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Interactions between plant nutrients, water and carbon dioxide as factors limiting crop yields

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SUMMARY

Biomass production of annual crops is often directly proportional to the amounts of radiation intercepted, water transpired and nutrients taken up. In many places the amount of rainfall during the period of rapid crop growth is less than the potential rate of evaporation, so that depletion of stored soil water is commonplace. The rate of mineralization of nitrogen (N) from organic matter and the processes of nutrient loss are closely related to the availability of soil water. Results from Kenya indicate the rapid changes in nitrate availability following rain.

Nutrient supply has a large effect on the quantity of radiation intercepted and hence, biomass production. There is considerable scope for encouraging canopy expansion to conserve water by reducing evaporation from the soil surface in environments where it is frequently rewetted, and where the unsaturated hydraulic conductivity of the soil is sufficient to supply water at the energy limited rate (e.g. northern Syria). In regions with high evaporative demand and coarse-textured soils (e.g. Niger), transpiration may be increased by management techniques that reduce drainage.

Increases in atmospheric [CO_2] are likely to have only a small impact on crop yields when allowance is made for the interacting effects of temperature, and water and nutrient supply.

1. INTRODUCTION

The general relations between crop growth, water use and nutrient acquisition can be approximated by a series of simple equations. Crop dry matter is produced as a consequence of the conversion of radiant energy to chemical energy during photosynthesis and the amount of dry matter (W) per unit area can be written as

$$W = \int qfS\partial t, \qquad (1)$$

where q is the efficiency with which intercepted radiation is converted to dry matter, f is the fraction of incoming radiation intercepted by the canopy, S is the amount of incoming radiation per unit area, and t is time (Monteith 1986). In the absence of water, nutrient and disease limitations the value of q tends to be conservative for a given crop variety growing in a given location. During the exchange of CO_2 between the atmosphere and the crop canopy there is a concomitant exchange of water vapour which may be approximated as

$$W = \int (k/d)\, T\partial t, \qquad (2)$$

where k is a crop-specific constant which depends strongly on the biochemistry of photosynthesis, d is the mean saturation deficit of the atmosphere weighted in favour of the time of day when transpiration is most rapid, and T is the amount of water transpired (Monteith 1986). The dry matter (W) is not simply carbohydrate but is elaborated into more complex assimilates with a requirement for other elements such as nitrogen (N), phosphorus (P) and magnesium (Mg); the enzymatic and biochemical processes also have requirements for specific elements. As crops grow, the concentration of nutrient per unit of dry mass (X) normally decreases with time as more structural materials are produced, but W and X are, by definition, related:

$$W = U_n/X_n, \qquad (3)$$

where U_n is the cumulative uptake of nutrient n, and X_n is the average concentration of the nutrient in the plant tissue. Rearranging equations (1)–(3) to express the demands for nutrients and water by a growing crop gives:

$$U_n = X_n \int qfS\partial t, \qquad (4)$$

$$T = (d/k) \int qfS\partial t. \qquad (5)$$

These equations can be used to explore the basis of nutrient and water effects on crop production. Both water and nutrient availability may affect the size of the canopy thereby influencing f. Short-term shortage of water is more likely to affect q than a shortage of nutrients because of the different buffering capacities of the plant with respect to water and nutrients. For example, a crop of 5 t dry mass ha^{-1} growing at 0.2 t ha^{-1} d^{-1} may well be subjected to a demand for water of 4 mm d^{-1} (equivalent to all of the water stored in the plant), compared to an N demand of 0.01 t ha^{-1} (equivalent to only 4% of the N stored in the plant). Hence, large tissue water deficits can accumulate within a few hours, resulting in stomatal closure and a reduction in *q*, whereas tissue nutrient deficits accumulate sufficiently slowly that plants can maintain a balance between supply and demand through modification of *f*, and so conserve *q*. Only in extremely nutrient deficient soils is *q* likely to be reduced by inadequate nutrition. The parameters *d* and *k* can be slightly affected by water supply (midday stomatal closure in water-stressed plants will reduce the contribution of high midday saturation deficit to the daily weighted mean) and nutrient supply (N deficient soils will reduce *k*), but these effects are generally small in relation to the effects on *f* and *q*. For nutrients made available in soils by biological processes (particularly N, P and S), availability is affected substantially by water.

Much of the crop-producing area of the world is characterized by climates in which the amount of rainfall during the period of most rapid crop growth is considerably less than the potential rate of evaporation, so that considerable depletion of the soil water reservoir is commonplace. The interactions of water and nutrients are particularly important in arid and semi-arid regions, where not only is water supply erratic but soil nutrient reserves are also low. For example, Stoorvogel *et al.* (1993) calculated nutrient balances for arable land in 38 countries of sub-Saharan Africa and concluded that there is gross nutrient mining throughout. Average nutrient losses exceed inputs and by the year 2000 will be 26 kg N, 3 kg P and 19 kg K ha^{-1} yr^{-1}. This net imbalance is currently at the expense of soil reserves and is, therefore, unsustainable unless it can be reversed with judicious use of crop residues, manures and inorganic fertilizers. The ability of animal manure to supply the nutrients required is limited. Fernández-Rivera *et al.* (1995) estimate that if all animals were used for manure production, there would be an average of 680 kg manure ha^{-1} yr^{-1} for seven West African countries. This rate of manure production is only sufficient for maintaining fertility in 18% of the presently cropped area at current levels of production. Williams *et al.* (1995) also conclude that manuring alone cannot sustain crop yields and that inorganic fertilizers are needed. The efficient use of both the limited manure and the purchased inputs of fertilizer to produce crops in these environments will require a better understanding of nutrient–water interactions.

