Theoretical Production Ecology: reflections and prospects

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1 Conservative behaviour in the response of crops to water and light

J.L. Monteith

1.1 Transpiration and crop yields

Transpiration and Crop Yields was the first major monograph that de Wit (1958) published when he returned to Wageningen from Burma. It revealed his skill in using theoretical ideas to reinterpret and illuminate measurements which had been gathering dust for years on the shelves of libraries; and it demonstrated the value of the physicist's approach to the analysis of field experiments in contrast to the statistician's. Physicists analyse systems by looking, in the first instance, for consistency and reproducibility in behaviour. Statisticians often seem more concerned with establishing whether differences and anomalies in behaviour are 'significant' or not!

Clearly, crop ecology has no constants in the physicist's sense but it has yielded a number of useful conservative quantities that have played a major role in the models developed by de Wit, by his Wageningen colleagues and by their many disciples in other parts of the world. I have chosen the subject of transpiration and crop yields partly because it illustrates the principle of conservatism so well, partly because it was expounded to me by Kees de Wit the first time we met in 1959, and partly because the relation between rainfall and crop growth is fundamental to food production in the semi-arid tropics where I now work.

1.2 Hindsight and foresight

Although Woodward (1699) gets credit for the first publication dealing with transpiration and assimilation by plants, J.B. Lawes (1850) was probably first to explore the subject in terms of agricultural production. In a somewhat protracted report to the Horticultural Society of London, he described growing wheat, barley, beans, peas and clover in pots which he weighed regularly to estimate transpiration and eventually harvested to determine production. The gain in dry weight per unit loss of water (a ratio referred to as C/E hereafter) differed much less between species than the absolute gain in dry weight. He therefore expressed the hope 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 sources were mainly...in the atmosphere'.

The first major investigation of the relation between transpiration and production in arable crops was by scientists working in the Great Plains of the U.S.A. between 1910 and 1930. De Wit made extensive use of measurements by Briggs & Shantz (1914) and by Kiesselbach (1916), an acute observer who laid the founda-

tion for much future research. In addition to demonstrating that C/E was a function of the drying power of the atmosphere as measured with an evaporation pan, Kiesselbach explored the relation between transpiration and leaf temperature, the way in which transpiration by foliage in a stand humidifies the microclimate, the difference in C/E between what we now refer to as C_3 and C_4 species ('approximately double'), and the lack of correlation between leaf anatomy and C/E for sorghum and maize. The final section of his summary is worth quoting because it anticipated by nearly 20 years the major advance made by Penman (1948) in the physics of natural evaporation as well as much subsequent work in the Department of Theoretical Production Ecology at Wageningen Agricultural University.

Transpiration appears to be a purely physical phenomenon, depending primarily upon the moisture supply in the leaf and the evaporating power of the atmosphere, which is modified in some degree by temperature effects resultant within the leaf from chemical activity, transpiration, and from the absorption of radiant energy.

Penman's own attitude to C/E was ambivalent. A key paper by Penman & Schofield (1951) drew attention to the fact that the rate of carbon assimilation by plants was much smaller than predicted from the assumption that the concentration of CO_2 in intercellular spaces (c_i) was zero. Laboratory measurements demonstrating the conservatism of c_i were still far in the future, so it was perhaps not surprising that Penman & Schofield described C/E as a 'normally useless concept'. They showed foresight in concluding that 'a luxuriant crop grows with a concentration of gaseous CO_2 inside the leaf which in only 10 to 20% less than that in outside air'. In hindsight, they failed to appreciate the finer points of stomatal control of gas exchange when they wrote '...it is obvious that in many assimilation problems all that need be known about stomata is whether they are open or shut'!

De Wit's monograph, the next major publication in this field, and still a standard reference, quotes Penman's conviction that 'there is little value in the concept of "transpiration ratio"'. De Wit demonstrated convincingly that this view was wrong (but was too diplomatic to make the point explicitly!). I never heard Penman admitting that de Wit had persuaded him to change his mind, but the fact remains that his later analysis of irrigation experiments at Woburn and Rothamsted, started in 1951, showed clearly that C/E was conservative and he used this fact to establish a limiting water deficit below which loss of dry matter was proportional to the amount of water lacking for transpiration (Penman, 1970).

