How Do Crops Manipulate Water Supply and Demand? [and Discussion]

J. L. Monteith and D. J. Greenwood

Phil. Trans. R. Soc. Lond. A 1986 **316**, 245-259
doi: 10.1098/rsta.1986.0007

Phil. Trans. R. Soc. Lond. A **316**, 245–259 (1986)
Printed in Great Britain

How do crops manipulate water supply and demand?

By J. L. Monteith†, F.R.S.

Hydrological Sciences Branch – Goddard Space Flight Center, Greenbelt, Maryland 20771, *U.S.A.*

The supply of water provided by the root system of a crop stand is defined in terms of the rate at which water is extracted by a root front moving downwards with a constant velocity, the available water per unit soil volume, and a time constant that is inversely proportional to root density. The demand for water, often identified with a potential transpiration rate, is defined in terms of a maximum crop growth rate multiplied by the conservative ratio of transpiration to dry-matter production. From experimental evidence, supported by theory, this ratio is proportional to the mean saturation vapour-pressure deficit.

As hypothesized, the root front accelerates during seedling establishment to keep demand and supply in balance. Once a maximum root velocity is reached (*ca.* 2–4 cm d^{-1}) transpiration is limited by water supply, except when the soil behind the root front is wetted by rain or irrigation, when it is limited by demand. Irrigation amounts and timing can both be estimated from this scheme.

INTRODUCTION

Plants grow in two media – soil and air – and survive by coordinating the operation of roots and shoots. In physiological literature, this coordination is often discussed in terms of a 'functional balance' (Brouwer 1983) or 'specific activity' (Charles-Edwards 1982). Most studies of functional balance have been concerned with the allocation of assimilates and substantial progress has been made towards understanding how a plant of fixed size manages to balance the loss of water from its foliage against the uptake by its root system. In contrast, few attempts have been made to explain how plants manipulate the growth of roots supplying water to match the growth of shoots transpiring water, not just on the day when an enthusiastic physiologist happens to be measuring water potentials and stomatal conductance but from the seedling stage through to maturity.

Irrigation is a technique that helps plants to meet a demand for water when the supply is limited by lack of rain. Most contemporary methods of calculating irrigation requirements fail to distinguish clearly between the physical states which determine potential rates of supply and demand and the physiological processes which set limits to these rates. In attempting to use limited supplies of water with maximum efficiency, agronomists are more likely to be guided by experience than by the complex prescriptions available in the literature. In this paper, I shall try to make a little progress towards distinguishing and quantifying 'supply' and 'demand' as a basis for improving the calculation of irrigation need and the timing of water applications.

SUPPLY

Not surprisingly, we know far more about the architecture, functioning and growth of foliage than about the corresponding properties of root systems. Sampling roots is a very tedious exercise and their penetration through soil cannot be observed without destroying them or

---

† Permanent address: University of Nottingham School of Agriculture, Sutton Bonington, Loughborough, Leicestershire LE12 5RD, U.K.

observing them through a glass darkly. What *is* surprising is that relatively few attempts have been made to interpret records of changes in soil water obtained by neutron moderation in terms of the downward movement characteristic of the root system of an annual crop and of the ability of an established root profile to extract water from the surrounding soil. Perhaps this is because most models of water uptake by roots (Tinker 1976; Molz 1981) deal with the radial diffusion of water from wet soil towards a stationary absorbing cylinder rather than with the movement of roots toward new sources of water that are deeper in the soil.

It is possible to estimate the rate at which a growing root system extracts water by combining models for the behaviour or a static root system with a function describing the downward penetration of roots. For simplicity, I have chosen a relation between the water content, θ (cm water per cm^3 soil), and time, t (d), suggested by Passioura (1983), namely,

$$\theta = \theta_a \exp(-klt), \tag{1}$$

where l is rooting density expressed in cm root per cm^3 soil and k is a constant with the dimensions of a diffusion coefficient (L^2T^{-1}). Because $\theta = \theta_a$ when $t = 0$, and $\theta = 0$ when t is infinite, θ_a can be defined as the maximum amount of water that roots are capable of extracting from the surrounding soil. The quantity $1/kl$ can be regarded as a time constant, the time needed for θ to decline to $\exp(-l)$ of its initial value.

At any depth z in the soil accessible to the root system, roots moving downward arrive at a time $t(z)$. I assume that when $t < t(z)$, $l = 0$ and $\theta(z) = \theta_a(z)$. For all values of $t > t(z)$, l has a fixed value and $\theta(z)$ decreases according to (1). This is not an unrealistic model of a growing root system because there often appears to be relatively little change in the root length at a specific depth once the front has moved deeper (Gregory *et al.* 1978; Gregory & Squire 1979).

To test this model and to obtain estimates of constants as a function of depth, I analysed measurements of soil-water extraction under sorghum and millet growing on two types of soil at the International Crop Research Institute for the Semi-Arid-Tropics (ICRISAT). For sorghum growing during the post-rainy season either on a vertisol (black cotton soil) or on an alfisol (sandy loam over clay), (1) described the measurements well from 30 cm downwards. It was not valid above 30 cm, presumably because of direct evaporation from the soil surface and the associated diffusion of water towards the surface as it dried. In the vertisol, values of $1/kl$ decreased from *ca.* 35 d at 30 cm to *ca.* 60 d at 90 cm. Values for the alfisol were much smaller, presumably because of the greater diffusivity of soil with larger pore spaces. For millet, grown on the alfisol only, $1/kl$ was about 10 d throughout the profile.

The downward progress of the root system was defined by plotting, as a function of depth, the time after emergence at which θ began to decrease below its initial constant value θ_a. Figure 1 shows the relation between z and t for millet and sorghum grown on both soil types in four seasons. During the main period of growth, the velocity of the root system was about 3.5 cm d^{-1}, and by extrapolation this rate started about 8 d after emergence. Other workers have obtained similar results by identifying the time at which soil water content starts to decline at a particular depth. Figure 6 of Day *et al.* (1978) shows that the velocity was approximately 2 cm d^{-1} for barley growing in a cool temperature summer, and figure 7 of Angus *et al.* (1983) working on a range of tropical crops in the Philippines, shows rates ranging from less than 1 cm d^{-1} for rice to more than 4 cm d^{-1} for cowpea.