In this paper we explore the interaction of water and nutrients (particularly N) in relation to those processes affecting nutrient availability in soils and those leading to losses from the production system. We then examine the influence of management practices on the use of water by crops to produce dry matter and yield under a range of soil and climatic conditions. Finally we summarize how increasing atmospheric concentration of CO_2 and temperature may interact with water and nutrients to affect future crop yields. Our examples are taken predominantly from semi-arid regions where the pressures to increase food supply are particularly acute (Brady 1990), and water and nutrients are often scarce.

2. NUTRIENT SUPPLY AND WATER

The strong interaction between water and the availability of nutrients to crops arises from the various effects of water on, (i) the release of nutrients from unavailable to available forms; (ii) the transport of nutrients to plant roots; and (iii) loss processes in the soil. The effects of water on transport processes in soils have been reviewed thoroughly elsewhere (Nye & Tinker 1977; Barber 1995). This paper concentrates on soil processes associated with the supply, particularly of N, to crops.

Nitrogen in humic substances accounts for over 90% of soil N in most soils but a remarkably constant proportion (1–3%) is mineralized each year (Wild 1988). However, the daily rate of decomposition varies widely according to temperature and soil water content and it is this rate that more directly affects the growth of crops. Incubation experiments, used to determine the rate of net mineralization over periods of about five to 15 days, have commonly shown that the rate of mineralization is negligible at wilting point and rises to a maximum at about field capacity. Between these limits, linear equations are often a satisfactory way of describing the relation (MacDuff & White 1985; Stanford & Epstein 1974). In soils wetter than field capacity, net mineralization generally decreases again. This shape of relation has been found in diverse soil types including many tropical soils (e.g. Choudhury & Cornfield 1978) although there are also reports of mineralization rate being relatively invariant over a broad range of water content above the permanent wilting point (Scholes *et al.* 1994). This phenomenon occurs particularly in soils with little decomposable organic matter (common in xeric conditions) where mineralization may be substrate limited (figure 1).

Measurements of net mineralization represent the balance between mineralization and immobilization

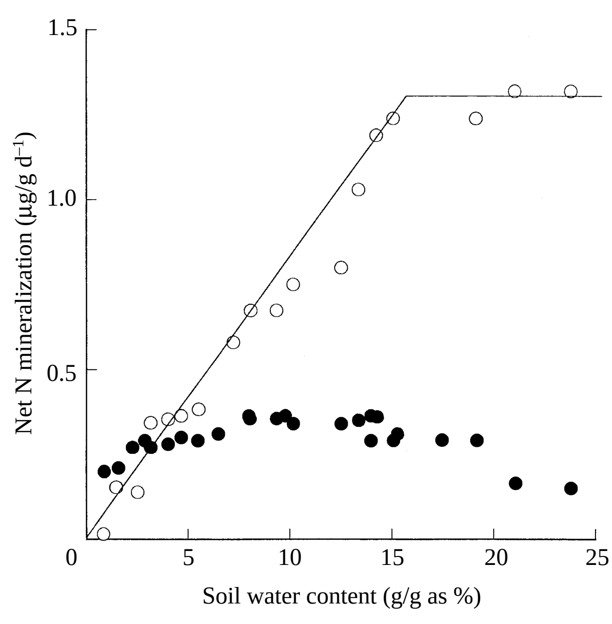

Figure 1. Relationships between net mineralization rate of nitrogen and water content for two Psamments from Nylsvley, South Africa; ○ 1.5% organic carbon, ● 0.6% organic carbon (from Scholes *et al.* 1994).

Table 1. *Influence of drying treatments at* 28 °C *on subsequent N mineralization* (μg g^{-1} *nitrate- and ammonium-N*), *during incubation for 21 days at* 25 °C *at a matric potential of* −7.5 kPa

(The matric potential of the initial soil was −10 kPa (from Seneviratne & Wild 1995).)

treatment	Thames series	Rowland series
untreated (−7.5 kPa)	29.0	9.2
dried to −100 kPa in 24 h	34.5	11.5
4 d at −100 kPa	40.2	11.7
dried to −1500 kPa in 24 h	46.2	14.5
4 d at −1500 kPa	60.1	15.2

consequent upon the continual cycling of humic materials to ammonium and back to humic materials. Gross mineralization can be assessed using $^{15}NH_4$ (Barraclough 1991), although only a few studies have been made in tropical soils (Pilbeam *et al*. 1993). In soils with sufficient amounts of carbon to allow significant immobilization, gross mineralization is usually substantially greater than net mineralization. For example, on a typic xeric Entisol in Western Australia, rates of gross mineralization of legume and weed residues applied to the surface were, on average, four times faster than those of net mineralization (Sparling *et al*. 1995). Measurements on an acriorthic Ferralsol at Kiboko, Kenya, showed a similar relation between rate of mineralization and soil water content as that found in other studies for net mineralization (Pilbeam & Warren 1995).

