Crop Growth in Semi-Arid Environments

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Abstract

Methods are presented for analyzing growth and yield of crops when water is limiting and not limiting. Examples are given from collaborative research between ICRISAT and the University of Nottingham, UK, on pearl millet grown in a range of controlled and natural environments.

Résumé

Croissance des cultures en milieux semi-arides : *La communication présente les méthodes d'analyser la croissance et le rendement des cultures sous conditions hydriques à la fois adéquates et déficitaires. Des exemples sont tirés des études effectuées en collaboration entre l'ICRISAT et l'Université de Nottingham en Angleterre, sur le mil cultivé dans une série d'environnements allant de naturel à contrôlé.*

Introduction

The semi-arid tropics is a region distinguished by large seasonal differences in important environmental factors. Rainfall is the dominant factor and influences to varying degrees solar radiation, air and soil temperatures, and the saturation vapor pressure deficit of the atmosphere (D). Generally, crops are grown during two contrasting seasons: the rainy season, when at least part of the soil profile is periodically rewetted by rain; and the postrainy season, when there is very little rainfall and the crop usually grows on a store of water in the soil. Of the other variables, saturation deficit changes most and is most tightly coupled to rainfall. It is unusual to find large saturation deficits when rain falls frequently vice versa. However, the coupling between rainfall and D is broken for isolated patches of irrigated land, which have little effect on the atmosphere around them.

At ICRISAT Center, where mean annual rainfall is 800 mm, mean monthly D ranges from 1-4 kPa, mean daily maximum temperature from 20-30°C, and insolation from 15-24 MJ $m^{-2}d^{-1}$. In certain other areas, daily mean temperature may rise above 30°C and saturation deficits above 4 kPa (Sivakumar et al. 1984), but these are probably extreme conditions during growing seasons.

In this review, growth and yield are examined in relation to two sets of conditions within the ranges experienced at Hyderabad, India (latitude 18°N). In the first set, rainfall is frequent, and consequently soil moisture is often near field capacity and D is 1.0-1.5 kPa (10-15 millibar). In the second, the crop is sown on a soil profile near field capacity; thereafter rainfall is sparse or absent, and D is generally

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much larger, about 2-4 kPa. Different environmental factors are limiting in these different circumstances, and they are examined separately for convenience. (Where appropriate, growth and yield are also considered in relation to the independent effects of D itself).

Examples are given from work mainly on pearl millet (*Pennisetum americanum*) and groundnut (*Arachis hypogaea* L.) which forms part of a collaborative research program between ICRISAT and the Department of Physiology and Environmental Science at Nottingham University, UK. The central analysis compares five stands of the pearl millet hybrid BK 560 grown in conditions ranging from the controlled environment greenhouses at Nottingham to very dry, postrainy seasons at Hyderabad and Niamey, Niger (latitude 14°N) (Table 1).

Terms used in this paper, and units, where appropriate, are defined as follows:

e = amount of dry matter formed per unit radiation intercepted (conversion coefficient) (g MJ^{-1})
f = fraction of mean daily insolation intercepted by the canopy
lv = root length per unit soil volume (cm cm^{-3})
p = fraction of total dry matter allocated to an organ
q = amount of dry matter produced per unit of water transpired (g K^{-1})
t = time (d)
D = saturation vapor pressure deficit (kPa)
E = amount of water that the crop extracts from the soil (kg m^{-2})
K = extinction coefficient
L = leaf area index (area of foliage per unit ground area)
Lm = maximum leaf area index
S = total radiation (daily mean) (MJ m^{-2})
T = mean daily temperature (°C)
Tb = base temperature (°C)
W = dry matter production (kg m^{-2})
α = water extraction front velocity (cm d^{-1})
θ_1 = thermal duration from sowing to 0.5 f (°Cd)
θ_2 = thermal duration from sowing to maturity (°Cd)

Dry Matter Production When Water is Not Limiting

The dry matter (W) produced by a stand growing on moist soil can be represented by

$$W = Sfet \quad (1)$$

This form of analysis is appropriate when radiation is limiting, either because the foliage is too sparse to intercept all the available radiation or because it exists for a small fraction of the year.

Interception of Solar Radiation

The area of foliage, represented by leaf area index (L), most strongly determines f at any time. For many tropical cereals and legumes grown at typical narrow row spacings, f can be related to L by an extinction coefficient (K) that depends mainly on the orientation and distribution of foliage. The value of K may change slightly with time if the organs intercepting most of the radiation change their orientation, or if the foliage becomes more randomly

Table 1. Stands of pearl millet.

Stand	Location	Year	Season	Daily maximum D (kPa)	Soil water	Planting density (m^{-2})	Reference
I	Nottingham	1979	-	1.4	W[1]	28.6	Squire et al. 1984b
II	Hyderabad	1978	Rainy	1.5-2.0	W	22.2	Reddy & Willey 1981 Marshall & Willey 1983 Gregory & Reddy 1982
III	Hyderabad	1977/78	Postrainy	2.4	W	26.6	Gregory & Squire 1979
IV	Hyderabad	1977/78	Postrainy	2.4	D[2]	26.6	Squire et al. 1984a
V	Niamey	1980/81	Postrainy	4.0	D	11.5	Azam-Ali et al. 1984a, b

1. W = rainfed or frequently irrigated.
2. D = irrigated to field capacity at sowing, and then irrigated no further.

oriented as the canopy closes but generally K may be treated as a constant for a given species and cultivar grown in wet conditions

