

# THE PRINCIPLES OF COTTON WATER RELATIONS AND THEIR APPLICATION IN MANAGEMENT

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## Abstract

The keys to understanding the principles of water relations that are specific to cotton are found in: (i) the ecology of the wild ancestors of cotton (xerophytic shrubs), (ii) the basic pattern of development (the orderly and regular production of mainstem nodes, lateral fruiting branches and fruiting sites, and the progression at each fruiting site from floral bud through to open boll or shed fruiting form), (iii) relative sensitivity of these developmental processes, and the growth physiological processes, to water stress. The biological and agronomic responses to variation in water supply are reviewed and interpreted in light of this understanding. Cotton is well adapted physiologically for both rain grown and irrigated production, and economically for both production on plantations and small holdings. The relative importance of rain grown and irrigated cotton on a global scale are considered. The management requirements of each in respect to optimising use of water discussed. Effects of excess water (water logging) are as important as water deficits.

Technological developments relevant to water relations can be broadly classified as software (rules of thumb, indices, plant mapping, osmotic adaptation, computer models and decision support systems) and hardware (neutron probes, pressure chambers, infra-red thermometry, drip irrigation, lateral shift and centre pivot irrigation). Their use in management and research applications is discussed. Management should aim to optimise the use of limited water resources, be it rainfall or irrigation supply, by maximising returns per unit input and minimising environmental impact. Management decisions have to be made at policy, strategic and tactical levels and appropriate software and hardware selected. There are specific important challenges and opportunities: management of limited irrigation water supplies; environmental impact of irrigation on salinity, and pesticide and nutrient pollution; the use of urban domestic wastes and saline drainage water; interaction of water with other factors; and risk analysis.

## Introduction

While it is axiomatic that water is essential for the growth of cotton, as it is for any crop, cotton's xerophytic adaptation confers a distinctiveness on the water relations of the crop that is unusual if not unique among field crops. Despite these xerophytic origins cotton is widely grown as an irrigated crop. There has been no definitive study of the proportion of the global cotton crop that is irrigated, although Ayalon (1983) says that most cotton in the world is rainfed and Waddle (1984) asserts that more than 60% of the world's cotton is irrigated. By collating all the available data (see Appendix) it is estimated that 53% of the area of land growing cotton in the world is irrigated. Figure 1 shows that this percentage is not uniformly distributed around the globe but varies among climatic regions.

A broad belt of irrigated cotton extends across the world from Spain in the west to the Punjab of Pakistan and India in the south east and Xinjiang province of China in the north east. It includes countries bordering the Mediterranean (Greece, Morocco, Egypt, Turkey, Syria and Israel), takes in the Sudan to the south, and passes through Iran, Afghanistan and the Central Asian republics (Azerbaijan, Turkmenistan, Uzbekistan, Kazakhstan, Tadjikistan, and Kirgystan). There are similar areas in the west of North and South America. These regions have mediterranean or desert climates, and cotton is fully irrigated without significant rainfall during the growing season.

By contrast, in Central and South America, and in Africa south of the Sahara, cotton is almost entirely rainfed. These are tropical and subtropical summer rainfall areas. Cotton is also rainfed in the Gujerat of India and in SE Asian countries.

Between these extremes cotton is grown with varying amounts of supplementary irrigation in semi-arid and humid regions. The percentage of the crop irrigated depends on both the amount of rainfall and the extent of technological development. In eastern Australia, with a semi-arid climate, about 90% of the crop receives supplementary irrigation. In United States the proportion of supplementary irrigation declines to the east -43% in the south west (Texas and Oklahoma), 30% in the Delta and 11% in the south east. China irrigates most of its non-desert cotton despite a more humid climate; 75% is irrigated according to Bell and Gillham (1989), 95% according to ICAC (1993b). In India with the largest area of cotton in the world and a monsoon climate, outside the fully irrigated Punjab and the fully rainfed Gujerat, 13% of the crop in the central region and 18% in the southern region receives supplementary irrigation.