Rates of mineralization are affected by the recent history of wetting and drying (Birch 1958; Sorensen 1974). Table 1 shows that for two soils from the Reading area in the UK, the greater the intensity of drying in laboratory conditions, the greater the N mineralized after rewetting (Seneviratne & Wild 1985). The importance of this is considerable in those parts of the tropics with clearly defined wet and dry seasons. The classical studies of Birch (1958, 1960) showed that the flush of mineral N at the start of the wet season in East Africa was a result of the population dynamics of the soil microbes. Immediately after rain, the young population increases rapidly, utilizing relatively easily decomposable materials. These are derived in part from the drying and death of most of the old population, and in part from soil organic matter made decomposable by physical and chemical changes brought about by wetting and drying. Similarly, in anaerobic conditions, rates of denitrification may be influenced by the antecedent water regime (length of flooding) independently of the current water content probably as a result of temporary changes to the microbial population and supply of readily decomposable organic material (Dendooven *et al*. 1996).

Once mineralized, N may be rapidly lost by various processes including leaching, denitrification, and immobilization, depending upon the rainfall and wetness of the soil. This can be observed in results obtained under bare fallow at Machang'a, Kenya (figure 2). After the initial wetting and flush of nitrate-N, rain and increases in soil water were accompanied by decreases in nitrate concentration, while dry periods were accompanied by increases in nitrate (Warren *et al*. 1997). On all occasions following the initial rewetting, soil water content > 10 % was accompanied by a substantial decrease in nitrate concentration. Whether lost by leaching, denitrification or re-assimilation by soil organisms, such rapid changes in nitrate concentration are unfavourably matched to crop demand for nitrogen. The initial mineralization of N occurs at a time when crops are not established and later losses during rain showers occur when crops should be growing rapidly; in many cases, fertilizer N added early in the season would be lost before it could be taken up by crops.

The practical relevance of the flush of mineral N at the start of the growing season has been recognized for some time. The highest nitrate concentrations are typically found in tropical soils during the transition from dry to wet seasons (Wong & Nortcliff 1995). Semb & Robinson (1969) observed the flush of N at 13

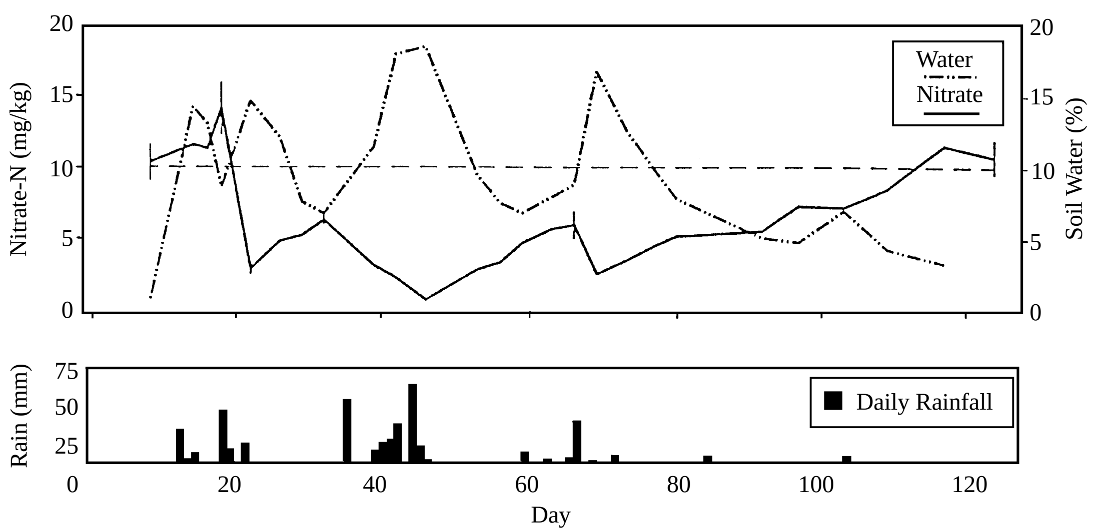

Figure 2. Soil water content and soil nitrate-N concentration under bare fallow at Machang'a, and daily rainfall. For nitrate, the bars are twice the standard error of the mean at days 8, 18, 22, 32, 66 and 124.

East African sites and found that it varied from 13 to 183 kg N ha^{-1}. This amount of N, if it were all to remain available, could contribute significantly to the N requirements of subsequent crops. A concentration of 10 mg N kg^{-1} soil (figure 2) in the upper 15 cm of the soil profile is equivalent to about 20 kg N ha^{-1}, sufficient to supply about 25% of the season's requirement for N in a crop of maize yielding 2 t grain ha^{-1}. Mineralization continues throughout the season and a soil with a total N content of 0.05–0.1% (typical of semi-arid regions) will supply 10–60 kg N ha^{-1} if 3% of the total soil N is mineralized.

Given the number of processes and transformations contributing to the concentration of mineral N in soil solution, it is hardly surprising that responses of crops in rainfed conditions are difficult to predict. The water–N relations are different for different processes and, as stated before, depend on the water content not just at the time but also in preceding periods. The result is that the supply of N to plants varies in a complex manner.