De Wit re-examined the role of stomata in determining both transpiration and carbon assimilation, used a Penman-type equation to estimate transpiration and developed a new formula for crop photosynthesis – the origin of much subsequent modelling and experimental work in the Department of Theoretical Production Ecology. However, he was unable to link assimilation and transpiration directly,

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because so little was then known about the connection between stomatal conductance and c_i. Instead, he reanalysed measurements of dry matter production (or yield) and transpiration for a wide range of species and sites where plants were grown either as groups in containers or as stands in the ground. He showed that in cool, temperate climates, production increased in proportion to transpiration up to a ceiling, whereas in hot climates it was necessary to divide transpiration by pan evaporation to obtain consistent proportionality. This conclusion neatly summarized a bewildering mass of evidence, extracting from it a few simple conservative quantities.

1.3 New perspectives

1.3.1 Single leaf model

In the 30 years following the publication of de Wit's monograph, understanding of how photosynthesis and transpiration are coupled expanded rapidly, stimulated by the development of highly sensitive and stable CO_2 analysers, portable porometers and other convenient equipment that plant physiologists can use either in the laboratory or in the field.

The first major advance was made by Bierhuizen & Slatyer (1965) whose measurements with several common crop species in the laboratory established that photosynthetic rates were approximately proportional to transpiration rates divided by the mean saturation vapour pressure deficit of the ambient air (D_a). Saturation deficit therefore replaced the rate of pan transpiration which de Wit had used as a surrogate for the drying power of air. Rijtema & Endrödi (1970) soon demonstrated that the mean rate at which stands of potato accumulated dry matter was proportional to E/D_a but crop physiologists and agronomists were somewhat slow to grasp the significance and usefulness of this relation. Similar evidence for a number of cereal and legume species has been reviewed by Tanner & Sinclair (1983) and by Monteith (1989).

To explore this line of work, I begin with gaseous exchange by a single leaf and then proceed to a homogeneous canopy treated as a 'big leaf' to avoid the complexities of canopy microclimate which are not relevant at this level of analysis.

For a single leaf,

$$E = \rho_w (e_i - e_a)/(p \, r_s)$$

Equation 1

where e_i is the partial pressure of water vapour in air within intercellular spaces, usually identified as the saturation vapour pressure at the temperature of mesophyll tissue (Pa); e_a is the partial pressure of water vapour of air in contact with the epidermis; ρ_w is density of water vapour at atmospheric pressure and at the mean temperature of the system (g m^{-3}); p is the atmospheric pressure (Pa); and r_s is the resistance of the epidermis to water vapour diffusion, usually treated as a stomatal component when this is much smaller than the cuticular component (s m^{-1}).

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For most types of green leaf, it is legitimate to neglect small differences of temperature that may exist between the mesophyll tissue of a leaf and its epidermis so that $(e_i - e_a)$ can be replaced by the saturation deficit of air in contact with the epidermis (D_e).

The flux of CO_2 assimilated by a leaf, as measured net of photorespiration, can be expressed similarly as

$$N = \rho_c (c_e - c_i)/(p \, r_s')$$
Equation 2

where c_e is the partial pressure of CO_2 in air at the epidermis of a leaf (Pa); c_i is the partial pressure of CO_2 in the intercellular spaces; ρ_c is the density of CO_2 at atmospheric pressure and at the mean temperature of the system (g m^{-3}); and r_s' is the resistance to the diffusion of CO_2 through the epidermis (s m^{-1}). If the rate of photorespiration is R, the *gross* uptake of CO_2 proceeds at the rate

$$N + R = \rho_c \, c_i/(p \, r_x)$$
Equation 3

an equation which defines r_x, a carboxylation resistance (Goudriaan et al., 1985). If c_e is set equal to c_i so that N becomes zero, Equation 3 reduces to

$$R = \rho_c \, \Gamma/(p \, r_x)$$
Equation 3a

where Γ is a minimum intercellular pressure of CO_2, in effect, the decrease in partial pressure across r_x associated with photorespiration. Eliminating N and R from Equations 2 to 3a leads to an equation given by Goudriaan et al. (1985) in the form

$$c_i = f(c_e - \Gamma) + \Gamma$$
Equation 4

The important ratio

$$f = (c_i - \Gamma)/(c_e - \Gamma) = r_x/(r_x + r_s')$$
Equation 5

behaves conservatively when the environment of a leaf is changed in a way that affects r_x directly, e.g. through changes of leaf illumination or nutrient status (Goudriaan & van Laar, 1978; Wong et al., 1978) or even through exposure to SO_2 (Kropff, 1987). The implication is that r_s' changes more or less in proportion to r_x, giving values of f which range from around 0.3 for C_4 species to around 0.7 for C_3.