In the perspective of global irrigation, irrigated cotton accounts for 7.3% of irrigated land in the world, compared with 61% for rice. Cotton uses much less than 7.3% of the water resources, given the quantities required by rice. In the countries that grow cotton, the crop occupies 26% of the irrigated land **not** used for rice. It must be stressed that these percentages relate to areas of irrigated land, not quantities of irrigation water.

Not unexpectedly the higher the proportion of the crop irrigated in a country the heavier is the yield. Statistical analysis shows that one third of the variation in mean national yield amongst the countries is associated with the percentage irrigated. The mean global yields of rainfed and irrigated cotton are 391 and 854 kg lint per ha respectively. However the heavier yield associated with irrigation cannot be attributed to irrigation alone because irrigated crops usually receive heavier technological inputs such as fertiliser and pesticides. Because irrigated crops on average yield 2.26 times as much a rainfed crops, 73% of cotton fibre in the world is produced under irrigation from 53% of the land growing cotton.

Water relations play a role in distinguishing tropical from temperate production, as well as rainfed from irrigated production. In tropical production the beginning and length of the growing season are determined by water supplies, whether rain or irrigation, whereas in temperate production they are dependent on temperature.

In most countries, whether crops are rainfed or irrigated, cotton production is limited by crop water supply (Bielorai *et al.*, 1983). For rainfed crops rainfall is a major determinant of yield, and crops experience droughts of varying severity in some if not all years. Supplies of irrigation water are limited in many regions, and irrigators face increasing competition from urban users and environmental needs. Using water efficiently is therefore a key issue, whether for rainfed or irrigated production. It is significant and pleasing to see so many papers at this conference referring to water use efficiency (P.O. Cull, and D. Robson, pers. comm.; Gerik and Landivar, these proceedings; M.R. Ghaemi and H. Siadat, pers. comm., Hutmacher *et al.*, these proceedings; V.R. Reddy and B. Acock, pers. comm.; S.M. Farah and A.A.A. Rahman, pers. comm.; J.C. Gutierrez, M. Lopez and E.O. Leidi, pers. comm.; M. Malik, pers. comm.).

The theme of water use efficiency (WUE) will recur throughout this review. Many of the topics covered are not specific to cotton, such as evapotranspiration, osmotic adjustment, irrigation technology and irrigation, and these will not be dealt with in as much detail as topics that are specific to cotton. While built on the foundations of previous reviews (Hearn, 1979; Jordan, 1982; Bielorai *et al.*, 1983; Grimes and el Zik, 1990), this review attempts not to supplant them but to complement them, by being global rather than national in its scope, ecological as well as agronomic in its perspective, and strategic as well as tactical with regards to management.

## **Principles: the Biology of Water Relations**

### *The ecology of the wild species of cotton*

The wild species of cotton and the centres of origin of the cultivated species are found in the arid and semi-arid tropics and subtropics. When discussing water relations of cotton it is almost mandatory to allude to these xerophytic origins, as a source of drought resistance (Ray *et al.*, 1974). Although mandatory, the reference to xerophytic origins is usually cursory, and has been largely

ignored in studying the physiology of the water relations of the crop. Wild species have been studied more for genetic sources of drought tolerance, than for understanding water relations. The keys to understanding the water relations of the crop lie in the xerophytic origins. Sound management depends on understanding and manipulating the mechanisms and strategies which adapt the crop to hot arid environments.

The genus *Gossypium* comprises some 50 species of which only four are cultivated. The wild species are xerophytic perennial shrubs found in three broad regions of the arid and semi-arid tropics and subtropics: Africa-Arabia, America and Australia. These regions include both summer and winter rainfall areas, as well as deserts. The common feature is long periods of drought which the genus is well adapted to survive.