3. WATER USE AND AGRONOMIC MANAGEMENT

Water is often considered to be the principal factor limiting crop production in rainfed agriculture and optimizing the amount of water that can be transpired underlies much agronomic management. Manipulation of the water balance equation allows the water use efficiency (*WUE*) to be written:

$$WUE = (W/T)/[1+(E_s+R+D)/T], \qquad (6)$$

where *WUE* is defined in terms of biomass produced per unit of water lost from the soil profile, E_s is evaporation from the soil surface, R is runoff and D is drainage below the root zone. This equation makes clear that improved *WUE* (and hence crop dry matter production) can come about by either crop improvement that increases W/T (for examples, see Farquhar & Richards (1984), Dingkuhn *et al.* (1991)), or agronomic management practices that maximize T by reducing the other losses (i.e. water conservation). Increasing the total amount of water available to a crop (by, for example, irrigation) may increase crop yield but will only increase *WUE* if T is increased proportionately more than $[E_s+R+D]$ (Gregory 1989).

Several workers have drawn attention to the small proportion of rainfall transpired in rainfed cropping systems (Cooper *et al.* 1987*b*; Siddique *et al.* 1990; Pilbeam *et al.* 1995). Figure 3 shows how transpiration, as a proportion of total evaporation (E_s+T), varies with seasonal rainfall at sites in Kenya, Syria and Western Australia. In each location–season combination there are several data points, each of which was obtained from crops grown with different management. The Kenyan data are measurements from maize, bean or maize–bean intercrops grown at different plant densities (with or without N fertilizer) (see Pilbeam *et al.* 1995). The Syrian data are from winter barley (with or without N and P fertilizers) and either winter- or spring-sown chickpeas (see Gregory *et al.* 1984; Brown *et al.* 1989; Allen 1990). The Australian

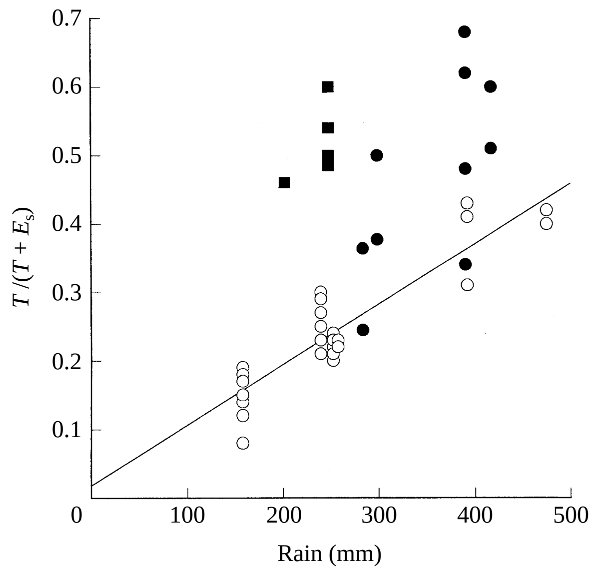

Figure 3. Relationship between $T/(E_s+T)$ and rainfall for Kiboko, Kenya (○), Breda and Tel Hadya, Syria (●), and Merredin and East Beverley, Western Australia (■).

data are from barley and wheat crops with either a range of planting densities or genotypes (see Gregory *et al.* 1992*a*; Yunusa *et al.* 1993). In all cases, T was obtained from the difference between total evaporation, estimated from the soil water balance, and the amount evaporated directly from the soil surface; E_s was estimated by a combination of direct measurement with microlysimeters and the use of simulation models verified in the appropriate environment.

Figure 3 shows that T, as a proportion of (E_s+T), increases with rainfall, so that in low rainfall environments a large proportion of rainfall is not used in transpiration and hence, crop production. There are several reasons for this low utilization of water, which are illustrated by the Kenyan data. First, more extensive canopies in wetter seasons reduce E_s as a result of several factors including (i) shading of the soil surface, (ii) impeded aerodynamic transfer of water vapour away from the soil surface, (iii) humidification of the air in the canopy immediately above the surface, and (iv) water extraction by roots, which reduces soil hydraulic conductivity and the upward flux of water through the soil matrix towards the soil surface. Second, wetter seasons tend to have more rain per rainfall event, resulting in a greater depth of wetting, which increases the total storage and reduces the proportion of rainfall lost as E_s in the few days immediately following rainfall (when E_s is relatively fast). Finally, wetter seasons tend to have more frequent rainfall events which results in a smaller average E_s per rain event.

Figure 3 also shows that crop management can have a substantial impact on the amount of transpiration (and hence dry matter production) in a given growing season. For the crops shown, D and R were negligible so that the principal effect of agronomic management practices was attributable to the effects on E_s. The Kenyan and Syrian results provide an interesting contrast with respect to the scope for reducing E_s

Table 2. *Comparison of evaporation from the soil surface from bare and cropped plots with sandy soils*

location	texture	leaf area index of crop	days of measurement	evaporation (mm) bare	cropped
Niamey, Niger (1991)	sand	0.8 max.	42 of 86 d	46	40
Niamey, Niger (1993)	sand	0–2.7	24 of 59 d	43	36
Beltsville, USA (1995)	sandy loam	1.8	10 after rain	10	8.2
Beverley, W. Australia (1992)	sand	2.0 max.	4 of 40 d	3.6	1.7

through improved crop management that can be related to differences in climate and soil. In northern Syria, rain occurs as frequent showers during the cool winter when evaporative demand is typically low (about 1–1.5 mm d^{-1}), so that the soil surface evaporates freely, though at a slow rate, for most of the rainy season. The soils at the Syrian sites were medium- to fine-textured with an unsaturated hydraulic conductivity sufficiently high to maintain E_s close to the evaporative demand. In contrast, the rainfall in Kenya was infrequent and often intense, and the evaporative demand was much greater (typically > 5 mm d^{-1}). The soil was a sandy loam with an unsaturated hydraulic conductivity that was insufficient to maintain E_s at the potential rate, even on the day following heavy rainfall.

