CROP–WATER RELATIONS

Edited by

I. D. Teare

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PREFACE

Water relations in crops is the domain not only of the plant physiologist and soil physicist, but also of the micrometeorologist, ecologist, agronomist, and horticulturist. In consequence, we have prepared this book with two main objectives. The first of these is to present a review of current research on the physical and physiological aspects of water transfer in the biosphere. We have included research concerning the atmospheric factors that affect energy exchanges in the biosphere, particularly evaporation; the soil factors that affect soil water status and water supply to crop roots; the distribution, movement, and function of water in plant cells, tissues, and organs; and the development of internal water deficits in relation to physiological processes.

The second objective is to present a review of the water relations of the twelve most important food and fiber crops grown today. In dealing with individual crops, we have asked each contributor to emphasize root growth, the canopy structure, the interaction of the crop with its environment, and the applied aspects of irrigation. We have also asked them to identify physiological stages of development for each crop and to relate them to critical water demand periods.

Technical terms from all fifteen chapters are included in a glossary at the end of the book. Symbols, however, are listed separately at the end of each chapter in their order of usage.

The subject matter coverage was developed from a course of lectures given to advanced graduate students at Kansas State University entitled "Crop Water Relations" during the years 1975 through 1978. At that time the senior author was a member of the Evapotranspiration Laboratory at Kansas State University and a Professor in the Department of Agronomy. We would like to acknowledge Dr. P. J. Kramer, Dr. Nasser P. Sionit, and other members of the Phytotron staff at Duke University for their generous assistance during the period this book was being prepared.

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ATMOSPHERIC DEMAND FOR WATER

Blaine L. Blad

INTRODUCTION

Water has many unique properties including its ability to exist in the solid, liquid, or vapor phase within the range of air temperatures occurring on earth. It is possible for all three phases to exist at the same time, but it is the change from one phase to another that is of interest to us, particularly the change from liquid to vapor. The phase change from ice to water requires 80 cal g^{-1} (334 kJ kg^{-1}). The change from liquid to vapor, the latent heat of vaporization (L), requires approximately 585 cal g^{-1} (2.44 MJ kg^{-1}) at 20°C.

The physical process for the change of liquid water to gaseous water vapor is called evaporation (E). Evaporation occurs from oceans, lakes, ponds, rivers, soil, or other wet surfaces. Transpiration (T_p) is the evaporation of water that has been absorbed through plant roots, transported through the plant, and then removed from leaf surfaces. It is controlled by the stomatal aperture and by the vapor pressure gradient from the leaf to the air. The term evapotranspiration (E_t) is commonly used to describe the total process of water vapor transfer into the atmosphere from vegetated land surfaces.

ENERGY EXCHANGE AMONG LEAF, CANOPY, AND ENVIRONMENT

General

The vast quantities of energy consumed in E_t are supplied almost entirely by sources traceable to the sun. This energy may come from direct, diffuse, or reflected sunlight; it may come from solar radiation absorbed by molecules and particles in the air or from objects on the surface of the earth where it is reradiated as long-wave radiation; or it may come through energy transferred to cool plants from air heated by solar radiation.

Solar radiation received at the earth's surface is concentrated primarily in the 0.30–3.0 μm waveband portion of the electromagnetic spectrum (short-wave radiation), and is composed of a direct beam and a diffuse component. Long-wave radiation, radiation concentrated primarily in the 3.0–40.0 μm waveband, also contributes energy for E_t. The difference between the incoming and the outgoing radiation streams is termed net radiation (R_n) and may be stated in the form of an equation as follows:

$$R_n = R_s - \alpha R_s + R_a - R_g \qquad (1.1)$$

where R_s and αR_s are incoming and outgoing short-wave radiation and R_a and R_g are incoming and outgoing long-wave radiation, respectively. The sign convention adopted in this chapter is such that fluxes toward the surface are positive and those away from the surface are negative. Maximum midday values of R_n over actively growing vegetation will seldom exceed about 1 cal cm^{-2} min^{-1} (697 W m^{-2}).