What do these velocities imply in terms of rates of water extraction? In the vertisol at

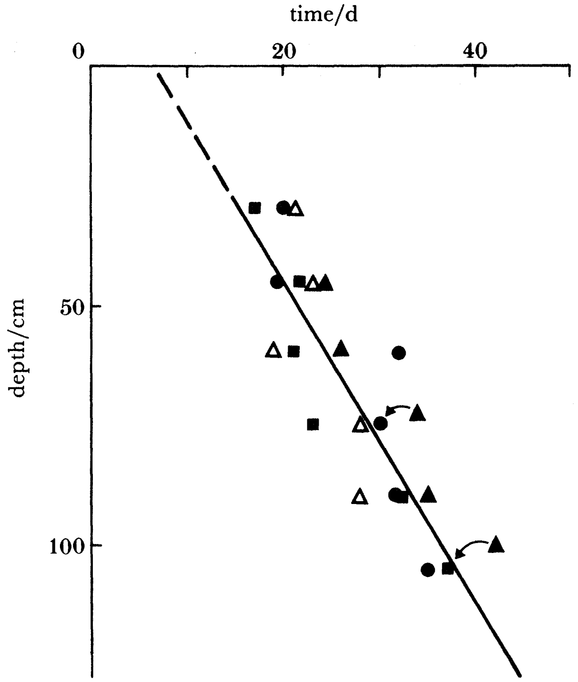

FIGURE 1. Increase in apparent depth of root front with time from emergence in three stands of sorghum (▲, alfisol; ●, vertisol) and one of pearl millet (△, alfisol) grown at the International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India. (Data supplied by Dr Piara Singh.)

ICRISAT, θ_{a} at 75 cm was about 0.16 $\mathrm{cm^3\,cm^{-3}}$ and kl was 0.015 $\mathrm{d^{-1}}$; corresponding figures for the alfisol were 0.05 $\mathrm{cm^3\,cm^{-3}}$ and 0.05 $\mathrm{d^{-1}}$. Assuming a maximum root velocity of 3.5 cm $\mathrm{d^{-1}}$, the maximum rates of extraction to be obtained from (1) are about 0.15 cm $\mathrm{d^{-1}}$ from the vertisol and 0.12 cm $\mathrm{d^{-1}}$ from the alfisol. Both rates are substantially less than the loss of water from a class A pan in the same environment – about 0.6–0.7 cm $\mathrm{d^{-1}}$. It follows that the rate of transpiration must have been limited by the supply of water to the shoots, as determined by the apparent velocity of the root front and the parameters of (1). In general, when crops grow on water stored in the soil profile, the loss of water by transpiration is likely to be limited by the rate of extraction so that the behaviour of stomata and the adjustment of water potential in cells and xylems must depend primarily on the size and activity of the root system.

DEMAND

Although the concept of a 'demand' for water imposed by the atmosphere is entrenched in the literature of crop ecology, rigorous definitions are hard to find. Demand is sometimes treated as synonymous with potential transpiration, defined by Penman (1948) as the rate at which water is lost from a short green crop, completely covering the ground and freely supplied with water. But what happens if the crop is not short or the ground cover is incomplete? Does the state of the vegetation determine the demand? And what constitutes a free supply of water? Does demand depend on supply? These difficulties can be resolved in part by using a form of the Penman equation in which the wind function is replaced by an aerodynamic resistance depending on surface roughness as well as on wind-speed, and in which a canopy resistance, r_c, is introduced to account for the diffusion of water vapour through stomatal pores (Monteith 1981). The canopy resistance depends on leaf-area index as well as on water supply, and for complete ground cover the minimum resistance for many arable crops is about 50 s m^{-1}.

It would be possible to define 'demand' as the rate of transpiration from a crop with an arbitrary minimum canopy resistance, as in the United Kingdom Meteorological Office model for soil-water balance (Gardner & Field 1983). On this basis, demand would depend partly on a set of physical variables (radiation, temperature, humidity, wind) as in the original Penman formula and partly on the canopy resistance treated as a physiological constant. This definition is still unsatisfactory for foliage not providing complete ground cover, because r_c will then exceed 50 s m^{-1} even though the crop is well watered.

I believe it may be possible to make some progress in defining 'demand' by standing the whole subject on its head. For many years, 'demand' in the form of a potential transpiration rate has been used as a guide to the amount of water needed to achieve maximum production of dry matter. Is this the right way round? Why not start from a potential rate of growth and use this figure to estimate a potential transpiration rate?

There are many ways of calculating the maximum rate of growth of a crop from the photosynthesis of individual leaves but most of them involve a large number of assumptions (about the angular distribution of leaves, for example) and include many disposable constants. Starting instead from field evidence, a very simple method of calculation can be based on the fact that during the vegetative growth of many crops, accumulated dry mass is nearly proportional to the integral of photosynthetically active radiation (p.a.r.) intercepted by or absorbed by the canopy. For C3 species growing in Western Europe, the factor for converting intercepted p.a.r. to a dry matter equivalent is about 1.5 g$(\mathrm{MJ})^{-1}$ (Monteith & Elston 1983). For C4 species growing in the tropics, it can be as large as 2.4 g$(\mathrm{MJ})^{-1}$ (Ong & Monteith 1984).

There is also a wealth of experimental evidence that the amount of water transpired by a crop in a given environment is proportional to the amount of dry matter accumulated in the same time, presumably because both quantities are tightly coupled to the amount of radiant energy received per unit field area and to the fraction of this energy absorbed by foliage as p.a.r. The amount of dry matter gained per unit of water lost is often called the 'water-use efficiency', an incongruous title because the water lost by transpiration is not 'used' metabolically, and because the quantity does not have a maximum value of unity corresponding to perfect efficiency in the thermodynamic sense. I shall therefore use the less contentious but somewhat clumsier term 'dry-matter/water ratio' (d.w.r.) with a symbol q, chosen because there is little danger of confusion with other quantities in crop ecology. Conveniently analogous quantities are the 'carbon/water ratio' for physiological studies and the 'yield/water ratio' for agronomy.

