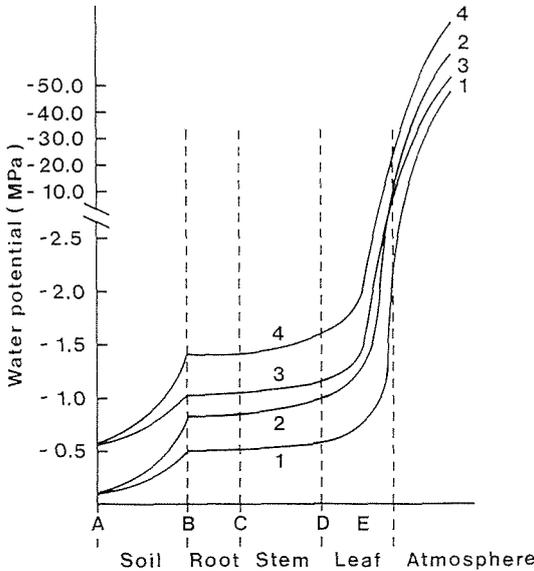


FIG. 3 Idealized water potential gradients through the soil-plant-atmosphere continuum. Curves 1 and 2 represent plant water removal from relatively wet soil at low and high transpiration rates, respectively; curves 3 and 4 represent plant water removal at low and high transpiration rates, respectively, after the soil water potential has been reduced to -0.6 MPa. (After Hillel, 1980).

chemical, and soil physical factors which are difficult to measure and quantify. The concept of potential evapotranspiration was introduced many years ago to define the upper limit of water loss from a vegetated surface under given climatic conditions. Earlier attempts at estimating evapotranspiration were based on corrections to the evaporation from a free water surface (evaporation pan) and to easily measurable climatic variables (empirical regression equations). Such methods can only be of a limited use because they do not consider all factors involved.

Previously, potential evapotranspiration was considered to be independent of the vegetation cover. However, it is now recognized that vegetation characteristics such as albedo and crop structure also influence the rate of evapotranspiration, see e.g. the definition by Doorenbos and Pruitt (1977).

The first physically-based equation for predicting potential evapotranspiration E_p was developed by Penman (1948) from energy balance and aerodynamic transport considerations. This equation was later improved by Monteith (1965) who included a rigorous formulation of turbulent transport of momentum, heat, and vapour resulting in the following formulation

$$E_p = \frac{\Delta(R_N - G) + \rho_a c_p \delta_e / r_a}{\lambda(\Delta + \gamma)} \tag{6}$$

where Δ is the slope of the saturation vapour pressure-temperature curve, R_N the net radiation, G the heat flux into the ground, ρ_a the air density, c_p the specific heat of air, δ_e the vapour pressure deficit, r_a the aerodynamic resistance, λ the latent heat of vaporization, and γ the psychrometric constant. In this equation it has been assumed that the surface resistance r_s is zero implying that there is no restrictions on the water supply to the evaporative surface. As opposed to other formulations this equation explicitly considers the structure of the vegetation surface, and it seems to provide an operational and reliable method for prediction of potential evapotranspiration.

When the water supply is restricted, the actual evapotranspiration is less than the potential. For large-scale problems such as catchment areas actual evapotranspiration, E_a , is often predicted by relating the ratio E_a/E_p to the soil water content in the root zone. Several empirically-based relationships of this kind have been proposed, see e.g. Tanner (1967). Some physically-based relations will be presented in section 7.

6. MEASUREMENTS OF ACTUAL EVAPOTRANSPIRATION

A number of techniques have been developed for measurement of evapotranspiration. As discussed by Sharma (1985) the various methods may be grouped in three categories: (a) water balance, (b) micrometeorological, and (c) plant physiological methods.

The first category involves application of the water conservation law to the scale of interest, and the evapotranspiration component is calculated as a residual term by measuring or estimating all other components appearing in the equation. This method is widely used in catchment hydrology, and if a larger time span is considered (in the order of years), evapotranspiration is often estimated as the difference between precipitation and surface runoff. Application of this method offers the advantage of integrating the effects of spatial variability of soil and vegetation within the catchment.

The water balance method may be applied to any larger and smaller scale down to a single soil profile. Furthermore, the method is applicable for any time span. However, when calculating short-term evapotranspiration problems of measuring the change in water storage may arise, particularly for larger scales.

The water balance method is widely used in combination with weighing lysimeters, where each component of the water balance equation is measured accurately, and the evapotranspiration term is consequently determined by the weight loss. Although problems may occur in relation to the representativeness of the isolated soil-vegetation and the microclimate, the lysimeter method is potentially the most accurate method of estimating actual evapotranspiration.

The second category includes the micrometeorological methods by which evapotranspiration is estimated from meteorological variables measured above the evaporating surface. The category includes (1) the profile method by which the water flux is estimated by measurement of the humidity gradient in combination with measurement of the wind profile in order to estimate the turbulent transfer coefficient; (2) the Bowen ratio method by which the incoming energy is measured

directly while the partitioning into latent heat and sensible heat is expressed by the Bowen ratio, which is estimated from measurements of dry and wet bulb temperature gradients; and (3) the eddy correlation method involving measurements of the instantaneous vertical wind and humidity components thus making possible the estimation of vapour flux as the product of these two quantities.