The total amount of radiation intercepted by a stand also depends on the period over which an intercepting surface is present The extent and size of this surface was examined in terms of f for four of the stands of pearl millet shown in Table 1 which began intercepting radiation at about 10 days after sowing (DAS), and were harvested at about 75 DAS (Fig 1) Stand I intercepted most radiation and grew in a humid atmosphere and moist soil in a glasshouse with controlled environment at Nottingham It achieved a maximum L of about 6 corresponding to a maximum f for total radiation (S) of 0 85 (0 93 for photosynthetically active radiation) Mean f was 0 34 between sowing and anthesis (45 DAS) and 0 83 S thereafter From sowing to maturity mean f was 0 54 averaged over a year it was 0 11

These values of f were achieved by stands for which emergence was successful for which the canopy expanded rapidly in the absence of drought and nutrient deficiency and for which there was negligible senescence after anthesis Such successful emergence and rapid expansion of the canopy have also been observed in wet conditions in the semi-arid tropics but there leaf area usually decreases as a result of senescence to reduce f by about 10% after flowering (Reddy and Willey 1981 Alagarswamy and Bidinger 1985) Fractional interception may be reduced considerably more than this in the field by a shortage of nutrients but there is a dearth of reliable quantitative information on such effects when water is also not limiting

In a simple model of light interception by pearl millet canopies well supplied with water and nutrients Squire et al (1984b) showed mean f to depend on three main factors (a) maximum f (b) the time from sowing to the time when f achieved half its maximum value and (c) the time from sowing to maturity Work in controlled environments at Nottingham showed that variation in solar radiation

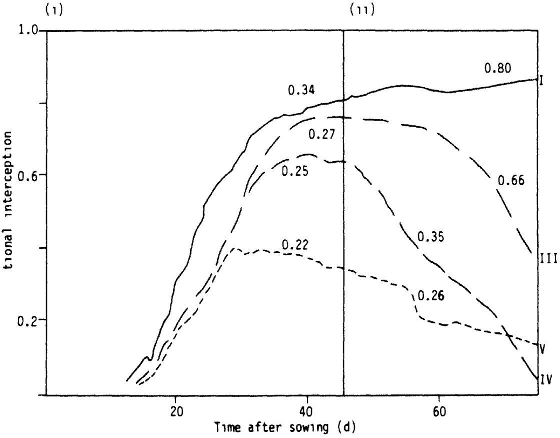

Figure 1. Fractional interception of total solar radiation (f) for four stands of pearl millet (BK 560) (i) before and (ii) after anthesis. Numbers I-V refer to crops in Table 1 Numbers above each curve show mean f.

over the range that occurs in the field, had little effect on any of these factors, but temperature strongly affected (b) and (c), although it had little influence on (a). Temperature governed (b) through its control of emergence (Mohamed et al. 1986), initiation of leaf primordia (Ong 1983a), and expansion of leaf laminae (Squire and Ong 1985), the rates of which increased linearly with temperature above a common base of 10°C. Consequently, the period between sowing and when f was half its maximum could be represented by a thermal duration (θ_1), which is an integral of time and temperature above an appropriate base (Squire et al. 1984a). Most of the period between sowing and final harvest was also strongly governed by temperature (Fussell et al. 1980, Ong 1983b), and was represented by a second thermal duration (θ_2). As temperature increases, the duration of the foliage (θ_2-θ_1) decreases and the canopy intercepts less radiation whereas, if temperature decreases, the canopy grows more slowly over a longer period, and therefore intercepts more radiation.

Conversion of Intercepted Radiation

The conversion coefficient (e) is the weight of dry matter produced per unit of solar radiation intercepted. In a range of moist environments including northern Australia (Begg 1965), Hyderabad in the rainy season (Reddy and Willey 1981, Marshall and Willey 1983, Alagarswamy and Bidinger 1985), and the controlled environments at Nottingham (Squire et al. 1984b), e measured over several weeks was around 2.5 g MJ^{-1} of the total radiation (for further discussion see Ong and Monteith 1985). This maximum value of e was achieved from sowing to harvest only by stand I (Fig. 2). At Hyderabad, this maximum was measured only between sowing and anthesis, and was reduced thereafter by senescence as shown by stand II. Senescence clearly had a considerable effect on productivity, but it is not known why it was absent in stands grown at Nottingham (Squire et al. 1986).

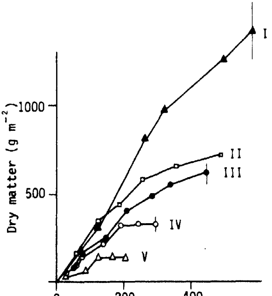

Figure 2. Dry matter production (above ground) and intercepted total solar radiation for five stands of pearl millet (cv. BK 560). Table 1 gives details of crops.

Unlike f, e was only weakly affected by temperature over the range at Hyderabad, although it decreased at temperatures below 20°C (Fussell et al. 1980, Squire et al. 1984b).