Fryxell (1986) identifies several strategies that different groups of wild species use to enable them to survive arid conditions (Table 1). One group has life cycles adapted to growing vegetatively when water is abundant and deferring fruiting until the start of dry season, followed by dormancy during the rest of the dry season. Another group has morphological adaptations including a compact habit and a leaf structure to minimise water loss but in contrast to the first group these species simultaneously grow vegetatively and reproductively. A third group is adapted to occupy (grow preferentially in) dry stream beds subject to flash floods. The plants remain dormant waiting for a flood. As soon as water recharges the root zone, a new cycle of development and growth starts. As the stored water is exhausted, morphological development (morphogenesis) stops and existing fruit are matured. The plant becomes dormant again until the next rainfall or flood event not only restarts the cycle but disperses the seeds which fell into the litter at the base of the plant (Hearn, 1968).

Although drought tolerance in cotton has been questioned (Karami *et al.*, 1980; Krieg and Sung, 1986), and Passioura *et al.* (1993) have made a strong case for abandoning the term for all crops, it is useful to compare Fryxell's groups in Table 1 with May and Milthorpe's (1962) widely accepted classification of drought resistance. There is a partial matching. The first two items in each list clearly correspond, but there is a mismatch of the third items. Fryxell made no claim that his list was exhaustive. His groups may not be mutually exclusive, and his first and third group probably overlap. and cultivated species show some aspects of both, as well as osmotic adjustment which would confer May and Milthorpe's third type of resistance, drought tolerance with low plant water potential.

In describing a wild *G. hirsutum* that clearly belongs to Fryxell's first group with lifecycle adaptation, Lee (1984) identifies three environmental factors that trigger fruiting: (i) soil water insufficient to sustain vegetative growth, (ii) a temperature differential between day and night, (iii) decreasing photoperiod. Hutchinson *et al.* (1947) observe that some wild species and primitive races of the cultivated species are also sensitive to wet conditions which trigger facultative shedding of fruiting forms (floral buds and fruit). This response delays the setting of fruit while vegetative growth continues. Thus these wild species and races behave as though they are sensitive to "signals" regarding the water supply at both the wet and the dry end of the range. Plants that have started to produce floral buds appear to respond to these "signals" by switching solely to vegetative growth at the wet end by shedding buds and fruit, solely to reproductive growth at the dry end by terminating vegetative growth, and to concurrent vegetative and reproductive growth between the wet end and the dry end. These adaptive responses to the water regime are expressed diagrammatically in Figure 2 in which "wet" and "dry" reflect both atmospheric and soil conditions. At the wet end of the range the soil is near the upper limit of plant available water and the atmospheric demand is low, and visa versa at the dry end. The nature of the "signals" will be discussed later in the section entitled "Evapotranspiration, Water Deficits and Stress".

During domestication modern varieties have largely lost sensitivity to temperature differential and photoperiod, though there are vestigial effects (Mauney, 1966; Low *et al.*, 1969). However modern varieties are still sensitive to the water regime. With dry conditions vegetative growth is terminated while reproductive growth continues. Once this happens, it is very difficult to restart vegetative growth and produce more squares (floral buds) until the bolls (fruit) already set have matured, even though the water supply is restored. The plant behaves as though it senses a signal

from the dry end which triggers a switch which cannot be reversed until the end of the fruiting cycle.

Although Hutchinson (1947) says that facultative shedding at the wet end of the range has been lost from modern varieties, they are still sensitive under some conditions. For example, in the Shire Valley, Malawi (Hearn, 1962) and the Ord Valley, Australia (Hearn, 1975a,b) crops respond to more frequent irrigation with an increase in shedding of young bolls in hot humid conditions. It is as though in hot humid weather plants can sense a signal from the wet end which triggers facultative shedding. This response contributes to the rank growth syndrome that can occur under such conditions and which is characterised by shedding of fruit, long internodes, and excessive height and leaf area.

The sensitivity to the water supply has a profound effect on crop performance which is important for managing the crop, particularly maintaining the balance between vegetative and reproductive growth. These adaptive responses to the water regime confer reproductive flexibility on the plant in the face of a variable and unpredictable water supply. The indeterminate habit confers further flexibility which has largely been ignored in drought resistance of cotton, though its ecological role is widely recognised (Stebbins, 1974). The role of the indeterminate habit is considered in the next section.