There are two differences between the Kenyan and Syrian experiences shown in figure 3. First, for a given rainfall, the proportion of total evaporation that is transpired is greater in Syria. This is because the low evaporative demand results in a smaller proportional loss of rainfall than is the case in Kenya, even though the surface is effectively wet for much of the growing season. Second, there appears to be less scope for agronomic management to influence the partitioning of T and E_s in Kenya. In Syria, the large effects of fertilizer on reducing E_s have been well-documented (e.g. Cooper *et al.* 1987*a*), and have led to practical trials and recommendations for increased fertilizer usage (e.g. Jones & Wahbi 1992; Pala *et al.* 1996). In Kenya, however, the majority of E_s occurs during periods when it is limited by the movement of water through the soil rather than by the amount of radiation incident on the soil surface (i.e. evaporation is supply limited). Consequently, agronomic treatments such as fertilizer applications, although resulting in increased canopy size, have relatively small effects on E_s, whereas in Syria the same total amount of soil water will be evaporated by whatever route, so that management to minimize E_s is possible.

In other environments, too, increasing canopy size through better fertilization, increased plant density and use of improved varieties does not change E_s greatly (table 2). Typically the difference in E_s between bare and cropped soils is < 20% (except for the frequently rewetted sand in Western Australia), representing some 0.2–0.4 t ha^{-1} of grain in these crops. For millet crops grown in Niger on sandy soils, Daamen *et al.* (1995) found that improved agronomy reduced E_s by 12% and 16% in two seasons. They concluded that the effects of the canopy on the amount of radiation incident on the soil surface and on the aerodynamic transfer of water away from the soil surface were small compared with the greater drying of the near surface by root water uptake.

Although the scope for altering the balance between T and E_s may be limited, particularly in regions with high evaporative demand and with coarse-textured soils, there may still be scope for increasing T if significant water loss occurs through either R, or D, or both. Cultivation of Alfisols at Machakos, Kenya, into furrows and benches resulted in less runoff and increased maize yield (Kilewe & Ulsaker 1984). Daamen *et al.* (1995) compared a 'traditionally-managed' millet–cowpea intercrop (low plant density, no fertilizer, local varieties), with improved management (higher plant density, 45 kg ha^{-1} N and P, short-duration varieties) grown on a deep sandy soil during the rainy season in Niger. The total shoot mass produced by the improved treatment (3.4 t ha^{-1}) was almost twice that of the traditional crop (1.9 t ha^{-1}), although E_s from the improved crop (220 mm) was only about 15% less than evaporation from a bare fallow. Assuming that millet plants produce about 5 g dry matter (roots and shoots) per kg water transpired (Payne *et al.* 1992), and that root mass is 20% of total mass, then the improved crop must have transpired about 36 mm more water than the traditional crop. It was concluded that most of this water was derived from water that would otherwise have been lost by drainage below the root zone.

On sandy soils in seasons with high evaporative demand, improved agronomic management may have a greater influence on D than E_s. This is demonstrated in an analysis of drainage beneath millet crops grown on sandy soils in the Sudano–Sahelian zone (figure 4; Gaze 1996). The solid line is a regression for studies conducted on farmer-managed fields with no, or very low, fertilizer inputs and low plant populations. These studies suggest that about 80% of the seasonal rainfall > 240 mm was lost by drainage. In contrast, data from experiments at research centres on similar soils, where the crops were more intensively managed, showed much less drainage. These data suggest that there is scope for agronomic management to increase productivity although this may be at the expense of groundwater recharge. In Western Australia, the change from perennial vegetation to annual crops has increased groundwater recharge allowing saline watertables to rise (McFarlane *et al.* 1992). Current research seeks to develop management approaches that will improve crop yields and concurrently minimize drainage and land degradation (Greenwood *et al.* 1992; Gregory *et al.* 1992*b*).

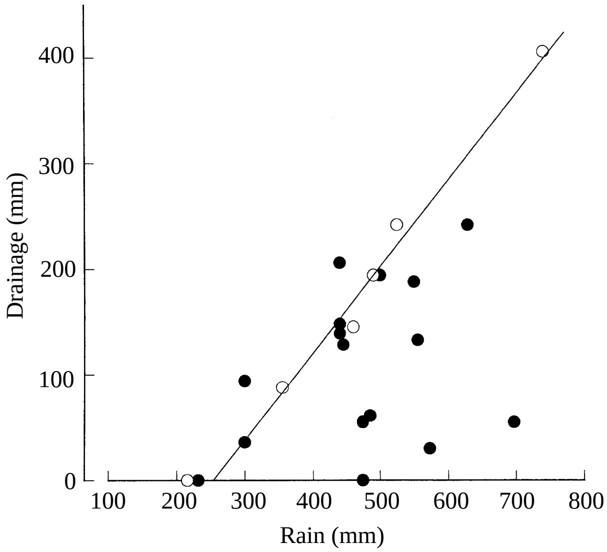

Figure 4. Values of drainage and rainfall determined for millet crops grown on sandy soils in the Sahel; crops grown on farmers fields (○) and on research stations (●). Adapted from Gaze (1996).