Net radiation provides energy for E_t, for heating the air, soil, and plants, and for photosynthesis. It is partitioned into the energy consuming processes:

$$R_n = -(LE + H + S + P_s + M) \qquad (1.2)$$

where LE is latent heat flux (energy used in E_t), H is the sensible heat exchange with the air, S is the soil heat flux, P_s is the energy for photosynthesis, and M is the term for any miscellaneous energy exchanges including energy for metabolic activity or energy storage in the plant canopy. Most of the energy supplied by R_n is consumed as LE, lesser but significant amounts go into H and S, while the amount utilized in P_s and M is generally less than 1–2% of the total. Thus, Eq. (1.2) can be simplified to:

$$R_n = -(LE + H + S) \tag{1.3}$$

Leaf

Both sides of a leaf exchange radiation with all objects "seen" by the leaf (Fig. 1.1). For a horizontal leaf above the soil surface the net amount of radiant energy absorbed by the leaf (R_l) is:

$$R_l = R_s - \alpha_l R_s + \alpha_g R_s - \alpha_l \alpha_g R_s + R_a + \epsilon_g \sigma T_g^4 - \tau_l R_s - \tau_l \alpha_g R_s$$
$$- (1 - \epsilon_l)R_a - (1 - \epsilon_l)\epsilon_g \sigma T_g^4 (1 - \epsilon_g)R_a - (1 - \epsilon_g)(1 - \epsilon_l)R_a \tag{1.4}$$

where σ is the Boltzmann constant; ϵ_g and ϵ_l are the emissivity of the soil surface and leaf, respectively; α_l and α_g are the reflection coefficients for the leaf and ground, respectively; T_g is the temperature (°K) of the ground; and τ_l is the transmission coefficient for the leaf.

Certain of the radiation streams, i.e., $(1 - \epsilon_l)R_a$, $(1 - \epsilon_g)R_a$, and $(1 - \epsilon_l)\epsilon_g \sigma T_g^4$, are very small and can be neglected. The equation can, therefore, be rearranged and simplified to give:

$$R_l = R_s(1 - \alpha_l)(1 + \alpha_g) + R_a + \epsilon_g \sigma T_g^4 - \tau_l(R_s + \alpha_g R_s) \tag{1.5}$$

The absorbed energy, R_l, is dissipated by reradiation, convection, and transpiration. The reradiated energy is equal to $2\epsilon_l \sigma T_l^4$ where T_l is the temperature (°K) of the leaf. This term may be combined with those in Eq. (1.5) to represent the net radiation of the leaf (R_{nl}) as follows:

$$R_{nl} = R_s(1 - \alpha_l)(1 + \alpha_g) + R_a + \epsilon_g \sigma T_g^4$$
$$- 2\epsilon_l \sigma T_l^4 - \tau_l(R_s + \alpha_g R_s) \tag{1.6}$$

Additional discussion of factors affecting net radiation of a leaf is contained in Monteith (1).

The following example is illustrative of typical values that might be encountered on a sunlit leaf during a clear, summer, midday period. $R_s = 1.4$ cal cm^{-2} min^{-1} (976 W m^{-2}), $R_a = 0.40$ cal cm^{-2} min^{-1} (279 W m^{-2}), $T_l = 300$°K, $T_g = 310$°K, $\alpha_l = 0.25$, $\tau_l = 0.25$, $\alpha_g = 0.15$, $\epsilon_l = 0.97$, $\epsilon_g = 0.95$. Using these values we have, by Eq. (1.6):

$$R_{nl} = 1.20 + 0.40 + 0.71 - 1.58 - 0.40$$
$$= 0.33 \text{ cal cm}^{-2} \text{ min}^{-1} \text{ (231 W m}^{-2}\text{)}$$

If this leaf were shaded by other leaves in a canopy, then R_{nl} could be drastically different. The solar radiation impinging on the leaf would be reduced to about one-fourth of full R_s so that R_s in Eq. (1.6) would