The relation between plant mass and water loss was explored by Lawes (1850) in a remarkable paper that also contains the first firm evidence that there is an energy cost for the biological fixation of nitrogen. Working with potted plants of wheat, barley, beans, peas and clover, Lawes found that the d.w.r. lay between 3.7 and 4.8 mg dry matter per gram of water. Anticipating research over the next 135 years, Lawes wrote: 'It seems to us more than probable that future experiments may fix a definite relationship between the amount of water given off and that of the non-nitrogenous proximates fixed in the plant . . . provided their source was mainly in each case the atmosphere, as in the instances of the seedling plants now under consideration . . . accumulating . . . their chief supplies during the period of the most powerful influence of heat and light upon the plants.'

A century later, Penman & Schofield (1951) made the first attempt to relate assimilation of carbon and transpiration of water by leaves to corresponding diffusion resistances. They demonstrated the existence of a large biochemical resistance for carbon dioxide responsible for 'building up of relatively high carbon dioxide gas concentrations inside the leaf – almost reaching the normal atmospheric value.' Presumably because they regarded the internal CO_2 concentrations as variable, they referred to the dry-matter/water ratio (or at least to its reciprocal) as 'normally a useless concept' with published values ranging from 0.7 to 5 mg g^{-1}. They did not refer to Lawes's contrary conclusions and Penman later made extensive use of q to analyse responses to irrigation!

Progress since 1951 has been much more rapid than in the preceding century. In his doctoral thesis, de Wit (1958) reviewed measurements of yield and water use for a larger number of experiments on crop plants grown in containers or as stands both in the western U.S.A. (for example, by Briggs and Shantz) and in the Netherlands. He demonstrated that, in a temperate climate, q was conservative for a given species but found larger differences between species than did Lawes. In a semi-arid climate, q increased with aridity as measured by the rate of evaporation from an open-water tank. Bierhuizen & Slatyer (1965) showed theoretically that a more appropriate index of aridity was the mean saturation deficit of the air, and found support from field experiments on arable crops. The same point emerged very clearly from a study of barley grown under a rain shelter at Rothamsted by Day *et al.* (1978) (figure 2) and by trials on potatoes grown in Wisconsin (Tanner 1981). Many other experiments leading to the same conclusions have been reviewed by Tanner & Sinclair (1983).

Because all irrigation is an attempt to increase the productivity of a crop by increasing its ability to lose water, it is relevant to consider the physiological basis of the dry-matter/water ratio in terms of the gas exchange of individual leaves. Briefly, the net uptake of CO_2 by an illuminated leaf surrounded by air with a CO_2 concentration of c_a can be written as

$$P = (c_a - c_i)/r, \tag{2}$$

where c_i is the concentration of CO_2 in the intercellular spaces, and r is the sum of the boundary layer resistance of the leaf to CO_2 diffusion and its stomatal resistance in series. The corresponding equation for transpiration is

$$E = A(e_i - e_a)/r', \tag{3}$$

where e_i and e_a are internal and external vapour pressure and r' is the total resistance to water-vapour diffusion. The constant A converts the vapour pressure difference into a difference in water-vapour concentration. (Strictly, equations (2) and (3) should be written in terms of differences in mixing ratio or molar concentration, but the form used here provides a simpler demonstration of basic principles.) Because the air in contact with intercellular tissue is saturated at the temperature of that tissue $(e_i - e_a)$ is the saturation deficit of the air surrounding the leaf, evaluated with respect to leaf temperature. When leaf and air are at the same temperature, $(e_i - e_a)$ is the true saturation deficit (D) of the air, a quantity that plant ecologists treat with increasing respect but which meteorological services never report.

Dividing (2) by (3) gives the ratio of net photosynthetic rate to transpiration rate as

$$P/E = (c_a - c_i)/[A'(e_i - e_a)], \tag{4}$$

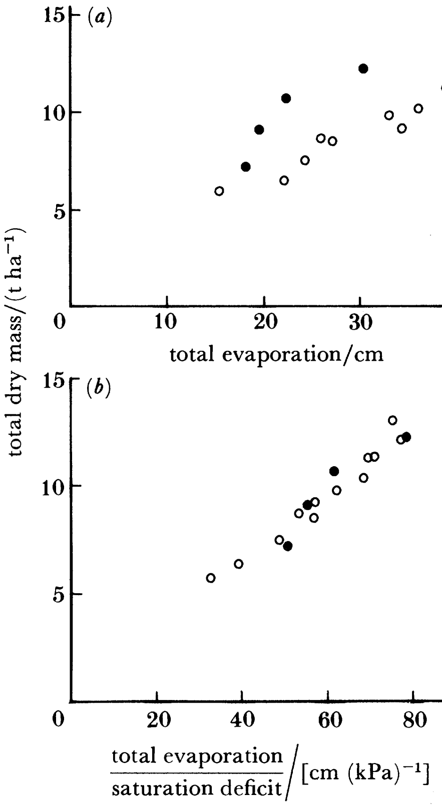

FIGURE 2. Relation between total dry-matter production for seasons 1976 (○) and 1979 (●), and corresponding water use for stands of barley grown at Rothamsted Experimental Station with rainfall excluded and water applied differentially. In (*a*), the *x*-axis shows water applied; in (*b*) it shows water applied per unit of mean saturation deficit. (Data supplied by Dr W. Day.)

where the new constant A' is the product of A and the conservative ratio of the resistances for CO_2 and water-vapour diffusion.