The converse is not generally true: environmental changes with a direct effect on r_s' do not necessarily induce proportional changes in r_x so in this case f is influenced by the state of the environment. The evidence can be summarized by appeal to experiments in which at least two of E, c_i and r_s' were monitored when the saturation deficit of ambient air, D_a, was increased. Two regimes can be distinguished:

– one for small values of D_a up to a limit D_l, often around 1 kPa but extending to 2 kPa in the measurements of Rawson et al. (1977). E increases almost in proportion to D_a implying that r_s is conservative so that c_i and N are also conservative

- and one for values of D_a above D_l, but below some upper limit D_u, usually poorly defined. E becomes almost independent of D_a at a rate determined by the ability of the root system to capture water (see Ackerson & Kreig, 1977, for an example). Consequently, r_s increases almost in proportion to D_a but the fashion for plotting the reciprocal of r_s against D_a (e.g. Bunce, 1985) obscures this fact. In this regime, c_i and N decrease (Sharp & Boyer, 1986; Cooper et al., 1988) implying either that r_x remains constant or that it increases more slowly than r_s. In either case, f decreases as D_a increases.

The conservative nature of f and of Γ, at least when plants have a good water supply or when the water demand is not very large, has major implications for the ratio N/E because Equations 1, 2 and 4 can be combined to give

$$N\,D_a/E = (c_c - \Gamma)\,(1 - f)\,(\rho_c\,r_s)/(\rho_w r_s') \qquad \text{Equation 6}$$

The ratio of densities ρ_c/ρ_w is 2.44 and for molecular diffusion through stomata r_s'/r_s is usually taken as 1.60. The term in square brackets therefore has a constant value of $z = 1.53$.

The quantity $N\,D_a/E$ should therefore be conservative in the absence of stress; with mild stress, it will increase somewhat if f decreases. With severe stress, both f and Γ may increase so that $N\,D_a/E$ decreases.

1.3.2 Canopy (big leaf) model

Following the procedure of Tanner & Sinclair (1983), Equation 6 can be applied to a uniform stand of vegetation rather than a leaf and to rates of dry matter production (C) rather than of net photosynthesis (N). This transformation involves a number of major assumptions but they lead to a conclusion fully consistent with the evidence that $C\,D_a/E$ is conservative in the field.

A major assumption is that Equations 1 to 6 which pertain to a single leaf can be applied to a canopy of leaves of different age and exposed to a range of radiation, temperature and saturation deficit according to the structure of the microclimate and the architecture of the foliage. This simplification, supported both by experiment and by theory (Monteith, 1981), leads to an equation for canopy transpiration analogous to Equation 1, viz.

$$E = \rho_w\,D_0/(p\,r_c) \qquad \text{Equation 7}$$

where r_c is the canopy resistance to the diffusion of water vapour analogous to the stomatal resistance of a single leaf; and D_0 is the saturation deficit of air at the effective level of the vapour source.

(Equation 7 is a link between alternative forms of the Penman equation in which the effective wetness of vegetation is allowed for by introducing either a diffusion resistance r_c or a saturation deficit D_0.)

Extending the analogy between leaf and canopy to carbon dioxide, the net rate of photosynthesis by a canopy can be written as

$$N = \rho_c\,(c_0 - c_{ic})/(p\,r_c') \qquad \text{Equation 8}$$

an equation in which concentrations and fluxes need to be carefully identified. The resistance r_c' is the effective resistance of the canopy for the diffusion of CO_2 through stomata and is therefore the analogue of r_c for water vapour. The concentration of CO_2 at the effective surface of the canopy (c_0) can be found from the concentration at the reference height c_a using the relation

$$c_0 = c_a - (N\, r_a p/\rho_c)$$ Equation 9

where r_a is the resistance to the diffusion of CO_2 between the reference height and the level of the effective sink for CO_2 within the canopy. Later, this level is assumed to be identical for CO_2, water vapour and heat on the grounds that exchanges of all three entities are dominated by the absorption of radiation. Because the resistances r_c and r_c' both pertain to molecular diffusion through stomata, it is logical to assume that $r_c'/r_c = r_s'/r_s = 1.6$.