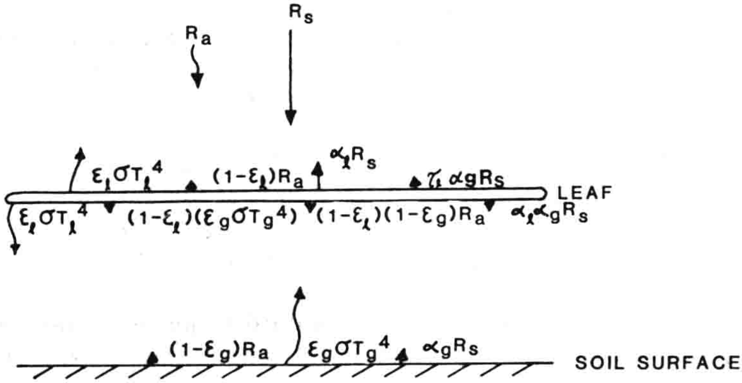

Figure 1.1. Diagram showing all radiation streams impinging on and leaving a leaf surface over the ground. Straight arrows indicate short-wave fluxes and wavy arrows indicate long-wave fluxes of radiation. Length of the arrows indicates relative flux densities that might be expected during a clear, summer midday period. R_s is incoming solar radiation, R_a is incoming long-wave radiation, ϵ_l and ϵ_g are emissivities, α_l and α_g are reflextivities, τ_l is the transmissivity of the leaf, and T_l and T_g are temperatures (°K) of the leaf and ground, respectively.

be replaced by $0.25R_s$ and the long-wave radiation from the sky, R_a, would be replaced by the radiation emitted by leaves "seen" by the shaded leaf. In this case a reasonable estimate of R_{nl}, if T_l remains at about 300°K, would be:

$$R_{nl} = 0.30 + 0.79 + 0.71 - 1.58 - 0.10$$
$$= 0.12 \text{ cal cm}^{-2} \text{ min}^{-1} \text{ (84 W m}^{-2}\text{)}$$

The difference in R_{nl} between sunlit and shaded leaves has important implications for leaf temperature, leaf transpiration, and the exchange of sensible heat with the surrounding air. Because R_{nl} of shaded leaves is low such leaves are generally at or near the temperature of the surrounding air, whereas the sunlit leaves may be a few degrees warmer than the air. Sunlit leaves can transpire large amounts of water but much less water is lost from shaded leaves. Shaded leaves exchange almost no sensible heat with the surrounding air but sunlit leaves may exchange a significant amount.

The sensible heat exchange (H_l) of a leaf with the surrounding air may be described by:

$$H_l = \frac{\rho_a C_p (T_a - T_l)}{r_a} \tag{1.7}$$

where T_a is the temperature of the air (°K), ρ_a is the air density, C_p is the specific heat of air at constant pressure, and r_a is the resistance to the flow of heat through the boundary layer of air surrounding the leaf. Heat is transferred either by natural convection (due to buoyancy effects) or by forced convection (due to windspeed effects). Except for very low windspeeds the amount of heat transferred by forced convection is much greater than that due to natural convection. Parlange et al. (2) show that, even for velocities as low as 60 cm/sec, forced convection carries 10 times more heat than natural convection. If the leaf is warmer than the air some fraction of R_{nl} will be utilized to heat the surrounding air. If $T_a > T_l$, heat will be transferred from the air to the leaf. H_l will, therefore, be an additional source of energy for transpiration or for increasing the leaf temperature.