Synthesis

In moist environments, where temperature and solar radiation are the main variables affecting productivity, equation 1 can be rewritten as

$$W = Se\,(1 - \exp\{-KLm\})\,[(\theta_2-\theta_1)/T)] \quad (2)$$

(Squire et al. 1984b). As e and Lm are only weakly affected by temperature, W decreases as the duration of the canopy decreases with increasing temperature. Figure 3 shows the modeled response of maximum W to mean temperatures between 20-30°C for stands of pearl millet using maximum values of e, Lm, θ_1, and θ_2 as given by Squire et al. (1984b). Such heavy crops have been grown in the controlled environments at Nottingham and occasionally in very moist conditions in the tropics (Begg 1965, Enyi 1977); but crops of these or comparable cultivars in rainy seasons in the semi-arid tropics are at most h[illegible] of the mass shown in Figure 3. One of the causes of this is the effect of senescence on e referred to earlier, but other causes may be limiting effects of other environmental factors such as saturation deficit or nutrient deficiency.

Limiting Factors

Saturation Deficit

There is now much evidence from work in controlled environments that the potential transpiration rate,

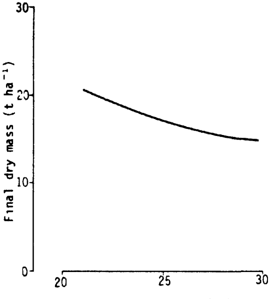

Figure 3 Modeled relation between mean temperature and final dry mass of pearl millet BK 560

as represented by the saturation vapor pressure deficit (D), has important effects on dry matter production, even on plants growing in moist soil Saturation deficit affects growth by reducing the rate of leaf expansion and by reducing leaf conductance and thereby the rate of photosynthesis (Schulze and Hall 1982)

There is little direct evidence on which to assess the effect of D by these mechanisms on productivity of stands in the field Work in controlled environments suggests that both f and e may decrease in response to increasing D by about 10% per kPa (Nagarajah and Schulze 1983, Squire et al In press) At a given site in the semi-arid tropics, D is closely coupled to rainfall, but D also varies between sites over a range of about 2 kPa and may therefore [illegible]fect productivity between different sites during the [illegible]ny season to an extent similar to that of temperature shown in Figure 3 Effects of D may be even larger on irrigated crops exposed to drier air

Nutrient Deficiency

The extent to which dry matter production is limited by nutrient deficiency is shown by the very large yield increases in response to fertilizer, both in rainy and dry postrainy seasons (Kanwar et al 1984, Huda et al 1985) However, there is little systematic information on how fertilizer affects interception and conversion of solar energy Work on temperate cereals shows that the main effect of applying nitrogenous fertilizer is to increase the rate of leaf expansion and therefore to increase the seasonal mean value of f In contrast the conversion coefficient is independent of nutrient status over a wide range These responses are generally consistent with those for pearl millet found by Coaldrake and Pearson (1985a and b) but the direct response of e to nutrients has still to be investigated

Dry Matter Production When Water is Limiting

Shortage of water in the soil may reduce the rate of leaf expansion and therefore delay formation of the canopy and reduce its size The shortage may also reduce (1) the effective duration of the crop in that the store of water may be used before the crop has reached maturity and (2) the rate of photosynthesis and thereby e through effects on leaf physiology These effects of water shortage (usually in combination with dry air) reduced f e, and dry matter production in postrainy seasons at Hyderabad and Niamey compared with moist environments considered earlier (Figs 1 and 2) Productivity over 75 d fell from 1 2 kg m^{2} to 0 15 kg m^{2} a factor of eight as the climate became drier

It is possible to examine such a range of productivity in terms of the factors in Equation 1 but for that analysis it is necessary to know how the balance between demand for water by the atmosphere and the supply of water from the soil controls water and turgor potentials in the plant and how these, in turn limit physiological processes such as photosynthesis and leaf extension At present, this analysis is impossible, simply because much of the information is fragmentary It is more feasible (and instructive) to analyze productivity in terms of the limiting factor itself the supply of water In this analysis, dry matter production (W) depends on two factors the amount of water that the crop extracts from the soil (E), and the amount of dry matter produced per unit of water extracted (q)

$$W = Eq \qquad (3)$$

Extractable Water

The total water supply in the soil depends on physical factors In many soils of the semi-arid tropics, the top 2 m holds from 100-250 mm of water at field capacity (Russell 1978, Williams 1979). A part of this (10-20%) can be lost to the atmosphere directly from the soil surface. The rest is available for transpiration. The fraction of this available water that can be removed by roots depends on factors such as the size and density of the root system.

Size of the Root System

The root system of crops sown at narrow row spacings can be considered to descend in the form of a two-dimensional front. The rate and duration of movement of the root front determines the volume of soil accessible to the root system. In soil columns within a controlled environment greenhouse, Gregory (In press) showed that roots extend at a rate strongly determined by temperature at the shoot meristem. Comparing root profiles below stands II, IV, and V of Table 1, suggests that the rate at which roots penetrate the soil may be influenced by wetness and density of the soil (Fig. 4). In a uniform sandy soil of low bulk density (stand V), this rate averaged 4.5 cm d^{-1} over the first 30 d, during which it reached a maximum of 7 cm d^{-1}. By comparison, in Alfisols at Hyderabad it was less than half these rates, although it was faster below a drying soil (stand IV) than one rewetted by rainfall (stand II).