Equation (4) provides a physiological foundation for the evidence that $q \times D$ is a conservative quantity, but several assumptions and approximations are needed to link laboratory measurements on single leaves over a few minutes to field measurements on crop stands over a whole growing season. One major source of uncertainty was removed by the discovery that c_i/c_a is not sensitive to irradiance (above a small minimum value) or to the nitrogen status of leaves, but it has been shown to increase somewhat as D increases (Morison & Gifford 1983). From the work of Wong *et al.* (1979), c_i/c_a is often taken as 0.7 for C3 species and 0.3 for C4 species, but within these major groups the range of c_i/c_a may be substantial and may depend on environmental history in ways which are not yet understood.

Another source of uncertainty is the amount of assimilated carbon that is subsequently lost by maintenance respiration (in addition to the component recycled within leaves during daylight). If maintenance respiration were proportional to the dry mass of the stand as McRee (1983) suggested, q would be expected to decrease as the mass of the stand increased, but there is no firm evidence for a trend of this kind. The field evidence for constancy of q therefore suggests that the rate of maintenance respiration, when integrated over periods of several weeks, is nearly proportional to the net uptake of carbon by photosynthesis integrated over the same period.

The relation between q and P/E also depends to some extent on the carbohydrate composition and on the protein and fat content of plant organs. Useful conversion factors are given by Tanner & Sinclair (1983).

Finally, it is not clear how the vapour-pressure difference $(e_i - e_a)$ should be averaged over all the leaves in a canopy. Simple integration is possibly only when there are no gradients of temperature or of vapour pressure in the canopy and when all leaf tissue is at the same temperature as the surrounding air. In practice, however, the difference between leaf and air temperature may range from less than −5 °C for a well-watered crop growing in a very dry environment to more than +5 °C for a crop running short of water and exposed to bright sunshine.

In summary, the form of (4) appears to be consistent with the general observation that the dry-matter/water ratio of crop stands is conservative for a particular species (Vaux & Pruitt 1983), but is inversely proportional to the mean saturation deficit of the air to which the crop is exposed over the period when q is measured (Tanner & Sinclair 1983). However, uncertainty about representative values of c_i, rates of maintenance respiration, and microclimatic structure preclude the use of (4) to predict absolute values of q, which must therefore be determined empirically.

Having reviewed the experimental evidence for the conservatism of qD and having outlined its physiological basis, we are now ready to define the 'demand' for water by a crop stand over any specified period as follows:

$$\begin{aligned}\text{demand} &= \text{amount of water transpired by a stand when water is freely available,}\\ &= (\text{rate of production of dry matter})/q.\end{aligned}$$

When the maximum accumulation of dry matter over a period can be expressed as the product of a conversion factor, e, the fraction of intercepted radiation, f, and the time integral of solar radiation (Monteith 1977), a useful operational definition of demand is

$$\text{demand} = efS/q, \tag{5}$$

which makes explicit the dependence of demand on the size of the canopy as expressed by f.

Although q may be inversely proportional to D, (5) should not be interpreted as a statement that demand is proportional to D. The primary effect of increasing D is to slow the growth of leaves, thereby decreasing f. If stomata close in response to increasing D, e must also decrease, but field evidence (Legg *et al.* 1979) suggest that this effect may be small compared with the decrease of f.

MANIPULATION OF SUPPLY AND DEMAND

We are now ready to consider how, at different stages of growth, a plant contrives to satisfy the laws of supply and demand. For simplicity, the total amount of water transpired by a plant over 24 h will be assumed to be equal to the amount absorbed by the root system, because the change in storage over this period will always be a very small fraction of the throughput.

To become established, a seedling needs to balance very carefully the gain of carbon against the corresponding loss of water, especially when the environment is hostile. Figure 3 is an attempt to represent the main features of this balance. Starting from the top, assimilate is used to produce new leaf or new root and the relative growth of these organs is determined by the need to ensure