The remaining term in Equation 8, c_{ic} is an effective intercellular partial pressure of CO_2 within the 'big leaf' formed by the canopy. This quantity can be estimated when all the other terms in Equation 8 are known, following a procedure often used for single leaves. It is then possible to define a non-dimensional parameter for a canopy with the same physiological significance as f for single leaves, viz.

$$f_c = (c_{ic} - \Gamma)/(c_0 - \Gamma)$$ Equation 10

The validity of this type of analysis is intuitive because few attempts have been made to establish the conservatism of c_{ic} and f_c experimentally. Values of c_{ic} estimated from profiles of water vapour and carbon dioxide over a field of wheat ranged from about 19 to 25 Pa (Monteith, 1963).

Estimating f_c in the absence of water vapour and CO_2 profiles is possible when the ratio of dry matter production to transpiration is known. To follow this route, it is first necessary to estimate the dry matter equivalent of the net CO_2 flux using factors proposed by Tanner & Sinclair (1983), viz. x_1 is the mean mass of plant material synthesized per unit of CO_2 assimilated, as estimated from the work of Penning de Vries (1975) (see Table 1); x_2 is the fraction of daily integral of N remaining after accounting for maintenance respiration, assumed to be 0.6; and x_3 is the fraction of accumulated dry matter harvested (which usually excludes roots, dead leaves, etc.) assumed to be 0.80.

Then the rate of dry matter production (in $g\, m^{-2}\, d^{-1}$) corresponding to a net photosynthesis rate of N is given by

$$C = x_1\, x_2\, x_3 N$$ Equation 11

Equations 7, 8, 10 and 11 can now be combined to give

$$C\, D_0/E = z\, x_1\, x_2\, x_3\, (c_0 - \Gamma)\, (1 - f_c)$$ Equation 12

Two difficulties remain. First, unlike C and E, D_0 cannot be measured directly, but from Equation 7, D_0/E is defined by the value of r_c which can be estimated in a number of ways. Second, Equation 12 is valid for instantaneous rates of photo-

Table 1. Values of $\bar{C}\,\bar{D}_a/\bar{E}$ and e reported for three crop types (Monteith, 1989) and of parameters used in model.

Crop type	Reported values		Assumed values		
	$\bar{C}\,\bar{D}_a/\bar{E}$ (g kg^{-1} kPa)	e (g MJ^{-1})	e (g MJ^{-1})	Γ (Pa)	x_1
C$_4$ cereals	8.3–9.5	1.2–1.7	1.5	0	0.51
C$_3$ cereals'	2.9–3.1	1.0–1.3	1.2	5	0.51
C$_3$ legumes*	3.9–4.8	0.6–0.75	1.0	5	0.41

Excluding groundnut.

synthesis and transpiration, whereas C and E are usually measured as daily mean rates for periods of a week or longer. Because all the terms in the expression $C\,D_0/E$ depend on the diurnal cycle of radiation, they are strongly correlated. It follows that the value of this ratio derived from daily means of its components, i.e. $C\,D_0/E$ will generally differ from the daily mean of instantaneous values $C\,D_0/E$ as Tanner & Sinclair (1983) pointed out.

A simple model for diurnal changes of weather is needed at this stage so that several forms of the ratio dry matter/water can be compared in terms of their dependence on weather and on f_c.

1.3.3   Weather model

Solar radiation S was assumed to be a sine function of time with a maximum of S_m at noon, at phase angle increasing monotonically from 0 at sunrise to π at sunset, and a daylength of 14 h. To find the net radiation R_{ni} received by a canopy if its foliage were at air temperature, the reflection coefficient α was assumed to be 0.2 and the net long-wave loss was taken as $(S_m/900) \times L$ where $L = 100$ W m^{-2} was assumed to be the net loss to a cloudless sky from a surface at air temperature. Then the isothermal net radiation at any time is

$$R_{ni} = (1 - \alpha)\,S - (S_m/900)L \qquad\qquad \text{Equation 13}$$

The additional long-wave flux associated with the difference between foliage and air temperature was combined with the flux of sensible heat so that a single resistance could be used for heat transfer by turbulence and long-wave radiation (Monteith, 1973). The aerodynamic component of this resistance was assumed to have a value of 30 s m^{-1} characteristic of arable crops.