Measurements of changes in the water content and water potential in a soil suggest that the deepest layer from which water is extracted by a stand growing on stored water (the water extraction front) lags slightly behind or keeps pace with the root front. The extraction front velocity (α) is about twice as fast for pearl millet and sorghum as for groundnut, consistent with the difference in rates of root extension for these species (Fig. 5). The relation shown for the cereals is the mean of measurements on four stands, for which α was similar in both Vertisols and Alfisols. In contrast, α was different from 50 d after sowing for the two groundnut stands of the same

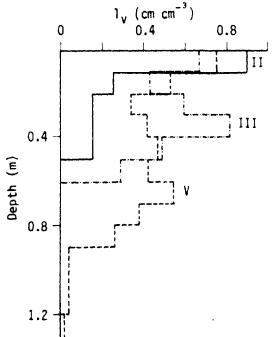

Figure 4. Rooting profiles at about 32 d after sowing for pearl millet stands grown at Hyderabad in the rainy season (——) Hyderabad in the postrainy season (.....), and Niamey in the postrainy season (- - -). L-v is the length of root per unit soil volume. Table 1 gives references.

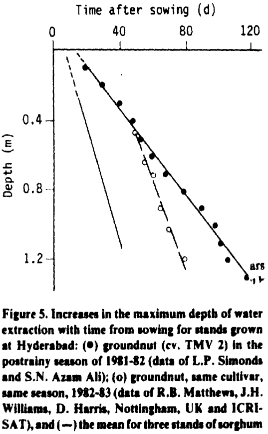

Figure 5. Increases in the maximum depth of water extraction with time from sowing for stands grown at Hyderabad: (●) groundnut (cv. TMV 2) in the postrainy season of 1981-82 (data of L.P. Simonds and S.N. Azam Ali); (o) groundnut, same cultivar, same season, 1982-83 (data of R.B. Matthews, J.H. Williams, D. Harris, Nottingham, UK and ICRISAT), and (—) the mean for three stands of sorghum and one of pearl millet (data of Piara Singh, ICRISAT).

cultivar grown in successive seasons. (The reason for this difference is not known).

The duration of a moving front appears to be similar to the duration of vegetative production above ground. For the pearl millet hybrid BK 560 examined in Hyderabad, this duration closely matched the duration over which the canopy formed, about 550°Cd, equivalent to 37 d at a mean meristem temperature of 25°C, by which time the front had descended about 1.0-1.5 m.

Root Length per Unit Soil Volume

The quantity of roots in any layer of soil is most conveniently described in terms of a length of root per unit soil volume (lv). This quantity usually decreases with depth, implying that tertiary and higher order branches continue to be initiated and to expand while the front moves below them. The extent of root proliferation in a soil layer above the front appears to depend on the frequency of rewetting surface soil layers, and on soil structure. In the rainy season at Hyderabad (stand II), most roots were in the surface layers, where lv was 1.0-1.5 cm cm^{-3} at anthesis, even though the front descended to 1 m (Gregory and Reddy 1982). In the postrainy season at Niamey (stand V), lv ranged between 0.4 and 0.6 cm cm^{-3} down to 0.8 m, below which roots were present in small quantity to 1.4 m. In the postrainy season at Hyderabad, similar values of lv to those at Niamey were observed down to 0.5 m, but below this, lv decreased abruptly as a result of a soil layer of high bulk density.

It is not yet clear how lv influences the minimum volumetric content to which water is reduced. Some authorities (Ritchie 1972, Russell 1978) assume that if roots are present in a soil layer, they extract water to a volumetric content equivalent to an arbitrary but realistic soil water potential of -1.5 MPa. They are then able to define a volume of extractable water for a given soil. For Vertisols and Alfisols at Hyderabad, the extractable water in the top 1.5 m of the profile ranges from 95-200 mm (Russell 1978).

The idea of a volume of extractable water forms the basis for a model of water extraction by roots being developed at ICRISAT (Monteith 1986). However, this concept cannot be applied indiscriminately to all crops and soils, as there is evidence that the volume of water extracted from a soil also depends on atmospheric conditions. If lv in that part of the soil profile supplying most of the water is so small that the maximum extraction rate is only a small proportion of the potential evaporation rate, the aerial organs may have to compensate by reducing leaf area and leaf conductance. This may effectively preclude further extraction (and dry matter production) even though water potential remains above -1.5 MPa. (Squire et al. 1984a, give an example of this for pearl millet, stand IV).

Dry Matter/Water Ratio (q)

It is well established that the amount of dry matter produced by a stand in a given atmospheric environment is directly proportional to the amount of water it transpires (Kanemasu et al. 1984). However, q is strongly affected by atmospheric conditions. It ranged from 6.4 to 2.1 g kg^{-1} for four stands of pearl millet, and was smaller in drier atmospheres such that the product of q and D varied only over a range of 27% of the mean of the four stands (Table 2). At least part of the relatively small differences in qD between stands may have been the result of sampling errors in estimating W and soil water content, or of using atmospheric saturation deficit rather than leaf-to-air saturation deficit, or of failing to distinguish properly between transpiration and evaporation from the soil surface.

An inverse relation between D and the ratio of photosynthesis rate to transpiration rate has been observed for many species and has a physiological basis. At any given value of leaf conductance, increasing D increases transpiration rate without affecting photosynthesis rate. The inverse relation between D and q implies that the proportion of photosynthate respired is conservative in a wide range of environments. (For further discussion see Bierhuizen and Slatyer 1965, Tanner and Sinclair 1983, Monteith 1986).

Table 2. Comparison of dry weight (W), transpired water (E), dry matter-water ratio (q), saturation deficit (D) and the product of q and D for four of the millet stands shown in Figures 1 and 2.