4. WATER AND THE RESPONSE OF CROPS TO FERTILIZER

Many reviews of semi-arid production systems have shown that the efficiency of N and P fertilizers depends on the rainfall received by the crop (e.g. Christianson & Vlek 1991) and that the response to N, in particular, is very limited in dry years. Similarly, studies in the Sahel have concluded that soil fertility is often a more important factor in rangeland and crop productivity than rainfall, so that effective management of water cannot be achieved without also correcting soil fertility constraints particularly N and P (Penning de Vries & Djitèye 1982; Payne *et al.* 1992). The result is that the limiting factors to crop growth during any particular season could be either water, or nutrient availability, or both.

Modest applications of N and P fertilizers have been shown to increase yields and water-use efficiency at a range of semi-arid locations (table 3), even in years of low rainfall. On the highly P-deficient soils of northern Syria, applications of P fertilizer to soils with sufficient N enhanced the rate of crop development so that anthesis and maturity occurred up to two weeks earlier (Shepherd *et al.* 1987). This advanced maturity as a consequence of P fertilizer has important implications in conferring a 'drought escape' mechanism on the crop as well as increasing yield. The effects of fertilizer on the growth of root systems are mixed. Penning de Vries & Djitèye (1982) found only very small effects of N and P fertilizers on root length of natural rangeland vegetation in the Sahel, although in northern Syria, root growth of barley was increased by fertilizer applications and this led to earlier water extraction in some seasons (Cooper *et al.* 1987*a*). In parts of New South Wales, Australia, where wheat crops are dependent almost wholly on stored soil moisture, applications of fertilizer or N fixed by previous legume crops may promote early growth and cause all available water to be used early in the season, resulting in crop death and no grain yield (Passioura 1986). This pattern of behaviour has rarely been reported elsewhere except during prolonged drought or conditions of extreme wind.

Field studies of the interactive effects of water and fertilizer generally show that crop response to N application is proportionately greater as rainfall increases, whereas responses to P are proportionately greater as rainfall decreases (Russell 1967; Jones & Wahbi 1992). Analysis of 75 trials conducted over four seasons in northern Syria showed that grain and straw yields of barley responded positively to N and/or P in 74 of the trials although the responses were highly variable (Jones & Wahbi 1992). Second-order multiple regressions based on mean rainfall values accounted for only 40% of the variance in yield response. Similarly analysis of 70 trials with wheat in slightly wetter locations also found variable responses to N (Pala *et al.* 1996). On average there was no response to N when rainfall was < 250 mm and the optimum grain production was achieved with applications of 40 kg N ha^{-1} at 350 mm rainfall, and 80 kg N ha^{-1} at 450 mm. In such environments it is impossible to specify widely applicable fertilizer recommendations because the rainfall is not known at the start of the season and conventional fertilizer trials provide only retrospective analysis.

The practical problem to be resolved in many semi-arid regions is how to apply the optimum amount of fertilizer to produce economically viable outputs in each season. Some have recommended the devel-

Table 3. *Effects of modest applications of fertilizer on shoot dry matter, water use and WUE*

(Data for crops of barley at Breda, Syria (from Cooper *et al.* 1987) and pearl millet at Sadore and Dosso, Niger (ICRISAT).)

crop	season	rainfall (mm)	fertilizer	dry matter (t ha^{-1})	water use (mm)	*WUE* (kg ha^{-1} mm^{-1})
barley	1981–82	324	+	6100	231	26.4
			–	4540	231	19.7
	1983–84	204	+	2880	176	16.3
			–	1340	171	7.8
millet	1984	260	+	4750	165	28.8
			–	2417	163	14.8
	1984	380	+	5000	247	20.2
			–	3100	270	11.5
	1986	440	+	3850	268	14.4
			–	1140	211	5.4

opment of 'response' farming based on probabilistic analysis of the approaching rainy season. This provides seasonally-specific fertilizer recommendations that are modified as the season unfolds (Stewart 1989). Improved techniques for analysing rainfall distribution and quantities in specific regions are a prerequisite of effective fertilizer recommendations in many agro-ecological zones (see Sivakumar & Valentin 1997). Tactical management of fertilizer applications dependent on seasonal climate forecasting systems offer some promise for the future (Hammer *et al*. 1996). In a case study of wheat production in Queensland, Australia, allowing for the Southern Oscillation Index demonstrated significant increase in profit (up to 20%) associated with adjusting N fertilizer and cultivar maturity.