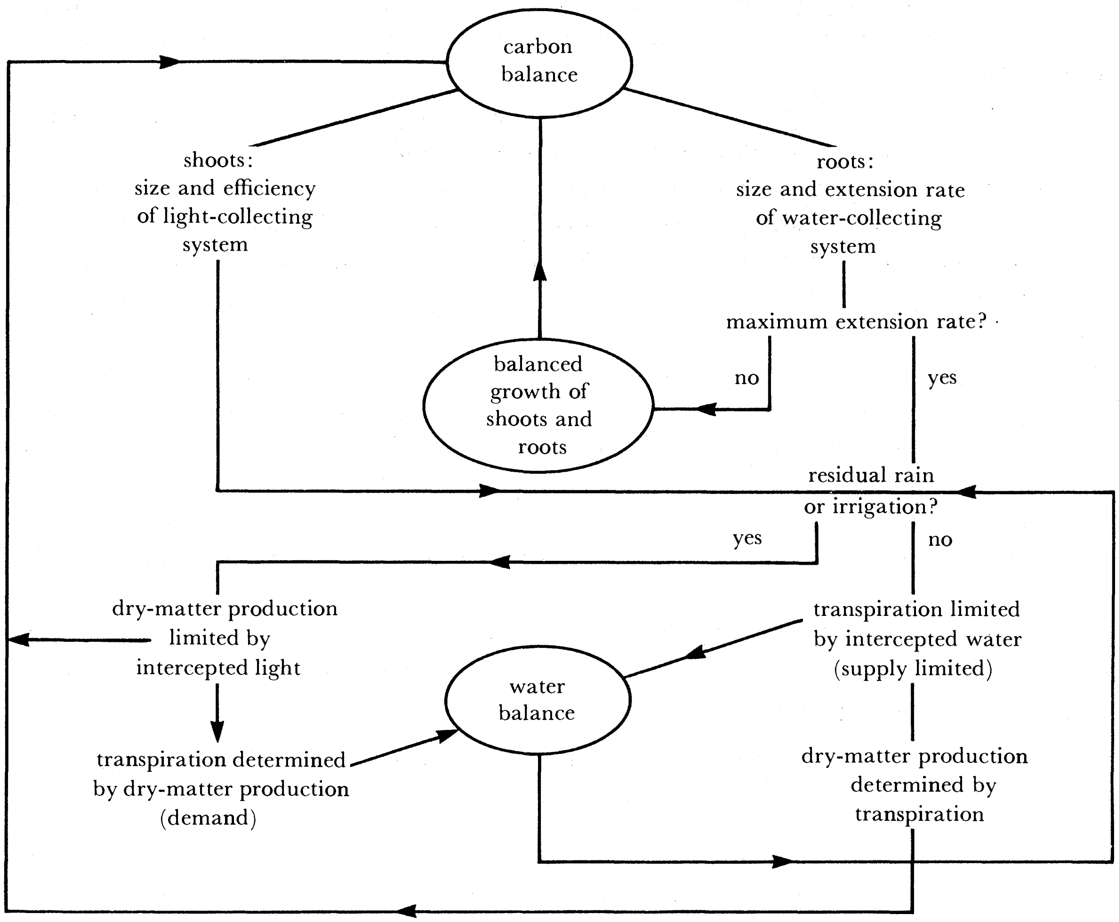

FIGURE 3. Manipulation of water supply and demand by a growing crop: see explanation in text.

that the rate of water supply as determined by the extension of the root system keeps step as far as possible with the rate of dry-matter production by foliage. If leaves grew too rapidly at the expense of roots, excessive loss of water from leaves would induce stomatal closure and would restrict the growth rate of the whole plant by restricting the photosynthetic rate (growth limited by water *supply*). If roots grew too rapidly at the expense of leaves, the rate of growth would again increase more slowly because the amount of light intercepted by a seedling is almost proportional to its leaf area (growth limited by water *demand*). When supply and demand are perfectly matched, both govern the rate of growth, which is the maximum that can be achieved for a prescribed rate of weather and soil (referred to as 'balanced growth' in figure 3). It can be shown that the optimal root density to achieve a maximum rate of seedling growth should decrease with time, and this behaviour is consistent with the observation that root density usually decreases systematically with depth.

As a seedling grows within a stand, its rate of transpiration must increase, and so must the rate of root extension, to maintain a maximum transpiration rate. Eventually a point must be reached where the root front achieves a maximum downward velocity, possibly determined by the rate of division and extension of meristematic cells near root tips. For sorghum, figure 1 suggests that a maximum rate between 3 and 4 cm d^{-1} is reached about 15–25 d after emergence. When there is no further input of water by rain or by irrigation, further growth of the plant will be limited by the supply of water (right-hand side of figure 3).

When the maximum rate of water supply is slower than the demand for water and when D is fixed, stomatal conductance must decrease until the flow of water into the roots (supplemented by changes of storage) is balanced by the loss of vapour from the leaves. An increase of D will then induce a proportional decrease of stomatal conductance. This is the basis for the so-called 'feedback' response operating through the water potential of leaf tissue. Models of plant-water relations usually represent feedback by an empirical relation between stomatal opening and plant-water potential, but in circumstances where this relation is simply a response to a conservative rate of water supply it would be more logical to model the supply system in terms of root performance rather than the complex behaviour of the stomatal valve.

Suppose now that the dry soil behind the root front is wetted by rain or by irrigation. Most crop plants respond rapidly to soil wetting by opening stomata within 24 h, and the photosynthetic rate responds equally rapidly. Under these circumstances, the rate of dry-matter production should quickly reach a maximum value determined by the amount of radiation captured by the canopy, and to a lesser extent by other weather variables, such as temperature and saturation deficit. The loss of water and the growth rate now depend on the demand for water (left-hand side of figure 3).

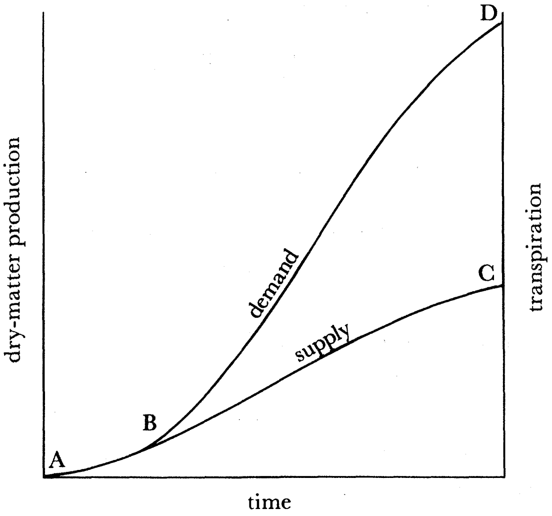

FIGURE 4. Seasonal increases of accumulated water supply and of water demand determined by accumulated dry-matter production.

Figure 4 puts these three modes of growth together. The horizontal axis represents time and the vertical axes are calibrated in dry matter or in water, related by a constant value of q. Seedling growth in a state of balance is given by the curve AB. With no input of water, growth would continue along BC at a rate slowly declining because of the decrease with depth of available water per unit soil volume. On the other hand, if the soil were re-wetted often enough, growth would follow BD, whose slope becomes constant when interception of light by the canopy is virtually complete. Approaching D, the slope may decrease because of senescence or because the production of new leaves has stopped at the beginning of reproductive growth, as in cereals.

RESPONSE TO IRRIGATION

Before moving on to the implications of figure 4 for irrigation practice, the relation between total dry mass, W, and harvestable yield, Y, must be considered. It is usually expressed by a harvest index, h, such that $Y = hW$. Fortunately for the rapid transfer of ideas from crop physiologists concerned with carbon uptake to agronomists concerned with yield, there are many arable crops for which h is a varietal characteristic, changing little from season to season. However, it does not follow that h will be independent of water supply in an irrigated system. A fractional decrease in Y in response to a shortage of water can therefore be written

$$\delta Y/Y = \delta W/W + \delta h/h. \tag{6}$$

A general relation between the fractional change in dry mass associated with a fractional change of evaporation, E, is

$$\delta W/W = \beta \delta E/E, \tag{7}$$

where $\beta = 1$ if the ratio $q = W/E$ is constant as assumed hitherto.