Stand	W ($g\ m^{-2}$)	E ($kg\ m^{-2}$)	q ($g\ kg^{-1}$)	D (kPa)	qD ($kPa\ g\ kg^{-1}$)
I	1440	220	6.4	1.4	9.0
III	600	150	3.9	2.4	9.5
IV	310	70	4.5	2.4	11.0
V	170	80	2.1	4.0	8.4

The conservative nature of qD is extremely valuable for modeling productivity in dry areas

Synthesis

Whereas temperature and solar radiation set the upper limit for productivity of a given cultivar in wet climates, extractable water and saturation deficit set this limit in dry environments Relations have been calculated between W and D for pearl millet at two extreme values of extractable water corresponding to the range defined by Russell (1978) for soils at Hyderabad (Fig 6) The total mass of pearl millet in postrainy seasons is unlikely to rise above 10 t ha^{-1} and will generally be much smaller

Limitations to Productivity—Summary

Productivity and its causative factors, for the stands in Table 1, are expressed as a fraction of stand I the most productive (Table 3) For the two stands for which water was not limiting, W was reduced mainly through effects on the conversion coefficient (e) mean fractional interception was reduced by only 20%, a consequence of unknown factors mainly affecting maximum leaf area The reduction in e (0 61) for stand II, which grew in a similar atmospheric environment to stand I was entirely related to senescence after anthesis This effect was by far the largest limiting productivity in moist conditions The additional reduction in e (0 56) for stand III may have been caused by the effect of D on photosynthesis referred to earlier

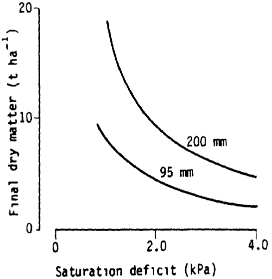

Figure 6. Modeled relation between final dry mass of pearl millet and saturation deficit for representative soils. Numbers by curves show volumes of extractable water in the top 1.5 m of soil.

Table 3 Main factors determining final standing weight

(a) Soil water not limiting			
Stand	W^1	f^2	e^3
II	0 50	0 83	0 61
III	0 42	0 80	0 56
(b) Soil water limiting			
Stand	W	E^4	D^5
IV	0 22	0 31	0 60
V	0 12	0 36	0 35

1 W dry matter production
2 f fraction of mean daily insolation intercepted by the canopy
3 e amount of dry matter formed per unit radiation intercepted (conversion coefficient)
4 E amount of water that the crop extracts from the soil
5 D saturation vapor pressure deficit

For the two stands, IV and V, for which water was limiting, W was reduced through effects both of extracted water (E) and of D operating via qD In the extreme case of stand V for which productivity was reduced by a factor of about 8, both E and q in Equation 3 were reduced by factors of about 2 8 The difference in W (a factor of almost 2) between stands IV and V growing in very different environments but extracting a similar amount of water was predominantly caused by a difference in D

Partition of Assimilate

In wet climates, the amount of dry matter allocated to the organs that constitute yield can be considered in terms of the factors in Equation 1, with the addition of a fraction (p) defined as the fraction of total dry matter (TDM) allocated to the relevant organ As the process of allocation usually coincides with an associated developmental phase, its duration is strongly governed by temperature above a base and can be defined as a thermal duration (Ong 1983b, 1984, G R Squire, personal communication) In controlled environments at Nottingham, the partition fraction changed little (about 0 4) over the temperature range at Hyderabad, and the final mass of stems and panicles was determined mainly by corresponding thermal durations Mass decreased as temperature increased (as for total plant mass shown in Fig 3)

This conservatism of the partition fraction appears to depend upon the size of the sink within the reproductive organ, in the form of units such as grains or pods, being matched with the final mass of the organ This matching of number and plant mass appears to operate through a physiological mechanism that senses the thermal growth rate of the plant at some specific stage in its life Thermal growth rate is defined as the rate of dry matter production per unit of thermal time Very tight relations between thermal growth rate before anthesis and grain number have been found for maize (Hawkins and Cooper 1981) and pearl millet (Ong and Squire 1984)

The coordination between grain number and mass breaks down if one of the physiological processes determining number is affected by other factors For example, when low temperature affected pollination and grain set in pearl millet (Fussell et al 1980) the panicle filled more slowly and the partition fraction was much less than at higher temperatures (Squire 1984a)

Partitioning when Water is Limiting

For a crop growing on stored water, yield may be reduced not only because TDM production is reduced, but also because the dry conditions may affect two other important factors

- the distribution of assimilate between roots and shoots, and
- the timing of developmental events in relation to the availability of water in the soil

Root/Shoot Ratios

The rate at which water is extracted from the soil by a root system must equal the rate at which it is transpired through the leaves Plants have several mechanisms to achieve this equilibrium the root system may be increased relative to leaf area, leaf area may be reduced, leaf conductance may be reduced, and leaves of some species may change their orientation to effectively reduce leaf area

As conditions became drier, the root system of pearl millet both descended and proliferated more rapidly (Fig 4) and the root length per unit leaf area increased by a factor of three (Table 4) This difference in root-length/shoot-area ratio may have been caused to some extent by the different soil conditions but it is notable that the ratio increased more or less in proportion to the saturation deficit at the three sites (Table 2) and that the ratio divided by D is 10 times less variable between sites than the ratio itself As D is a factor that strongly determines transpiration rate this conservatism implies that the root/shoot ratio responded to match the water extraction rate with the transpiration rate

The modification of the root length/leaf area ratio had a relatively small effect on root mass at anthesis (not shown) but root/shoot mass ratio increased considerably with increasing dryness from 0 045 for stand I to 0 29 for stand V In relation to the very large differences in total plant mass the mass of roots was virtually constant in these different environments