5. GLOBAL CO_2 AND CROP PRODUCTIVITY

Substantial experimental and modelling work has been undertaken recently to determine the effects of elevated concentrations of CO_2 on crop productivity. Atmospheric [CO_2] is projected to increase from its current level of about 370 μmol mol^{-1} to twice that value by 2100, with a concomitant increase in mean surface temperature of 1–3.5 °C. The profitable use of supplemental CO_2 in glasshouses in the horticultural industry has demonstrated that elevated [CO_2] can accelerate plant growth and could potentially increase agricultural production. Typically, experiments have been conducted at ambient and twice ambient [CO_2] and show an increased productivity for C_3 plants averaging about 30% (range: −10 to +80%; Rogers & Dahlman 1993). The measured response for C_4 crops is much smaller than that for C_3 crops (table 4) and there have been few comparative studies with woody, perennial crops. The wide range of measured responses to elevated [CO_2] reflects not only differences between species but also the different experimental systems employed and the varying weather and soil conditions.

Although the basic physiological responses of photosynthesis and respiration to [CO_2] and temperature are well understood, responses of field-grown crops are less readily predictable because of year to year variations in weather and interactions with other environmental factors such as water and nutrients. The free air carbon dioxide enrichment (FACE) experiments (with 550 μmol CO_2 mol^{-1}) with cotton and wheat at Maricopa, Arizona illustrate this. Net photosynthesis of both crops responded similarly to increased [CO_2] but the seasonal changes of leaf area (affecting f in equation (1)), biomass and final yields responded differently (Pinter *et al*. 1996). Net photosynthesis was increased 20–30% at individual leaf and canopy levels in both crops when nutrient supply was good but by mid-season, the increase in biomass was about 20% in wheat and 40% in cotton. This advantage was maintained until the end of the season in cotton resulting in a 60% increase in lint yield in crops irrigated to replenish potential evaporation, and a 52% increase in crops irrigated to a proportion of potential evaporation. For wheat, however, the yield advantage was only 8% in the fully irrigated crop but still 20% in the partially irrigated crop (Kimball *et al*. 1995). Possible explanations for the different responses lie in the differences in growing period (wheat is a winter crop and cotton a summer crop in Arizona implicating a strong, positive [CO_2] by temperature interaction) and growth habit (wheat is determinate whereas cotton is indeterminate and has newly added fruits to provide a fresh sink for additional photosynthate). Additionally, elevated [CO_2] partially closed stomata in wheat, increasing canopy temperature by 0.6 °C in the fully irrigated crop. This resulted in senescence, and maturity was advanced by about one week thereby shortening the duration of grain-filling. These results and the outputs from various modelling exercises (e.g. Matthews *et al*. 1995) demonstrate that a major consequence of climate change is a shortening of the growing period in response to increasing temperature which may have either harmful or beneficial effects depending on the crop's growth habit and the water supply.

The interacting effects of [CO_2] and temperature have rarely been investigated in crop stands because of the experimental difficulties. Batts *et al*. (1997) grew diverse cultivars of winter wheat under fully irrigated and fertilized conditions in polythene tunnels and found that elevated [CO_2] increased the rate of canopy development (and hence f) even during the cool winter period. Effects on yield varied with genotype but generally there were negative interactions between elevated [CO_2] and temperature so that the beneficial effects of doubling [CO_2] on grain yield were negated by an increase of only 0.7–2.0 °C in mean seasonal temperature. Carbon partitioning between roots and shoots was also affected by temperature and [CO_2], showing a decline as temperature rose and an increase with elevated [CO_2].

Because the value of k (equation (2)) is related to the difference in [CO_2] inside and outside the leaf, increasing ambient [CO_2] increases the *WUE* of crop production. By inducing partial stomatal closure, water is conserved and transpiration reduced (table 4).

The interactions between nutrient availability and elevated [CO_2] are complex and the subject of much argument. Bazzaz (1990), among others, has suggested that plants respond less to elevated [CO_2] as the availability of nutrients (particularly N and P) in soils decreases. However, Lloyd & Farquhar (1996) reviewed 18 experiments (including trees and crops) in which N and [CO_2] were varied and showed that in half of the studies the relative growth at doubled [CO_2]

Table 4. *Effects of doubling atmospheric [CO_2] on transpiration, biomass and yield of selected crops*

(The values are the percentage change and 95% confidence limits (from Rogers & Dahlman 1993).)

crop	transpiration	biomass	yield
rice	-16 ± 9	$+27 \pm 7$	$+15 \pm 3$
wheat	-17 ± 17	$+31 \pm 16$	$+35 \pm 14$
maize	-26 ± 6	$+9 \pm 5$	$+29 \pm 64$
soyabean	-23 ± 5	$+39 \pm 5$	$+29 \pm 8$
potato	-51 ± 24	-15	$+51 \pm 111$

was as great under conditions of low N as at high N. They further produced a simple model based on three equations, one describing the dependence of photosynthesis on leaf [N], a second describing the rate of N uptake from the soil solution, and a third relating photosynthesis to growth. They demonstrated that low N availability can result in either higher or lower growth enhancement than well-fertilized plants. A key process in these estimates is the effect of N on respiration.