The latent heat flux from a leaf is the third major mechanism for the exchange of energy between a leaf and its environment. This flux may be described by:

$$LE = \frac{M_w/M_a}{P} L\rho_a \frac{(e_l - e_a)}{r_a + r_s} = \frac{\rho_a C_p}{\gamma} \frac{(e_l - e_a)}{r_a + r_s} \qquad (1.8)$$

where M_w/M_a is the ratio (0.622) of the mole weights of water vapor (M_w) and air (M_a), P is the atmospheric pressure, e_l is the vapor pressure at the leaf surface, e_a is the vapor pressure of the air, γ is the psychrometric constant ($\gamma = PC_p/LM_w/M_a = 0.66$ mb °C^{-1} at 20°C and P = 1000 mb), and r_s is the diffusive resistance to the flow of water vapor from the internal to the external surface of a leaf. This latter term is principally the resistance to the diffusion of water vapor through the plant stomata. Only minor amounts of water vapor may, in some plants, diffuse through the leaf cuticle. r_s is usually on the order of 1 to 10 or 20 sec cm^{-1} and r_a is generally 0.1 to 1 or 2 sec cm^{-1} (2). More detailed discussion of energy exchanges between a leaf and the surrounding environment can be found in Gates (3) and Montieth (1).

Plant Canopy

A plant canopy is composed of plants and their individual parts. The exchange of energy between the aerial environment and the canopy is more complicated than that just described for a single leaf. Leaves within a canopy exchange energy with neighboring leaves and other plant parts. The irradiance of leaves at various levels within a plant canopy is influenced by the amount of plant cover and by the manner in which plant, parts, particularly leaves, are arranged, distributed, oriented, and inclined within the canopy. A review describing procedures for estimating the penetration of short-wave radiation into plant canopies is provided by Lemeur and Blad (4). Net radiation generally decreases with increasing depth into the canopy and most of the radiation is captured in the upper canopy levels. Thus, for example, Denmead et al. (5) found that almost three fourths of the net radiation absorbed by a corn canopy was captured in the upper half of the canopy.

In the exchange of energy with the atmosphere, various levels within a plant canopy may serve either as sinks or sources for sensible heat, water vapor, CO_2, and other materials. Because of the complexities and difficulties associated with describing energy and mass exchanges within plant canopies there are few studies that have been made and few models developed which accurately simulate these processes. Begg et al. (6) conducted one of the few such studies of mass and energy exchanges using a crop of bulrush millet. One of the best simulation models of these processes was recently developed by Norman (7).

In some cases it is only necessary to understand what the entire canopy is doing and not what is happening at different levels within the canopy. In such cases, the radiation and energy exchanges between the canopy and the atmosphere can be determined by evaluating differences between the radiative and energy streams passing through some defined plane above the canopy and another plane just above the soil surface. The net radiation above the canopy (R_n) may be written as:

$$R_n = R_s - \alpha_c R_s + R_a - R_a(1 - \epsilon_c) - \epsilon_c \sigma T_c^4$$
$$= R_s(1 - \alpha_c) + \epsilon_c R_a - \epsilon_c \sigma T_c^4 \quad (1.9)$$

where α_c is the albedo of the crop, ϵ_c is the crop emissivity, and T_c is the crop temperature. Similarly, the net radiation below the canopy (R_{nb}) can be described. Each radiation stream will be modified significantly by the plant canopy. We are interested in the energy absorbed by the canopy, i.e., $R_n - R_{nb}$. This difference is related to the canopy energy balance by:

$$R_n - R_{nb} = T_p + H_c \quad (1.10)$$

where H_c is the sensible heat exchange between the canopy and the surrounding air. H_c may be calculated by:

$$H_c = \rho_a C_p \frac{T_a - T_c}{r_a} \quad (1.11)$$

The energy balance at the soil surface can be expressed as:

$$R_{nb} = E + H_s + S \quad (1.12)$$

where H_s is the sensible heat exchange between the soil surface and the air above.

Kanemasu and Arkin (8) show the differences in canopy energy balance between sorghum grown in wide (0.91 m) and narrow (0.46 m) rows. These data were obtained under conditions of a dry soil surface so that E is assumed to be negligibly small. Therefore, E_t is essentially the canopy transpiration in this case. Components of the energy balance in wide and narrow sorghum are shown in Fig. 1.2.