Timing of Development

The timing of the sequence of developmental events from emergence to final harvest is determined mainly by temperature, and in some species also by photoperiod (Mahalakshmi and Bidinger 1985a, Ong 1983a and b) The time available for growth is determined by the volume of water accessible to the roots divided by the mean rate at which it is extracted (here termed water-time, as by Monteith, 1984) If developmental-time and water-time are equal, development is able to proceed to maturity If the water-time is less than the developmental-time, then the yield will depend on there being

- sufficient water-time to support growth until the reproductive sink has been determined, and
- a capacity to retranslocate assimilate from other organs to the reproductive sink

Water-Time

Since water-time is calculated by the volume of accessible water divided by the mean transpiration rate, it is affected by attributes of the root system (e g , root front velocity), and of the canopy (mean conductance, area), the relations between which are not well understood Nevertheless, there are grounds for considering that the water-time provided by a

Table 4. Root and shoot characteristics for three of the stands shown in Figures 1 and 2 and Table 1, 31-33 DAS.

Stand	Root length per plant (m)	Root length per leaf area (m m^{-2})	Root weight per plant (g)	Root length per weight (m g^{-1})
II	63	980	0.98	64
IV	120	1540	0.75	160
V	370	3370	2.6	140

store of given volume may be somewhat insensitive to the atmospheric environment. As potential transpiration rate rises (for example, in response to an increase of D), leaf area and conductance tend to fall, thereby conserving the actual transpiration rate. Such a response was shown by the two stands of pearl millet (IV and V) that extracted a similar amount of water from the soil. Despite the large difference in D between these sites, mean actual transpiration rate from both stands was between 1.5 and 2 mm d^{-1}, a result of compensation mainly in leaf area. Consequently, the supply of water lasted about 45 d in both cases. The duration between sowing and anthesis for this hybrid grown without drought stress is also about 45 d at the prevailing temperature. The dry conditions had no effect on this duration so the water-time was just sufficient to support development to anthesis and grain set.

However, developmental- and water-time may not be so well matched for other varieties or in other environments. In several studies at Hyderabad, the ability of a variety to yield when grown on stored water depended on earliness (defined by the period between sowing and flowering) and susceptibility for development to be delayed by drought. Generally, earlier and less-susceptible cultivars avoided drought stress and thereby yielded more than later and more susceptible ones (Mahalakshmi and Bidinger 1985a; F.R. Bidinger, V. Mahalakshmi and Durga Prasada Rao, ICRISAT, personal communication).

This work also showed that the degree of synchrony in flowering of different tillers was an important factor to be accounted for when matching developmental-time to water-time (Mahalakshmi and Bidinger 1985b). When stands grew on a store of water which was not replenished later in the season, early synchronous flowering gave rise to more yield than late asynchronous flowering. But for stands whose store was replenished around anthesis, asynchronous flowering among tillers usually gave rise to more yield: the late-flowering tillers which grew in less stressed conditions compensated for the poor yield of the early-flowering tillers.

Retranslocation of Assimilate

In the case of stands IV and V, most of the foliage died shortly after anthesis, but the stem and panicle remained alive until the end of the thermal duration for the whole crop. Between anthesis and maturity, the panicles filled, apparently with assimilate translocated from the stem. Factors controlling the rate of retranslocation in these circumstances are not known. Azam Ali et al. (1984a) point out that [illegible] partition fraction for panicles at final harvest was remarkably constant (about 0.5) among the various experimental treatments of which stands IV and V were part. However, smaller fractions have been found in other experiments (Mahalakshmi and Bidinger 1985a).

The volume of extractable water at these two sites was at the lower end of the range defined by Russell (1978) for soils at Hyderabad. Therefore, cultivars with developmental-time requirements similar to BK 560 would generally be able to grow at least until anthesis, thus insuring some yield. The maximum yield of this cultivar growing on stored water can now be estimated from Figure 6, assuming that the maximum partition fraction for panicles is about 0.5. Within the range of mean maximum D from 2.5-4.0 kPa, panicle yield on a deep Vertisol would range from 3.8-2.4 t ha^{-1}, and on a medium Alfisol from 1.8-1.1 t ha^{-1}.

Opportunities for Plant Breeding

From work in controlled environments and in the field, one or two current genotypes of pearl millet can now be defined in terms of a set of important physiological characters. From a simple model currently being developed at Nottingham, it may be possible to estimate the effect of genotypic change in many of the characters on TDM production and yield.

For example, when water is not limiting, an increase in the base temperature (T_b) for development by 1°C would prolong the duration of the foliage (θ_2-θ_1) and thereby increase total productivity and panicle yield of pearl millet by 7%. Mohamed (1984) found evidence of considerable variation in T_b between cultivars germinated on a thermal gradient plate in the laboratory. As T_b appears to be similar for all processes, this technique may be useful to identify cultivars with a thermal duration suitable for a particular environment.

With respect to yield when water is limiting, the analysis indicated six attributes deserve the attention of plant breeders (and physiologists):

- the dry matter-water ratio,
- the root front (or water extraction front) velocity,
- the duration of movement of the front,
- root length per unit soil volume,
- developmental time in relation to water-time, and
- compensating mechanisms that affect harvest index (e.g., retranslocation of stored assimilate, degree of synchrony of tillering).