### *Influence of water supply on morphogenesis and development*

The morphological development of the plant follows an orderly and regular pattern. Development is indeterminate; the mainstem never terminates in a flower (to talk of determinate and indeterminate varieties is an absurdity). The mainstem produces a new node at regular intervals, usually every two to three days. The lateral fruiting branches are subtended from the mainstem nodes. The first usually appears between the 5th and 8th node in modern *G. hirsutum* varieties. Fruiting sites, initially occupied by floral buds, are produced at regular intervals along a fruiting branch, usually one every five to six days. The rate of site production on a lateral branch is closely coupled to the rate of mainstem node production so that there is a constant ratio between them. The characteristic pyramidal shape of the cotton plant results. The fruiting form at each fruiting site develops from the floral bud through anthesis to an open boll. The rate of morphological development (mainstem and laterals), and the rate of fruit development are both controlled by temperature. The effect of temperature can conveniently, but not very accurately, particularly in the case of fruit, be described by day degrees.

As the plant develops the number of fruit and their demand for assimilate initially increases exponentially, while assimilate supply increase asymptotically as leaf area increases. Consequently the inevitable result is increasingly severe competition for assimilates. In response, morphological development of the mainstem and laterals slows down, and eventually stops when the fruit load is large enough to monopolise the whole carbohydrate supply. By contrast development of individual fruit do not slow down. Instead an increasing proportion of fruit abort their development, and are shed, usually as young floral buds or young bolls.

The vegetative branches, which are produced on the mainstem below the first fruiting branch, and which replace the mainstem if the growing point is tipped out, develop in a similar manner to the main stem.

The simplest example of the influence of water supply on morphogenesis is a crop grown entirely on stored water from a single irrigation applied prior to planting and without rainfall. This ancient method of crop production is still practised in the deltas in the deserts bordering the Red Sea and the southern coast of the Arabian peninsula (Hearn, 1969). It is an ingenious way to use the erratic spate floods of short duration which run off nearby mountains and are impounded on the fields in order to store the water in the soil. The crop grows entirely on this stored water. Development and growth are unaffected by water supply until approximately three quarters of the supply is exhausted, whereupon morphological development and vegetative growth stop abruptly, while the fruit already set continue to grow and mature.

These conditions are remarkably similar to the natural environment of wild species already mentioned. This similarity is strikingly illustrated in southern Yemen where the indigenous wild species *G. areysianum* occasionally occurs as a weed in cultivated crops of modern varieties of *G. barbadense* and *G. hirsutum*, utilising the same adaptive features. The seed is carried by flood water from natural habitats to cultivated fields, often germinating and establishing plants along the high water mark on the banks that impound the flood waters that irrigate the crop (Hearn, 1968).

The root and shoot development resulting from different amounts of stored water are shown in Figures 3 and 4 respectively. The root system explores the soil to the depth wetted, and is capable of penetrating to a depth of at least 3 m. The plants with different amounts of stored water develop at the same rate unaffected by the amount of water, until approximately three quarters is exhausted, whereupon morphological development and vegetative growth stop abruptly. Consequently the final size and shape of the plants grown with different amounts of stored water look like successive stages of one crop, which in effect is what they are.

This pattern of development is well adapted for survival in arid and semi-arid environments where the water supply from rainfall or floods is erratic and variable. It allows the plant to make full use of supplies which can vary greatly from one event or season to the next. When the supply is large, development continues for longer to give a larger plant and heavier yield; when the supply is small the reverse occurs. The key is that the plant somehow recognises that the water supply is running out (the dry "signal" in Fig. 2), and in response stops further morphological development and concentrates on maturing the fruit already set.