When δE is the difference between the maximum (or potential) loss of water by transpiration (E_p) and the actual loss E_a, then

$$\delta E = E_p - E_a \tag{8a}$$

and corresponding equations for dry matter and yield are

$$\delta W = W_p - W_a; \quad \delta Y = Y_p - Y_a. \tag{8b}$$

Combining equations (6)–(8) gives

$$(1 - Y_a/Y_p) = \beta(1 - E_a/E_p) + \delta h/h. \tag{9}$$

Variants of this equation have been used by many workers either to analyse yields from irrigation experiments or to predict irrigation need in a specified environment.

In the first category of application, irrigation trials on grass and on arable crops grown on a sandy loam at Woburn were summarized by Penman (1971), who expressed the difference between potential and actual transpiration as the difference between a theoretical maximum soil-water deficit D_m and an actual deficit D_l, where the subscript l implies a limit set by the size and activity of the root system and by the water-holding capacity of the soil.

The maximum deficit was found from

$$D_m = E_p - i,$$

where E_p is the potential transpiration, calculated from the Penman formula, and i is the input of water from rain and irrigation. The limiting deficit was found from a relation assumed between yield and water use, namely,

$$Y_a = k(i + D_l). \tag{10}$$

Paraphrasing Penman's explanation, D_l was first determined by inspection and then adjusted by trial to make Y_a proportional to $(i + D_l)$. Values of D_l are given in table 1.

Equation (10) is consistent with equation (9) only when $\delta h/h = 0$, $\beta = 1$ and $k = Y_p/E_p$, i.e. $k = hq$ for a fully watered crop. Most of the values of k determined from (10) were between 0.25 and 0.5 t dry matter ha^{-1} per centimetre of water. Taking an arbitrary harvest index of 0.5, the corresponding range of q is 0.005–0.01.

TABLE 1. VALUES OF LIMITING DEFICIT

	sandy loam[1] (Woburn) D_1/mm	clay loam[2] (Rothamsted) D_1/mm
early potatoes, clover	25	—
spring beans	30	80
spring wheat	30	140
main-crop potatoes	35	84
grass (cocksfoot), grass–clover mixture	38	—
spring barley	40	100
Italian ryegrass	50	—
sugar beet	100	—
lucerne	110	—

[1] Data from Penman (1971).
[2] Data from French & Legg (1979).

In 1964, Penman began irrigation trials on a flinty silty clay loam at Rothamsted and measurements for the 13 seasons to 1976 were analysed by French & Legg (1979) and compared with the Woburn record. For a few crops, they were able to determine β from (9), having made the implicit assumption that $\delta h/h = 0$. For beans grown at Woburn, β was 1.8 compare with 1.1 at Rothamsted. Corresponding values for potatoes were 1.3 and 1.1 (not significantly different from 1.0). For barley at Woburn, β was 0.6.

From such limited evidence, it is not possible to determine whether β departed from unity because (*a*) the dry-weight/water ratio was not constant for different irrigation treatments; (*b*) the harvest index was not constant; and (*c*) E_p calculated from climatological records may be either greater or less than the water loss from a crop stand. Values of β exceeding unity imply that water stress probably imposed an irreversible check to growth. The most common type of check is a restriction in the expansion of the canopy responsible for a loss of light energy (decrease of f in equation (5)), but after a period of more severe stress, the efficiency of photosynthesis (represented by e in equation (5)) may not return to its original value. Even without anomalous changes in f or e, a decrease in harvest index following drought ($\delta h/h > 0$) would make β appear to exceed unity if $\delta h/h$ was assumed to be zero in (9). A value of β less than unity implies an improvement in the performance of the plant in response to drought, probably as a consequence of an increase of harvest index. In cereals and grain legumes, harvest index can increase when assimilates stored in stems are used to fill grains when photosynthesis is checked by a shortage of water after anthesis (Gregory & Squire 1979).

In the United States, variants of (9) have been used extensively, both for the analysis of yields from irrigation trials and to predict irrigation need (Hanks 1974; Stewart *et al.* 1977). The same equation was adopted by Doorenbos & Kassam (1979) in a comprehensive F.A.O. report on *Yield responses to water*, which reviewed work on a large number of irrigated crops (but did not refer to Penman's unique set of trials at Woburn and Rothamsted). Rather than starting from the conservative nature of the dry-matter/water ratio, as de Wit and Penman did, Doorenbos & Kassam calculated potential yield Y_m and potential evaporation E_m by two unrelated methods. First, the maximum dry mass W_m was found from a model based on solar radiation and temperature, and this quantity was multiplied by a crop-specific harvest index to obtain Y_m. The corresponding value of E_m was estimated either from the Penman equation for open-water evaporation or from pan evaporation, in each case by applying coefficients which changed during the season to allow for changes in ground cover initially and for senescence before harvest. Actual evaporation, E_a, was then determined from the total amount of water held in the root zone, from a 'soil-water depletion factor' depending on E_m, and from the frequency of irrigation. Finally, values of β for specific types of crop at specific stages of development were obtained from a table based on experimental evidence. This is a lengthy procedure: even when E_m is estimated from pan records, figures must be extracted from 13 tables before Y_a can be determined for a given irrigation régime.

In the work considered so far, the dry-matter production and yield of a crop were assumed to be linear functions of the loss of water during growth either by transpiration alone or by the sum of transpiration and soil evaporation. Jensen (1968) and others preferred to use exponential relations that can be derived by assuming

$$\mathrm{d}Y/\mathrm{d}E = \beta'(Y/E), \tag{11}$$

(cf. equation (7)), which can be integrated to give

$$(Y_a/Y_p) = (E_a/E_p)^{\beta'}. \tag{12}$$

In an extension of this method, (Y_a/Y_p) is expressed as the product of a series of terms $(E_a/E_p)_i^{\beta_i'}$ where the subscript i identifies values of (E_a/E_p), and of β for specific stages of growth. The main objection to this procedure is that the values of β' cannot be interpreted in terms of measurable physical or physiological variables and are probably specific to experimental design and to season.

The form of analysis proposed earlier in this paper is a step towards combining the relative simplicity of Penman's approach (which depends on the experimental determination of a dry-matter/water or yield/water ratio, treated as conservative) with seasonal differences in water supply and demand which are a central feature of the Doorenbos & Kassam method.