In general the micrometeorological methods require advanced and costly instruments and data logging equipment, and the methods are therefore most suitable for research programs and less applicable for routine measurements.

The last category includes the plant-physiological methods which are described in section 4.

7. PHYSICALLY BASED MODELS IN ACTUAL EVAPOTRANSPIRATION

If a small scale is considered such as a group of plants or an agricultural field, a less empirical and more process-oriented approach to predicting actual evapotranspiration may be of interest. In principle the most universal and accurate model is produced if all flow processes through the soil-plant-atmosphere system are considered and formulated on the basis of the physical laws for water flow in the individual regimes. In fact, such a model should also consider uptake of nutrients and plant growth in order to fully represent the evapotranspiration process. However, such a model is not possible at the moment, because all processes involved are not fully understood yet, and, if so, they would involve a large number of parameters which would be impossible to quantify. Hence, simplifications must be introduced in the formulations in order to obtain a model of practical relevance even for research purposes. Numerous models of various complexity have been proposed covering different aspects of evapotranspiration, see e.g. review by Sharma (1985).

Several physically-based models for actual evapotranspiration E_a are developed from the Penman-Monteith combination equation where an additional parameter, the surface resistance r_s , is included to account for the extra resistance to water flow when the water supply is restricted

$$E_a = \frac{\Delta(R_N - G) + \rho_a c_p \delta_e / r_a}{\lambda(\Delta + \gamma(1 + r_s / r_a))} \quad (7)$$

The surface resistance reflects the response of the vegetated area to soil water deficit and other environmental variables, and various relationships of empirical nature have been proposed, e.g. Szeicz et al. (1973) and Russel (1980). However, the proposed functional relationships are often species-specific, and more research on the behaviour of the surface resistance is required in order to develop sub-models of general relevance.

More physical realism may be introduced into an evapotranspiration model by considering the total evapotranspiration as a sum of three components: Evaporation from the soil surface, transpiration from the plant community, and evaporation of water intercepted on the plant surface. For some purposes this separation may

be unimportant. However, due to the differences in the physical mechanisms involved in the three processes this partitioning seems superior in most cases. Particularly for tall vegetations like forests the consideration to evaporation from intercepted water is important because the evaporation from a wet canopy is much higher than from a dry canopy even in case of optimal water supply due to changes in the ratio of the surface and aerodynamic resistances.

It is common to assume that evaporation from intercepted water precedes transpiration and that the incoming radiation is divided in a part available for soil evaporation and a part available for interception/transpiration depending on the density of the vegetation community, see e.g. Hansen et al. (1990).

In this way upper limits of the various evapotranspiration components can be defined. The actual evaporation of intercepted water depends on the actual canopy storage, while the soil evaporation within the vegetation is a function of the water flux to the surface. The transpiration component representing the rate of water extraction by the root system is in general the most important process and also the one which is most difficult to quantify. Numerous model approaches have been proposed as reviewed by Molz (1981). In general it is very difficult to obtain data for the parameters involved such as root surface area and root depths and their dynamics for various crop species and under different soil conditions.

8. PROBLEM AREAS AND FIELDS OF DEMAND IN RESEARCH

The emphasis on leaf water potential and the physical linking of soil, root, leaves, and atmosphere as the basis for crop response to environmental variables including soil water status appear to be too simplistic. Current evidence (Schulze, 1986; Turner, 1986; Davies et al., 1990) indicates that the root may be considered as a "sensor" of soil water deficit and that growth regulators may play an important role in transferring the message of increasing soil water deficit to the shoot. Thus, as pointed out by Turner (1986) more emphasis must be placed on understanding root water relations in conjunction with soil water deficit and on the interactions, both hydraulic and chemical between root and shoot. Further studies on the hydraulic resistances of the plant are needed including the importance of osmotic adjustment as well as further studies on plant regulators in conjunction with plant water relations and the effects of plant regulators on crop growth and water use efficiency under water limited conditions.

Although progress has been made in the understanding of evapotranspiration processes, and thus a better platform has been established for developing process-oriented and physically-based models, a number of areas need to be explored, not only on the scale of a group of plants, but also for large-scale regional problems with due consideration to the spatial heterogeneity in climate, vegetation and soil conditions. More progress is also needed in measurement techniques in order to provide the required input parameters for the models and to obtain direct measurements of evapotranspiration for validation purposes.