The development of rainfed and irrigated cotton are variations of this basic pattern. A succession of drying cycles replaces the single prolonged cycle. The farmer controls length and amplitude of the cycle in an irrigated crop. Rainfed crops experience irregular cycles of varying length and amplitude. In either case, if the drying cycle continues long enough, the point is reached at which the plant recognises that the water supply is running out and stops morphological development. The crop matures the bolls already set. Even if rainfall or irrigation subsequently restores an adequate water supply, morphological development, and therefore production of more fruit, will not be resumed until the fruit already set have matured. In their classical study of the water requirements of cotton in Uganda, Hutchinson *et al.* (1958) identified the termination of exponential expansion of leaf area index (LAI) by water shortage as a major determinant of yield; the later it occurred, the larger the plant and the heavier the yield. It was triggered by a specific soil water status and was irreversible. Their observations and conclusions can be interpreted in terms of a dry end "signal" from the soil and a "switch" "in the plant. The aim of management is to keep the water regime between the wet and dry "signals" (Fig. 2) for as long as possible, either by selection of sowing date (Rijks, 1968) and conservation of rainfall for rainfed crops, or by timely irrigation.

#### *Influence of water supply on other physiological processes*

As well as influencing morphogenesis and development, water supply affects numerous physiological processes involved in growth, defined as the increase in size and mass of the organs produced by morphogenesis and development. In earlier reviews, Hearn (1979) and Jordan (1982, 1986) concluded that cell expansion is more sensitive than stomatal closure to water deficit. Consequently, processes dependent on cell expansion, such as expansion of leaf area and increase in height, are more sensitive to water deficits than those associated with stomatal closure, such as photosynthesis and transpiration. These conclusion have been confirmed by recent work (Turner *et al.*, 1986; Puech-Suarez *et al.*, 1989).

The processes involved in growth and affected by water deficit vary not only in their relative sensitivity, but also in their position in the sequential chain noted by Jordan (1982). Thus there are two dimensions to the effects of water deficit on physiological processes, and these have been represented diagrammatically in Figure 5. The first processes affected by a deficit, on the left in Figure 5, are cell expansion, mesophyll resistance and stomatal resistance. These are followed by the second order processes leaf growth rate and rate of photosynthesis at the leaf level, and so on until yield is affected. A third dimension, not shown in Figure 5, is the timing of the deficit in the

life cycle of the crop. As the canopy approaches closure, further cell expansion, leaf growth and LAI expansion become less important as determinants of yield that can be affected by water deficits.

Krieg and Sung's (1986) experiment is an exception to this well documented pattern. They found that leaf number was more sensitive to water deficits than leaf size, implying that node production was more sensitive than leaf growth.

Figure 5 shows that there are several routes between a deficit and yield. Consequently, as Jordan (1982) emphasised, water deficits can reduce yield by the most sensitive route (the uppermost, through cell expansion, leaf growth rate, LAI expansion, light interception and canopy photosynthesis) without affecting the rate of leaf photosynthesis. There are two routes for a deficit to affect leaf photosynthesis; stomatal control is more important in humid climates, and controlled environments while non-stomatal (or mesophyll) control is more important in hot arid climates.

Krieg and Sung (1986) state that the major direct effect of water deficits on photosynthesis is on source activity not sink activity. Translocation is less sensitive than photosynthesis to water deficits and as the deficit increases an increased percentage of exported assimilates accumulate in fruit (Krieg and Sung, 1986).

Krieg (1986) cites six papers reporting that water deficits induced stomatal closure in cotton, and thus greatly reduced gas exchange and photosynthesis, but he also notes other papers reporting that stomata remained open and maintained conductance under water deficit while photosynthesis was reduced by non-stomatal control. Ephrath *et al.* (1990) and Radin (1992) have since confirmed that stomata remain open despite a water deficit sufficient to cause zero turgor, visible wilting of leaves and reduced photosynthesis.