Figure 5 demonstrates how my scheme might be used to estimate irrigation need and the optimal scheduling of irrigation. The first implication is that water should be applied at the critical point where the demand, as determined by the photosynthesis of foliage, exceeds the supply, as determined by the extension of the root system. To minimize the direct loss of water from the soil surface as well as minimizing labour costs, the number of irrigations should be as small as possible, implying that water should be applied not before the critical point but as soon as possible thereafter, to avoid an irreversible loss of dry matter and usually of yield.

In figure 5, water is applied at B to stop the crop growing along BH at a supply-limited rate. This early irrigation should not exceed the amount extracted by roots (BE) plus direct evaporation from the soil surface shown as EF. Excess (FG) will be lost by drainage or runoff. Growth then proceeds along FH parallel to the corresponding portion of the demand-limited curve above it until the supply line is met at H, where all the applied water is exhausted. A second amount of water is then applied – HI – insufficient to wet the whole profile, but allowing growth to continue at a maximum (demand-limited) rate. The next phase of growth ends at the critical point J, after which no further water is applied in this example and the crop is harvested at C. The total amount of water transpired and the total dry matter accumulated are given by LK, which is CK (water extracted and corresponding growth without irrigation) augmented by the amount reaching the root zone after two irrigations, i.e. LC = BF + HI.

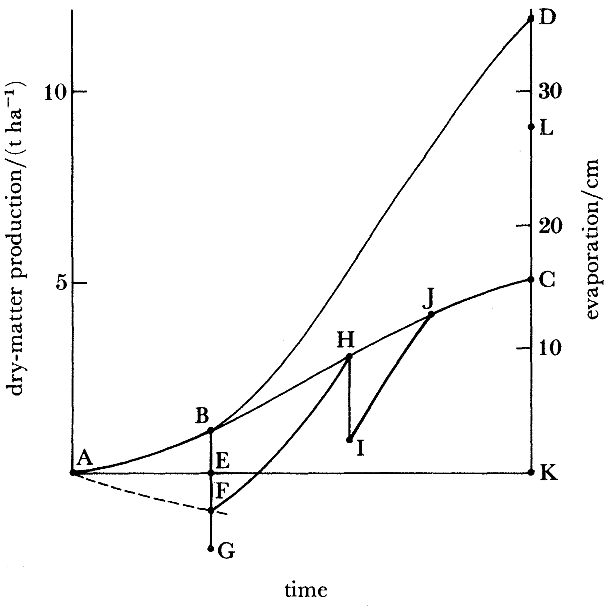

FIGURE 5. As figure 4, but irrigation applied as described in text. Assumed ratio of dry-matter production to evaporation is $q = 1/300$.

In the absence of irrigation, the total amount of water transpired would be CK and this quantity is equivalent to Penman's limiting deficit D_1. The maximum deficit D_m is given by the maximum possible water loss DK less the input of water LC, and the loss of dry matter as a result of inadequate watering is given by $D_m - D_1 = \mathrm{DK} - \mathrm{LC} - \mathrm{CK} = \mathrm{DL}$.

This scheme can be simplified by representing the supply and demand functions as two straight lines with appropriate slopes and intercepts; or it can be made more exact by keeping a day-by-day check of the soil water balance with the use of a computer program.

RÉSUMÉ

Traditional methods of calculating the irrigation need of a crop are based on the notion that a potential transpiration rate determined by the state of the atmosphere establishes a demand for water from transpiring leaves that roots may or may not be able to meet. Because the dry-matter/water ratio is usually conservative and stomatal control appears to be intimately related to carbon exchange, it seems more logical to express demand as the water equivalent of maximum dry-matter production. This procedure greatly simplifies the amount of information needed to estimate demand, as well as clarifying the distinction between supply and demand.

The procedure can be applied graphically (as in figure 5), analytically, or numerically, to estimate the rate of dry-matter production at any time during the growing season. This information may help to throw light on the sensitivity of yield to water stress at different stages of development. A theoretical basis for interpreting measurements of sensitivity is urgently needed to attack one of the central problems or irrigated agriculture: how to achieve the maximum yield (or the maximum economic return) from limited reserves of water.

I am grateful to the National Academy of Sciences and the National Research Council for a Senior Research Associateship while at Goddard Space Flight Center; to Dr Piara Singh of the International Crops Research Institute for the Semi-Arid Tropics for the measurements of soil water used to derive figure 1; and to Dr Bill Day of Rothamsted Experimental Station for figure 2.

References

Angus, J. F., Hasegawa, S., Hsiao, T. C., Liboon, S. P. & Zandstra, H. G. 1983 The water balance of post-monsoonal dryland crops. *J. agric. Sci., Camb.* **101**, 699–710.

Bierhuizen, J. F. & Slatyer, R. O. 1965 Effect of atmospheric concentration of water vapour and CO_2 in determining transpiration–photosynthesis relationships. *Agric. Meteorol.* **2**, 259–270.

Brouwer, R. 1983 Functional equilibrium: sense or nonsense? *Neth. J. agric. Sci.* **31**, 335–348.

Charles-Edwards, D. A. 1982 *Physiological determinants of crop growth.* Sydney: Academic Press.

Day, W., Legg, B. J., French, B. K., Johnston, A. E., Lawlor, D. W. & Jeffers, W. de C. 1978 A drought experiment using mobile shelters. *J. agric. Sci., Camb.* **91**, 599–623.

Doorenbos, J. & Kassam, A. H. 1979 Yield response to water. *F.A.O. irrigation and drainage paper.* Rome: F.A.O.

French, B. K. & Legg, B. J. 1979 Rothamsted irrigation 1964–76. *J. agric. Sci., Camb.* **92**, 15–37.

Gardner, C. K. M. & Field, M. 1983 An evaluation of the success of MORECS in estimating soil moisture deficits. *Agric. Meteorol.* **29**, 269–284.

Gregory, P. J., McGowan, M., Biscoe, P. V. & Hunter, B. 1978 Water relations of winter wheat: growth of the root system. *J. agric. Sci., Camb.* **91**, 91–102.