The air temperature at screen height was also assumed to be sinusoidal with a phase angle increasing from 0 at sunrise to π 18 h later, so that the temperature maximum occurred 2 h after noon. The difference between maximum and minimum temperature was assumed to be proportional to maximum solar radiation

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and was set at 20 °C for $S_m = 900$ W m^{-2}. Vapour pressure was assumed to be constant during the day so that the saturation vapour pressure deficit was determined by the relative humidity at dawn and the subsequent variation of air temperature.

With the diurnal change of weather specified in this way, corresponding changes in the components of dry matter/water ratios were found as follows.

In rigorous analyses, the relation between gross photosynthetic rate and the irradiance of single leaves is often assumed to be hyperbolic or exponential. As I was primarily concerned with daily totals of dry matter production and radiant energy, I made the simpler assumption that C was proportional to intercepted radiation throughout the day and took ground cover as complete. It was then possible to obtain values of the parameter $e = C/S$ from the literature (see Table 1) so that N could be evaluated as

$$N = e \, S/(x_1 \, x_2 \, x_3) \hspace{4cm} \text{Equation 14}$$

The literature contains convincing evidence (e.g. Kiniry et al., 1989) that, at least in the absence of stress, e is not sensitive to differences of environment for a particular species or group of species. Using a linear relation between C and S implies that r_c' will be somewhat overestimated in weak light and underestimated in strong light. The same proportional error then appears in r_c, so when dry matter/water ratios are calculated, resistance errors are partly self-cancelling.

The instantaneous rate of transpiration was estimated from the Penman-Monteith equation as a function of R_n, D_a, air temperature and vapour pressure, and transfer resistances. The canopy resistance for vapour transfer, r_c was evaluated as 1.6 times the CO$_2$ resistance, found by combining Equations 8, 9 and 10 to give

$$r_c' = (1 - f_c) \, (\rho_c(c_a - \Gamma)/(\rho \, N) - r_a) \hspace{3cm} \text{Equation 15}$$

with N found from Equation 14.

D_0/E was evaluated from Equation 7, knowing the value of r_c, and D_a was obtained directly from the weather model.

Changes in the dry matter/water ratio induced by a shortage of water were explored by setting an upper limit, E_m, to the hourly rate of transpiration, conveniently specified as the equivalent flux of latent heat. Using the procedure just described, the diurnal change of E was calculated first, to give the potential rate of transpiration. For hours in which E exceeded E_m, r_c was calculated from an inverse form of the Penman-Monteith equation and the net flux of CO$_2$ was calculated using $r_c' = 1.6 \, r_c$ and leaving the canopy equivalent of r_x unchanged so that f_c decreased as E_m decreased.

1.4   Output from the models

In Figure 1, four ways of calculating the dry matter/water ratio are compared, using daily solar radiation as the independent variable. Ratios are plotted on a

CE^{-1} (g kg^{-1})
$CE^{-1}D$ (g kg^{-1} kPa)
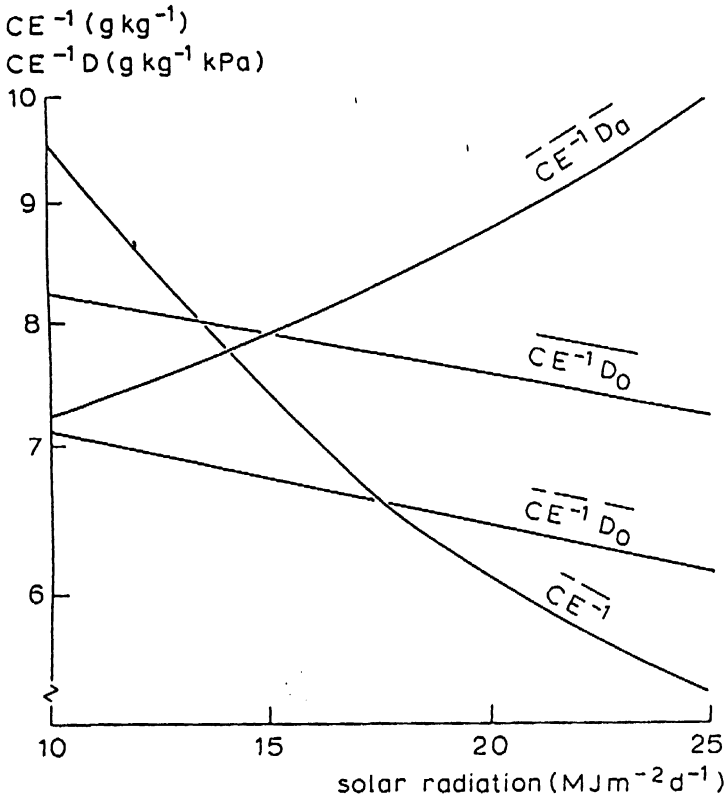
solar radiation (MJ m^{-2} d^{-1})