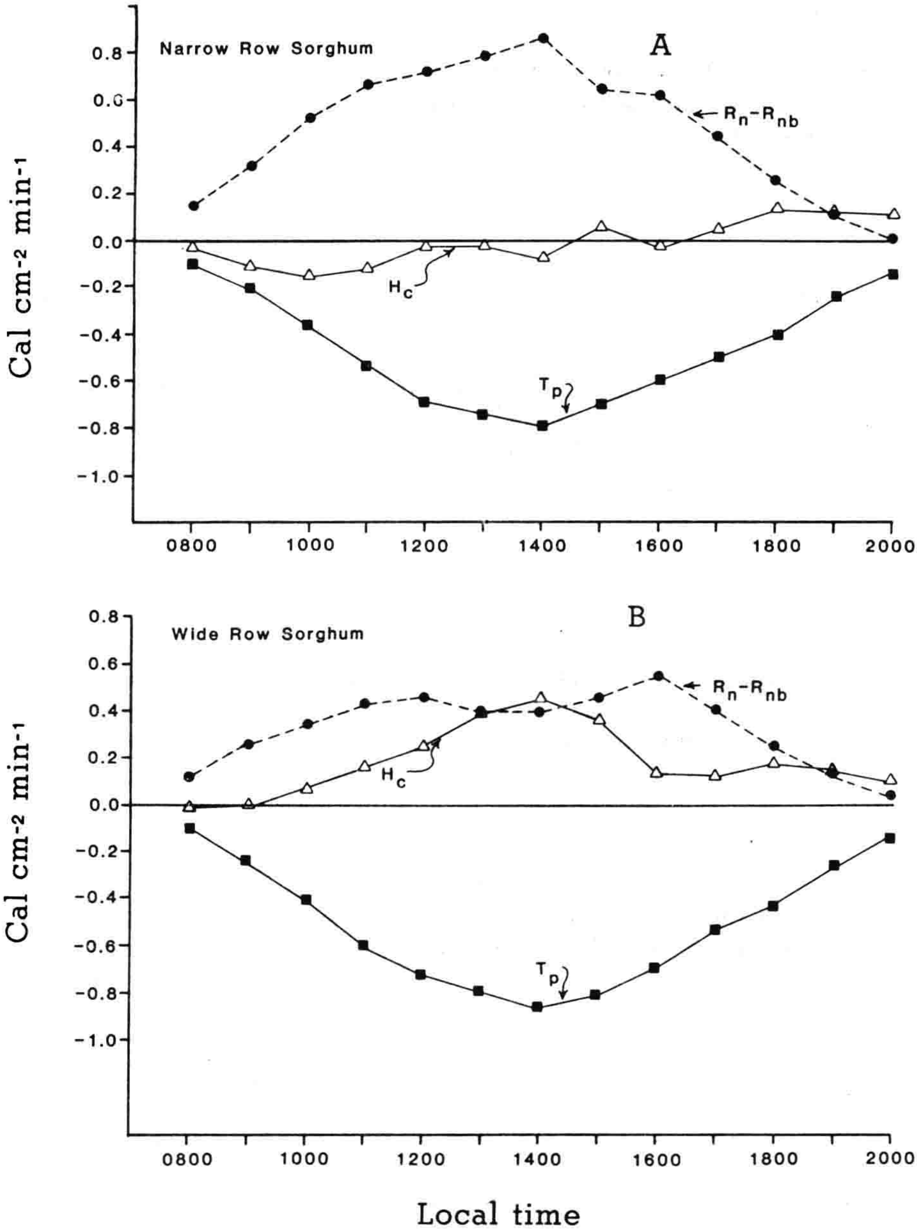

Figure 1.2. Above canopy minus below canopy net radiation ($R_n - R_{nb}$), transpiration (T_p), and sensible heat flux between the canopy and air (H_c) for narrow-row sorghum (A) and wide-row sorghum (B). [Adapted from Kanemasu and Arkin (8).]