Gregory, P. J. & Squire, G. R. 1979 Irrigation effects on roots and shoots of pearl millet. *Expl. Agric.* **15**, 161–168.

Hanks, R. J. 1974 Model for predicting plant yield as influenced by water use. *Agron. J.* **66**, 660–665.

Jensen, M. E. 1968 Water consumption by agricultural plants. In *Water deficits in plant growth* (ed. T. T. Kozlowski), vol. I, pp. 1–22. New York: Academic Press.

Lawes, J. B. 1850 Experimental investigation into the amount of water given off by plants during their growth. *J. hortic. Soc. Lond.* **5**, 38–63.

Legg, B. J., Day, W., Lawlor, D. W. & Parkinson, K. J. 1979 The effects of drought on barley growth. *J. agric. Sci., Camb.* **92**, 703–716.

McRee, K. J. 1983 Carbon balance as a function of plant size in sorghum plants. *Crop Sci.* **23**, 1173–1177.

Molz, F. J. 1981 Models of water transport in the soil–plant system. *Water Resour. Res.* **17**, 1245–1260.

Monteith, J. L. 1977 Climate and the efficiency of crop production in Britain. *Phil. Trans. R. Soc. Lond.* B **281**, 277–294.

Monteith, J. L. 1981 Evaporation and surface temperature. *Q. Jl R. met. Soc.* **107**, 1–27.

Monteith, J. L. & Elston, J. 1983 Performance and productivity of foliage in the field. In *The growth and functioning of leaves* (ed. J. E. Dale & F. L. Milthorpe), pp. 499–518. Cambridge University Press.

Morison, J. & Gifford, R. M. 1983 Stomatal sensitivity to carbon dioxide and humidity. *Plant Physiol.* **71**, 789–796.

Ong, C. K. & Monteith, J. L. 1984 Responses of pearl millet to light and temperature. In *Agrometeorology of sorghum and millet* (ed. S. M. Virmani & M. K. V. Sivakumar), pp. 129–142. International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India.

Passioura, J. B. 1983 Roots and drought resistance. *Agric. Wat. Management* **7**, 265–280.

Penman, H. L. 1948 Natural evaporation from open water, bare soil and grass. *Proc. R. Soc. Lond.* A **193**, 120–145.

Penman, H. L. 1971 *Irrigation at Woburn.* Report of Rothamsted Experimental Station, 1970, part 2, pp. 147–170.

Penman, H. L. & Schofield, R. K. 1951 Some physical aspects of assimilation and transpiration. *Symp. Soc. exp. Biol.* **5**, 115–129.

Stewart, J. I., Cuenca, R. H., Pruitt, W. O., Hagan, R. M. & Tosso, J. 1977 *Determination and utilization of crop water production functions for principal Californian crops.* W-67 Calif. Contrib. Project Report, University of California, Davis.

Tanner, C. B. & Sinclair, T. R. 1983 Efficient water use in crop production. In *Limitations to efficient water use.* (ed. H. M. Taylor, W. R. Jordan & T. R. Sinclair), pp. 1–27. American Society of Agronomy, Madison, Wisconsin.

Tanner, C. B. 1981 Transpiration efficiency of potato. *Agron. J.* **73**, 59–64.

Tinker, P. B. 1976 Transport of water to plant roots in soil. *Phil. Trans. R. Soc. Lond.* B **273**, 445–461.

Vaux, H. J. & Pruitt, W. O. 1983 Crop-water production functions. In *Advances in irrigation* (ed. T. T. Kozlowski), pp. 61–97. New York: Academic Press.

de Wit, C. T. 1958 *Transpiration and crop yields.* Versl. Landbouwk. Onderz. 64, no. 6: Institute of Biological and Chemical Research on Field Crops and Herbage, Wageningen.

Wong, S. C., Cowan, I. R. & Farquhar, G. D. 1979 Stomatal conductance correlates with photosynthetic capacity. *Nature, Lond.* **282**, 424–426.

Discussion

D. J. Greenwood (*National Vegetable Research Centre, Wellesbourne*). I want to refer to that part of Professor Monteith's argument dealing with growth when it is not limited by lack of water. I quite accept that when radiation intensities are low, photosynthetic rate can be proportional to the intensity of radiation. What impresses me is the extent to which measured increases in total plant dry mass appear to be buffered against substantial variations in temperature and radiation. Growth may often be limited by feedback mechanisms within the plant, and in particular by sink strengths. Their importance is well illustrated by the considerable reductions in growth rate that can be brought about by removing tubers of potatoes, seeds of grain crops and fruit of fruit crops. These treatments reduce the sink size; have no influence on the photosynthetic apparatus and yet reduce rate of dry-matter increase. Sink strength is roughly determined by plant mass. I think that growth rate may often be primarily determined by plant mass reflecting the plants' capacity to metabolize photosynthate, and that the effects of variation in intensity of radiation can be of secondary importance. Maybe this could be an alternative explanation for at least some of Professor Monteith's results.

Our work does, however, support the treatment of root penetration. We have found that the depth of 90 % rooting of some vegetable crops is linearly related to total plant mass of the above-ground parts.

J. L. Monteith. Dr Greenwood's thesis that growth rate is determined primarily by plant mass rather than vice versa may sometimes appear to be supported by the performance of individual plants growing more or less in isolation – as do some of the vegetables he is familiar with. This does not necessarily prove that sink size limits photosynthesis; I believe it simply demonstrates that photosynthesis *per plant* depends on light intercepted per plant, which depends on plant size in the absence of shading between individuals. For arable crops growing as a stand with fairly complete ground cover, many field trials show that growth rate *per unit of field area* stays approximately constant as mass per unit field area increases by a factor five or more, simply because the interception of light is approximately constant (and I think Dr Greenwood demonstrated this point very well in one of his own papers!). I am always worried about the interpretation of experiments in which parts of plants are removed in an attempt to demonstrate source–sink relations. Why should amputation not have traumatic consequences for plants as for animals?