Figure 1. Dependence on daily totals of solar radiation of several parameters which include the ratio of dry matter production to transpiration. Bars indicate mean values of individual components or of products of components over hours of daylight. Physiological parameters were chosen for a C_4 cereal (Table 1) with $f_c = 0.3$. The weather is specified in the text. Mean daytime temperature ranged from 16 °C at 10 MJ m^{-2} to 23 °C at 25 MJ m^{-2}; dawn relative humidity was 80%.

logarithmic scale so that proportional changes can be compared in terms of relative slopes. All ratios are for a C_4 cereal and a time step of one hour was used to estimate daily mean values.

For the range of radiation chosen (10 to 25 MJ m^{-2} d^{-1}) the smallest variation (about 7%) occurs in ratios normalized by the saturation deficit in the canopy, D_0. There would be no variation in the 'theoretical' ratio $\bar{C} \bar{D}_0/\bar{E}$ if the concentration of CO_2 in the canopy remained constant, but the microclimatic model allows it to decrease with increasing radiation because of increasing photosynthesis (Equation 9). The ratio obtained from daily mean values of components ($\bar{C} \bar{D}_0/\bar{E}$) was somewhat smaller than the mean of hourly values of the ratio ($\overline{C D_0/E}$) but depended on radiation in the same way.

A much larger difference appeared when the saturation deficit at a reference height above the canopy, D_a was substituted for D_0. The normalized ratio then increased with radiation and had a range of about 16%. The reason for this increase is that the diurnal cycle of D_a depends on the diurnal variation of

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temperature imposed by the weather model, whereas the microclimatic model makes D_0 depend both on D_a and on exchanges of sensible and latent heat in the canopy. For the conditions specified, D_a increases more rapidly than D_0 during the first part of the day because the vapour pressure of air at the reference height is assumed to be constant, whereas within the canopy it increases because of transpiration. This effect overrides temperature changes, which usually act in the opposite direction, at least during the morning.