Looking beyond the complexity at the single plant level to the response of agroecosystems, the possible interactions become even more complex. Several studies suggest that the N cycle is a major regulator of production responses to elevated [CO_2] but there is a poor understanding of the carbon and nitrogen fluxes and transformations via roots, exudates, litter and soil organic matter. This leads to contrasting hypotheses for the expected sign of the feedback linking changed C and N cycles in elevated CO_2 (Koch & Mooney 1996). If soil mineral N is immobilized because microbial populations increase (because of more rhizodeposition), there will be negative feedback, but if microbes receiving C mineralize more soil organic matter thereby increasing N availability to plants, the feedback will be positive.

6. CONCLUSIONS

The supply of water affects both the microbial and chemical processes influencing the supply and loss of nutrients in soils and the transport of nutrients to the roots. Because temperatures in tropical soils are higher than those in temperate regions, the transformation of N is faster and more rapid gains and losses may occur, ill-matched to the cropping cycle. Splitting of fertilizer applications and timing them in relation to predicted or actual rainfall will prevent losses in wet seasons and wastage in dry seasons.

There is considerable scope for encouraging canopy expansion to conserve water by reducing E_s in environments where there is frequent rewetting of the soil surface, and where the unsaturated hydraulic conductivity of the soil is sufficient to maintain E_s at the energy-limited rate for prolonged periods (i.e. fine textured soils in winter rainfall environments). In contrast, in places where the soil is rarely wetted and most E_s is supply-limited (e.g. sandy soils in summer rainfall environments), enhanced water uptake by crops is most likely to be at the expense of D or R.

The greatest scope for intensifying crop production through increased use of fertilizers is in environments where there is a source of water to meet the enhanced transpiration. In places such as northern Syria where, in essence, increased T (resulting from increased growth as a consequence of fertilizer application) is paralleled by decreased E_s, crop production can be increased. However, in places such as Kiboko, Kenya, where there is relatively little scope for reducing E_s and insufficient rainfall for drainage, the scope for increasing crop production is small.

The impact of the global increase of atmospheric [CO_2] on agricultural production is uncertain because of the interacting effects of temperature, and water and nutrient supplies. At a field scale, the fertilization effect of CO_2 is likely to be much smaller than in controlled conditions and will, in any case, be of only little direct benefit in feeding the additional 2.5 billion people expected by 2020.

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Discussion

T. Batey (*University of Aberdeen, Scotland*). Besides nutrients, the inherent ability of a soil to produce crops can also be adversely affected by soil structure and soil compaction. In situations where the inherent capability is low or root penetration is limited by compaction then additions of nutrients are unlikely to be effective. To what extent do physical conditions determine the interactions between water and nutrients?

P. J. Gregory. It is correct that soil physical conditions play a substantial part in the interactions between water and nutrients. For example, as equation (6) indicates, agronomic water use efficiency will be reduced if soil surface conditions allow runoff. Similarly, if water has penetrated the soil but physical conditions limit root growth and hence the accessibility of water, then crop growth will be reduced compared with a soil with that limitation removed. However, there are many soils on which positive responses to nutrients can be obtained without removing all of the physical defects.

J. K. Syers (*University of Newcastle-upon-Tyne, UK*). Given that soil moisture appears to be a key to efficient N use, how useful is it to consider water and nitrogen separately and not their interaction?

P. J. Gregory. For many semi-arid regions I think that it is essential to consider the interaction because the interseasonal variation in rainfall is larger than the yield advantage (and economic benefit) to be gained from adding fertilizer. As I mention in my paper, there is a great need to combine modern approaches to climate analysis with fertilizer response curves so that tactical management of fertilizer applications can be improved and within-season advice communicated to farmers.

J. S. Wallace (*Institute of Hydrology, Wallingford, UK*). First, I should like to comment that the discussion between those advocating water or nutrients as separate or even rival factors limiting crop production is artificial. In reality, the limiting factors can change dynamically in time and space so that, for example, a situation that is initially fertility-limited may be alleviated by the addition of fertilizer, but then the limiting factor may become water. Second, Professor Gregory showed that different agronomic treatments increased T relative to $(T+E_s)$ (figure 3) from 0.1 to 0.2 in Kenya but was somewhat dismissive of this increase. Surely a doubling of the fraction of water transpired is a significant improvement?

P. J. Gregory. Dr Wallace is quite correct in his comment that for many crops there is no clear distinction between water and nutrient limitations; either or both may limit crop growth in different parts of a field or at different times in a season. The reason that I did not make much of the scope for increasing T in the Kenyan results was that dry matter production was not significantly affected by any treatment. Poor root growth, possibly because of mechanical impedance, meant that although treatments affected T there was no effect on yield.

M. V. K. Sivakumar (*World Meteorological Organization, Geneva, Switzerland*). Professor Gregory referred to the effects of CO_2 enrichment on nutrient use efficiency. However, another aspect of climate change that has implications for organic matter dynamics is temperature. With the projected increase of 2–4 °C, semi-arid and arid regions could be adversely affected because their maximum temperatures are already 38–40 °C at the start of the season. Should we not pay more attention to the effects of the elevated temperatures on organic matter dynamics and nutrient mineralization?

P. J. Gregory. Dr Sivakumar is right to draw attention to the possible consequences of higher temperatures for soil organic matter dynamics. There is a large research programme investigating these effects both in national and international organizations. For example, the Global Change and Terrestrial Ecosystems (GCTE) project has an international group of experiments and modellers attempting to understand such effects through its Soil Organic Matter Network (SOMNET).