The model could be used to indicate the relative importance of physiological characters to stands growing on stored water (as in the example in Table 5). The first part of the table lists a set of environmental factors typical of a postrainy season. The second part lists the initial set of relevant physiological variables, based on pearl millet hybrid BK 560. Values for most of these variables are realistic, but those for three of them have been simplified for this example: the specific root length (m g^{-1}), root length per unit soil volume, and the volumetric water content of the soil when extraction has ceased, are assumed constant throughout the profile. The third part of the table shows calculations based on information in the first and second parts and gives panicle yield based on the initial set of characters as 88 g m^{-2}. The third part also shows the effect on this of a 10% increase in the value of one variable—the water extraction front velocity. Maximum rooting depth and the volume of extractable water increased, the latter by more than 10% since none of the extra water made available was lost from the soil surface. The extra dry matter produced (30 g m^{-2}) was much greater than the amount of extra root mass required (3 g m^{-2}), and yield increased by about 13 g m^{-2} or 15%. There is probably enough information on which to base comparable calculations for most other variables, except for lv, the effect of which on final volumetric water content is unclear.

Table 5. Demonstration of a procedure for predicting the effect of change in a physiological character (in this case extraction front velocity, α) on yield of pearl millet in a hypothetical dry environment.

1. Environmental factors		
Solar radiation	18 MJ m^{-2} d^{-1}	
Temperature	25°C	
Saturation deficit	3.5 kPa	
Total soil evaporation	25 mm	
Soil depth	>1.5 m	
Initial volumetric water content (uniform with depth)	0.2	
2. Initial physiological characters		
Sowing to anthesis	17 d + 460°Cd	
Specific root length	130 m g^{-1}	
qD	10.0 kPa g kg^{-1}	
lv (constant throughout profile; reduces volumetric water content to 0.1)	0.4 cm cm^{-3}	
Mean extraction front velocity (α)	2 cm d^{-1}	
Partition fraction for panicles (shoots only)	0.5	
3. Calculations	Control	With 10% increase in α
Maximum rooting depth (m)	0.96	1.06
Extractable water (kg m^{-2})	71	81
q (g kg^{-1})	3.0	3.0
Total dry weight (g m^{-2})	213	243
Weight of roots (g m^{-2})	37	41
Weight of panicles (g m^{-2})	88	101

Future Work

The effects of solar radiation and temperature on growth and crop yields in the semi-arid tropics are now relatively well understood compared to many of the effects of water. Future research in water relations should concentrate on at least these specific topics:

- the effect of saturation deficit (independently of soil water) on interception and conversion of solar radiation;
- the relation between some attribute of the root system, such as lv, on both the rate of water extraction and the water content when extraction has ceased; and
- the effects of high temperature (35-50°C) independent of saturation deficit, on leaf expansion, development, and dry matter production.

Research on all these responses should be continued in realistic controlled environments, but work on the second can be effectively performed only in the field.

The systematic effects of nutrient concentration in the soil are even less well-documented than those of water and need to be tackled within the structure of a model of growth and yield that takes into account the effects of solar radiation, temperature, saturation deficit, and water supply.

References

Alagarswamy, G., and **Bidinger, F.R.** 1985. The influence of extended vegetative development and d_2 dwarfing gene in increasing grain number per panicle and grain yield in pearl millet. Field Crops Research 11:265-79.

Azam-Ali, S.N., **Gregory, P.J.**, and **Monteith, J.L.** 1984a. Effects of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) grown on stored water. I. Growth of roots and shoots. Experimental Agriculture 20:203-214.

Azam-Ali, S.N., **Gregory, P.J.**, and **Monteith, J.L.** 1984b. Effects of planting density on water use and productivity of pearl millet (*Pennisetum typhoides*) grown on stored water. II. Water use, light interception and dry matter production. Experimental Agriculture 20:215-224.

Begg, J.E. 1965. The growth and development of a crop of bulrush millet (*Pennisetum typhoides* S. & H.). Journal of Agricultural Science 65:341-349.

Bierhuizen, J.F., and **Slatyer, R.O.** 1965. Effect of atmospheric concentration of water vapour and CO_2 in determining transpiration-photosynthesis relationships. Agricultural Meteorology 2:259-270.

Coaldrake, P.D., and **Pearson, C.J.** 1985a. Panicle differentiation and spikelet number related to size of panicle in *Pennisetum americanum*. Journal of Experimental Botany 36:833-840.

Coaldrake, P.D., and **Pearson, C.J.** 1985b. Development and dry weight accumulation of pearl millet as affected by nitrogen supply. Field Crops Research 11:171-184.

Enyi, B.A.C. 1977. Physiology of grain yield in groundnut. Experimental Agriculture 13:101-110.

Fussell, L.K., **Pearson, C.J.**, and **Norman, M.J.T.** 1980. Effect of temperature during various growth stages on grain development and yield of *Pennisetum americanum*. Journal of Experimental Botany 31:621-633.

Gregory, P.J. (In press.) Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). VIII. Root growth. Journal of Experimental Botany.

Gregory, P.J., and **Reddy, M.S.** 1982. Root growth in intercrop of pearl millet/groundnut. Field Crops Research 5:241-252.

Gregory, P.J., and **Squire, G.R.** 1979. Irrigation effects on roots and shoots of pearl millet (*Pennisetum typhoides*). Experimental Agriculture 15:161-168.

Hawkins, R.C., and **Cooper, P.J.M.** 1981. Growth, development and grain yield of maize. Experimental Agriculture 17:203-208.