REFERENCES

- Andersen, M.N., C.R. Jensen and R. Lösch (1991) Derivation of pressure-volume curves by a non-linear regression procedure and determination of apoplastic water. J. Exp. Bot. **42**; 154-165.
- Bannister, P. (1986) Water relations and stress. In: Methods in Plant Ecology, 2nd ed. (eds. P.D. Moore and S.B. Chapman). Blackwell Sci. Publ., Oxford, 73-143.
- Barrs, H.D. and Weatherley, P.E. (1962) A re-examination of the relative turgidity technique for estimating water deficits in leaves. Aust. J. Biol. Sci. **15**; 413-428.
- Beadle, C.L., M.M. Ludlow and J.L. Honeysett (1985) Water relations. In: Techniques in Bioproductivity and Photosynthesis. (eds. Combs et al.) Pergamon Press, Oxford, 50-61.
- Begg, J.E. and N.C. Turner (1976) Crop water deficits. Adv. Agron. **28**; 161-217.
- Bradford, K.J. and T.C. Hsiao (1982) Physiological responses to moderate water stress. In: Encycl. Plant Physiol. New Ser. **12B** (eds. A. Pirson and M.A. Zimmermann). Springer Verlag, Berlin, Heidelberg, New York, 263-324.
- Burquez, A. (1987) Leaf thickness and water deficit in plants: A tool for field studies. J. Exp. Bot. **38**; 109-114.
- Davies, W.J., T.A. Mansfield and A.M. Hetherington (1990) Sensing of soil water status and the regulation of plant growth and development. Plant, Cell and Environment **13**; 709-719.
- Dorenbos, J. and W.O. Pruitt (1977) Crop water requirements. FAO Irrig. Drain. Paper **24**.
- Hansen, S., H.E. Jensen, N.E. Nielsen and H. Svendsen (1990) Daisy. Soil Plant Atmosphere System Model. NPo-Research Report A10. National Agency of Environmental Protection, Denmark.
- Hellkvist, R., G.P. Richards and P.G. Jarvis (1974) Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. **11**; 637-667.
- Hillel, D. (1980) Applications of soil physics. Acad. Press, New York.
- Jones, H.G. (1983) Plants and Microclimate. Camb. Univ. Press, Cambridge.
- Kikuta, S.B. and H. Richter (1986) Graphical evaluation and partitioning of turgor responses to drought in leaves of durum wheat. Planta **168**; 36-42.
- Livingston, N.J. and E. de Jong (1988) Use of unsaturated salt solutions to generate leaf tissue water-release curves. Agron. J. **80**; 815-818.
- Marshall, D.C. (1958) Measurement of sap flow in conifers by heat transport. Plant Physiology, **33** (6); 385-396.
- Molz, F.J. (1981) Models of water transport in the soil-plant systems: A review. Water Resour. Res., **17**; 1245-1260.
- Monteith, J.L. (1965) Evaporation and environment. Symp. Soc. Exp. Biol. **19**; 205-234.
- Penman, H.L. (1948) Neutral evaporation from open water, bare soil and grass. Proc. R. Soc. London Ser. A **193**; 120-146.
- Savage, M.J., A. Cass and J.M. de Jager (1981) Calibration of thermocouple hygrometers. Irrig. Sci. **2**; 113-125.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet and E.A. Hemmingsen (1965) Sap pressure in vascular plants. Science, **148**; 339-346.

- Schulze, E.D., A.E. Hall, O.L. Lange and H. Walz (1982) A portable steady-state porometer for measuring the carbon dioxide and water vapour exchanges of leaves under natural conditions. Oecologia (Berlin) 53; 141-145.
- Schulze, E.D. (1986) Whole-plant response to drought. Aust. J. Plant Physiol. 19; 127-141.
- Sesták, Z., J. Catsky and P.G. Jarvis (1971) Plant Photosynthetic Production: Manual of Methods. Junk, The Hague.
- Sharma, M.L. (1985) Estimating evapotranspiration. Advances in Irrigation (ed. D. Hillel). Volume 3; 213-281.
- Slavik, B. (1974) Methods of Studying Plant Water Relations, Academia, Prague. Springer Verlag, Berlin.
- Stadelmann, E.J. (1984) The derivation of the cell wall elasticity function from the cell turgor potential. J. Exp. Bot. 35; 859-868.
- Swanson, R.H. and D.W.A. Whitfield (1981) A numerical analysis of heat pulse velocity theory and practice. J. Exp. Bot. 32 (126); 221-239.
- Szeicz, G., C.H.M. Van Bavel and S. Takami (1973) Stomatal factor in the water use and dry matter production by sorghum. Agric. Meteorol., 21 I; 213-226.
- Tanner, C.B. (1967) Measurement of evapotranspiration. Agron. Monogr. 11; 534-574.
- Turner, N.C. (1986) Crop water deficits: A decade of progress. Adv. Agron. 39; 1-51
- Turner, N.C. and J.B. Passioura (eds.) (1986) Plant growth, drought and salinity. Aust. J. Plant Physiol. 13.
- Turner, N.C. (1988) Measurement of plant water status by the pressure chamber technique. Irrig. Sci. 9; 289-301.
- Van den Honnert, T.H. (1948) Water transport in plants as a catenary process. Discuss. Faraday Soc. 3; 146-153.
- Wilson, J.R., M.J. Fischer, E.D. Schulze, G.R. Dolby and M.M. Ludlow (1979) Comparison between pressure-volume and dewpoint-hygroscopy techniques for determining the water relations characteristics of grass and legume leaves. Oecologia (Berlin), 41; 77-88.