In the real world, however, the lower atmosphere will often be coupled to the underlying surface in such a way that the ratio of D_a/D_0 changes less with radiation (or temperature) than the model predicts, in which case Figure 1 would exaggerate the dependence of $\bar{C}\,\bar{D}_a/\bar{E}$ on weather. Similarly, with small plots, as used by Day et al. (1978) for example, the type of microclimate assumed here (for a horizontally uniform canopy) will not exist and foliage at all heights will be exposed to air with a saturation deficit close to D_a. Here again, the value of $\bar{C}\,\bar{D}_a/\bar{E}$ would exhibit the same weak dependence on radiation (and on temperature) as $\bar{C}\,\bar{D}_0/\bar{E}$. This may be one reason why values of $\bar{C}\,\bar{D}_a/\bar{E}$ reported in the literature are more conservative than might be expected from the evidence of Figure 1.
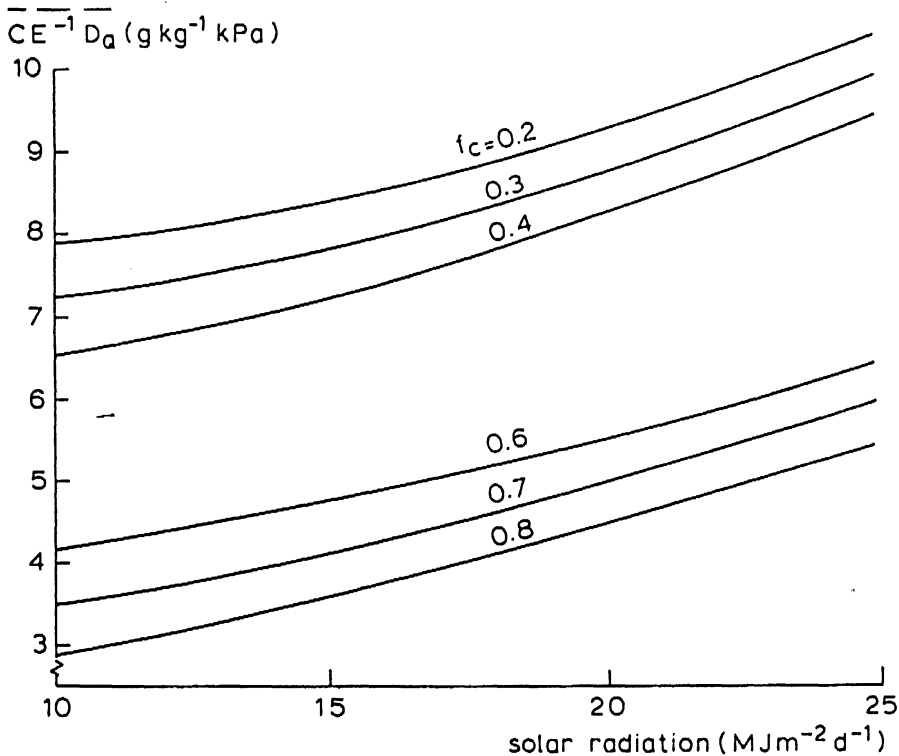

Figure 2. Dependence on daily totals of solar radiation and on f_c of $\bar{C}\,\bar{D}_a/\bar{E}$ for a C_4 (f_c = 0.2 to 0.4) and a C_3 species (f_c = 0.6 to 0.8). Mean daily temperatures corresponding to a range of 10 to 25 MJ m^{-2} were set at 16–23 °C for C_4 and 13–20 °C for C_3; dawn relative humidity was 80% (C_4) or 90% (C_3).

The value of the straight ratio C/E decreases with increasing radiation (because E depends on saturation deficit as well as on radiation) and has the largest range in Figure 1, about 28%.

Figure 2 shows how the value of $\bar{C}\,\bar{D}_a/\bar{E}$ for both C_4 and C_3 cereals depends on f_c. For sorghum, the mean measured value of the ratio is about 9 g kg^{-1}kPa and for an appropriate range of radiation (20 to 25 MJ m^{-2}d^{-1}); this is consistent with a value of f_c around 0.3, as reported for single leaves of C_4 species. The same value of f_c appears to be valid for maize, which has a somewhat larger value of e (1.75 compared with 1.5 g MJ^{-1} (Kiniry et al., 1989)), offset by a cloudier and slightly cooler environment for which radiation is usually in the range 15 to 20 MJ m^{-2}.