Huda, A.K.S., **Sivakumar, M.V.K.**, and **Rego, T.J.** 1985. An anlysis of agroclimatic data in relation to fertiliser use in dryland farming areas of India. Fertiliser News 30:35-41.

Kanemasu, E.T., **Piara Singh**, and **Chaudhuri, U.N.** 1984. Water use and water-use efficiency of pearl millet and sorghum. Pages 175-181 *in* Agrometeorology of sorghum and millet in the semi-arid tropics: proceedings of the International Symposium, 15-20 Nov 1982, ICRISAT Center, India. Patancheru, A.P. 502324, India: International Crops Research Institute for the Semi-Arid Tropics.

Kanwar, J.S., **Rego, T.J.**, and **Seetharama, N.** 1984. Fertiliser and water-use efficiency in pearl millet and sorghum in Vertisols and Alfisols of semi-arid India. Fertiliser News 29:42-52.

Mahalakshmi, V., and **Bidinger, F.R.** 1985a. Water stress and time of floral initiation in pearl millet. Journal of Agricultural Science 105:437-445.

Mahalakshmi, V., and **Bidinger, F.R.** 1985b. Flowering response of pearl millet to water stress during panicle development. Annals of Applied biology 106:571-578.

Marshall, B., and **Willey, R.W.** 1983. Radiation interception and growth in an intercrop of pearl millet/groundnut. Field Crops Research 7:141-160.

Mohamed, H.A. 1984. Varietal differences in the temperature responses of germination and crop establishment. Ph.D. thesis, University of Nottingham, Loughborough, UK.

Mohamed, H.A., **Clark, J.A.**, and **Ong, C.K.** (In press.) Genotypic differences in the temperature responses of tropical crops. I. Germination characteristics of groundnut (*Arachis hypogaea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). Journal of Experimental Botany.

Monteith, J.L. 1984. On time and Crop Production. Jennareddy Venkat Reddy Memorial Lecture, 1984. Patancheru, A.P. 502 324, India: International Crops Research Institute for the Semi-Arid Tropics. 15 pp. (Limited distribution.)

Monteith, J.L. 1986. How do crops manipulate water supply and demand? Philosophical Transactions of the Royal Society of London, B 316:245-259.

Nagarajah, S., and **Schulze, E.D.** 1983. Responses of *Vigna unguiculata* (L.) Walp. to atmospheric and soil drought. Australian Journal of Plant Physiology 10:385-394.

Ong, C K 1983a Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S & H) I Vegetative development Journal of Experimental Botany 34 322 336

Ong, C K 1983b Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S & H) II Reproductive development Journal of Experimental Botany 34 337 348

Ong, C K, and **Monteith J L** 1985 Response of pearl millet to light and temperature Field Crops Research 11 141 160

Ong, C K, and **Squire G R** 1984 Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S & H) VII Final number of spikelets and grains Journal of Experimental Botany 35 1233 1240

Reddy, M S, and **Willey, R W** 1981 Growth and resource use studies in an intercrop of pearl millet groundnut Field Crops Research 4 13 24

Ritchie, J T 1972 Model for predicting evaporation from a row crop with incomplete cover Water Resources Research 8 1204-1213

Russell, M B 1978 Profile moisture dynamics of soil in Vertisols and Alfisols Pages 75 87 *in* Proceedings of an International Workshop on the Agroclimatological Research Needs of the Semi Arid Tropics 22 24 Nov 1978 ICRISAT Center India Patancheru A P 502 324 India International Crops Research Institute for the Semi Arid Tropics

Schulze, E D, and **Hall, A E** 1982 Stomatal responses water loss and CO_2 assimilation rates of plants in contrasting environments Pages 181 230 *in* Encyclopedia of plant physiology (Lange O L Nobel P S Osmond C B and Ziegler H eds) New series Vol 12B Berlin Springer Verlag

Sivakumar, M V K, **Huda, A K S** and **Virmani, S M** 1984 Physical environment of sorghum and millet growing areas in South Asia Pages 63 83 *in* Agrometeorology of sorghum and millet in the semi arid tropics proceedings of the International Symposium 15 20 Nov 1982 ICRISAT Center India Patancheru A P 502 324 India International Crops Research Institute for the Semi Arid Tropics

Squire, G R, **Gregory, P J**, **Monteith, J L**, **Russell, M B**, and **Piara Singh** 1984a Control of water use by pearl millet (*Pennisetum typhoides*) Experimental Agriculture 20 135-149

Squire, G R, **Marshall, B.**, **Terry, A C**, and **Monteith, J L** 1984b Response to temperature in a stand of pearl millet VI Light interception and dry matter production Journal of Experimental Botany 35 599-610

Squire, G R., **Marshall, B.**, and **Ong, C K** (In press) Development and growth of pearl millet (*Pennisetum typhoides*) in response to water supply and demand Experimental Agriculture

Squire, G R, and **Ong, C K** 1983 Response to saturation deficit of leaf extension in a stand of pearl millet (*Pennisetum typhoides* S & H) I Interaction with temperature Journal of Experimental Botany 34 846-855

Tanner, C B, and **Sinclair, T R** 1983 Efficient water use in crop production Pages 1 28 *in* Limitations to efficient water use (Taylor H M Jordan W R and Sinclair T R eds) Madison Wisconsin USA American Society of Agronomy

Williams J B 1979 Physical aspects of water use under traditional and modern irrigation farming systems in Wadi Rima Tihamah Project Record no 27 Surbiton Surrey UK Land Resources Development Centre (Limited distribution)