It is evident that the wide-row sorghum in this study transpired more water than did the narrow-row sorghum. Over the entire season the wide-row sorghum was observed to use about 10% more water. A significant proportion of the energy used throughout the day in E_t in the wide-row sorghum was supplied by sensible heat (H_c has a positive sign). The narrow-row sorghum, on the other hand, absorbed sensible heat only after about 1400 hr. The major source of sensible heat consumed by the plants in the wide rows came from the air which was heated at the soil surface. This was especially true in the morning. In the afternoon sensible heat was also drawn from the warm air above the crop to the plants. Chin Choy et al. (9, 10) and McCauley et al. (11) also reported reduced water loss from peanuts and sorghum planted in narrow as compared to wide rows. However, in very wide rows (perhaps 2 m or wider) the total water use of the field will be decreased because evaporation from the soil, especially when the soil surface is not saturated, will be less than transpiration from the plants. In these very wide rows, much of the heat generated at the soil surface may not be captured by the plants that occupy only a relatively small portion of the total air–plant volume.

In regions where the soil surface is well supplied with water, E_t from wide- and narrow-row vegetation will be about the same. In humid regions R_n generally sets the upper limit on the amount of energy consumed in *LE* (12). Lemon et al. (13), for example, reported that R_n in the eastern United States in summertime was proportioned as follows: *LE* (40–90%), *H* (10–60%), *S* (5–10%), and P_s (1–5%). In contrast *LE* in arid regions may often exceed R_n because of the advection of sensible heat (14, 15).

Hanks et al. (16) identified various sources of advected energy. These include between row advection, energy advected from nearby fields, and energy transported from regions remote from a given area. Between row advection occurs when sensible heat is generated at the soil surface between the rows as illustrated in the previous discussion of wide- and narrow-row sorghum.

Sensible heat is advected to a crop from nearby fields when wind blows across a surface that is discontinuous in temperature and/or humidity. This so-called local advection is common in areas where irrigation is practiced because irrigated fields tend to be cooler and wetter than adjacent nonirrigated areas. It also occurs where fallowed fields are adjacent to crop covered fields. As the surface of a fallowed field dries it becomes a potential source of sensible heat for nearby crops. Local advection causes E_t rates to be greatest near the field border and to decrease with increasing distance into the field (16–19). Generally, the effects of local advection are minimal at downwind distances of about 80–100 m (18).

Regional advection occurs when sensible heat is transported from regions remote from the field. McIlroy and Angus (20) reported that regional advection of sensible heat caused E_t rates double that when net radiation was the only source of energy. In research conducted in the central Great Plains, Brakke et al. (19) found that local advection supplied 1–14% and regional advection supplied 7–40% of the total energy consumed in E_t. The contribution of regional advection was greatest on days of strong wind.

Thus, the atmospheric demand for water from vegetative surfaces depends on two sources of energy. The primary source of energy is R_n but especially in arid to subhumid climates advected sensible heat may contribute as much as 50% of the energy consumed in E_t.

The Soil–Plant–Atmosphere Continuum

The transpiration process involves the absorption of water by the plant roots, the transport of water through the conducting tissues of the plant, and the passage of evaporated water through the leaves and into the air, primarily through the stomatal aperture.

The hydraulic system within intact plants acts as a true continuum. This was demonstrated by research that showed that pressure changes at one end of the plant system, the roots, are faithfully manifest at the other end of the system, the leaves (21). The movement of water through the soil–plant–atmosphere system can be explained using laws and principles of thermodynamics. A detailed discussion of these laws and principles of thermodynamics will not be attempted here. Additional information on the thermodynamics of water movement in biological systems may be obtained from Leyton (22).

For the purposes of this chapter it is necessary only to know that water will move through the soil and into the plant, through the plant and into the atmosphere in response to a water potential gradient, that is, water

Table 1.1. Approximate magnitudes of water potential for a transpiring corn plant with soil moisture at field capacity and relative humidity of 50% and air temperature of 30°C

	Water Potential	
Component	$N\ m^{-2}$	Bars
Soil	-1×10^4	−0.1
Roots	-1.5×10^5	−1.5
Leaves	-8×10^5	−8
Air	-8×10^7	−800