For wheat grown in New Zealand and for barley in the U.K., values of $\bar{C}\,\bar{D}_a/\bar{E}$ close to 3 g kg^{-1} kPa have been reported. Assuming that daily solar radiation was in the range 10 to 15 MJ m^{-2}d^{-1} for most of the growing season, it appears f_c was about 0.8. Although this is somewhat larger than the round number of 0.7 often quoted for C_3 species, it is well inside the range reported in the literature.
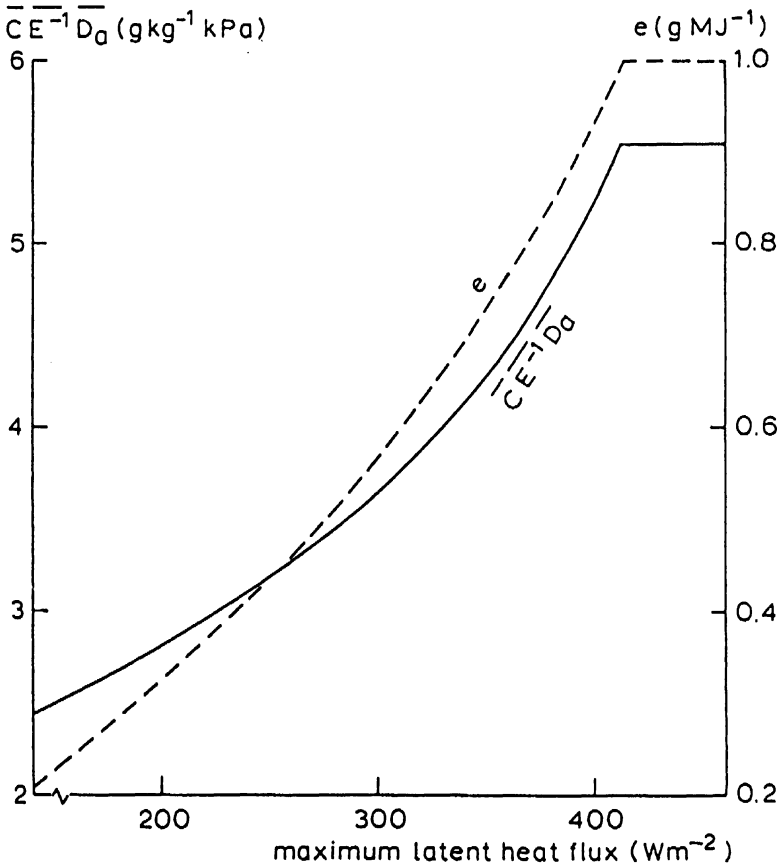

Figure 3. Dependence on maximum latent heat flux λE_m for a C_3 legume, of (e) daily mean value of dry matter per unit of intercepted radiation; and ($C\,D_a/E$) normalized transpiration ratio. Mean temperature 20 °C, radiation 20 MJ m^{-2} d^{-1}, dawn relative humidity 80%.

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For C_3 legumes grown in warm climates, values of $\bar{C}\,\bar{D}_a/\bar{E}$ are larger than for C_3 cereals (Table 1), possibly reflecting the influence of higher temperature and radiation as discussed in relation to Figures 1 and 2. Conversely, measurements of e are smaller than for C_3 cereals. To investigate whether an inadequate supply of water could account for this difference, e was assumed to have an upper limit of $1.0\ \mathrm{g\ MJ^{-1}}$ and both e and $\bar{C}\,\bar{D}_a/\bar{E}$ were evaluated as functions of λE_m, the upper limit for latent heat loss during the course of the daily cycle (Figure 3). For the weather chosen, $\bar{C}\,\bar{D}_a/\bar{E}$ decreased with λE_m below 400 W m^{-2}, because stomatal closure reduced C more than E. A value of λE_m in the range 320 to 370 W m^{-2} appears to be consistent with the values of e and $\bar{C}\,\bar{D}_a/\bar{E}$ reported for C_3 legumes (Table 1).

Although precise values of the ratios plotted in Figures 1 to 3 clearly depend on the level of variables chosen for the weather model, the general inferences drawn in this section do not depend critically on the mean values of these levels or on the specific diurnal variations they were assigned.

1.5 Postscript

In this analysis of transpiration and crop production, de Wit was the first to introduce a normalizing factor that took account of the role of atmospheric humidity. This idea was later refined by other workers and notably by his own colleagues in Wageningen whose work has benefited so much from his stimulation and encouragement.

The analysis in this paper goes one step further and is based on several clearly tenuous assumptions. However, it reaches the satisfactory conclusion that the conservative parameter f (ratio of non-stomatal to total physiological resistance to CO_2 diffusion) has similar values for single leaves in the laboratory and for canopies of the same species in the field, treated as a 'big leaf'. It also explores the implications and limitations of using the saturation deficit of air at a reference height as a convenient substitute for the value within foliage.

I am conscious that this tribute to the inspiration and guidance of an old friend lacks the rigour he has always maintained in his own work and within his Department; but at least it demonstrates an important de Wit precept that simulation modelling should be used to relate processes at two levels of organization, in this case, the leaf and the canopy. It also demonstrates that crop models that currently assume a constant value of $C\,D_a/E$ could be made more rigorous by introducing a microclimatic sub-model accounting for vertical gradients of saturation deficit and CO_2 concentration.

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