In the light of these conflicting observations, Radin (1989, 1992) found the widely accepted hypothesis of Cowan and Farquhar (1977) and Cowan *et al.* (1982) inadequate to account for stomatal response of cotton to water deficits. This hypothesis states that stomata open and close to optimise WUE of gas exchange, which is achieved by coupling the rate of photosynthesis and stomatal conductance in order to maintain constant internal CO<sub>2</sub> concentration. The coupling results in the stomata closing to the degree needed to match gas exchange (CO<sub>2</sub> and water) thus optimising the processes in order to maximise WUE. It is further postulated that the coupling is mediated by the hormone abscisic acid (ABA). After reviewing the evidence in relation to cotton, Radin (1992) concluded: (i) at high temperatures the rate of photosynthesis and stomatal conductance become uncoupled, because high temperatures reduce ABA levels; (ii) the result of the uncoupling is to maximise the rate of transpiration which causes substantial evaporative cooling of leaves below air temperature at the cost of failing to conserve water and maximise biological WUE, thus conferring heat tolerance, possibly at the cost of drought tolerance, and which has been enhanced by selection in modern varieties; (iii) coupling of turgor and stomatal closure are not obligatory because not only have stomata been observed open at zero turgor, but they close at high turgor when N is deficient (Radin *et al.*, 1985).

Consequently Radin (1992) proposed an alternative hypothesis which states that stomata open and close to optimise leaf temperature, referred to as the TKW hypothesis. (TKW is the thermal kinetic window which is the optimum range of leaf temperature for enzymatic action, a concept discussed in the next section.) The adaptations embodied in the WUE and TKW hypotheses cannot coexist simultaneously, but are not in conflict and are expressed as the environment demands.

Radin (1992) suggests that the effects of temperature on ABA may account for the well established difference between field-grown cotton and that grown in controlled environments in stomatal response to water deficits, e.g. Jordan and Ritchie (1971), rather than acclimation by past deficits and consequent osmotic adjustment. Both mechanisms probably contribute to the difference.

The loss of coupling of turgor, stomatal conductance and photosynthesis is a feature common to desert species (Raschke, 1975). Since it fails to conserve water and maximise WUE, its survival value must relate to evaporative cooling, heat tolerance being more important in a hot arid environment.

Nevertheless there are anomalous experimental results that are not consistent with these hypotheses. Experimenting at temperatures at least as high as Ackerson *et al.* (1977b) in Texas, if

not as high as Radin's in Arizona, Puech-Suanez *et al.* (1989) in California and Turner *et al.* (1986) in Australia found water deficits decreased stomatal conductance resulting in a nonlinear relationship between leaf photosynthesis and stomatal conductance as the deficit increased, whereas Ackerson *et al.* (1977b) found stomata remained open though photosynthesis decreased. Regardless of whether the stomata close or not, in the field there is a consistent response of net photosynthesis to increasing water deficit with a steady decline starting relatively early in the drying cycle (Table 2). In two out of three cases the final rate was still an impressive 25 or 30% of the rate with minimum deficit.

### *Evapotranspiration: water deficits and stress*

Clearly many physiological processes in cotton are affected by water deficits, but mechanisms by which deficits influence these processes are not clear. The concept of a "signal" was introduced with Figure 2. Is use of the term justified? The term "stress" has been avoided so far. Can water stress be defined? What degree of deficit constitutes stress? Discussion of evapotranspiration and the origin of water deficits will introduce answers to these questions.

Evapotranspiration (ET) is loss of water vapour from the crop to the atmosphere, and is the sum of evaporation from the soil surface (E) and transpiration through the plant (T). ET depends on evaporative processes that require energy. The potential ET depends on meteorological factors, the energy available and the sink strength of the atmosphere for water vapour. It is not influenced by crop factors apart from canopy "roughness" affecting turbulence (a secondary-level effect), it is common to all crops and there is not a rate specific to cotton. The physics of the process are beyond the scope of this review.

Actual ET equals potential evapotranspiration early in the drying cycle of a crop with full cover intercepting all incoming solar radiation. However actual ET is influenced by crop factors such as the rate at which the canopy develops to intercept solar radiation and the response of the crop to water deficits as the water supply is depleted. Both E and T are energy limited early in the drying cycle, and supply limited later in the cycle. There are many formulae and models for calculating both potential and actual evapotranspiration (Ritchie, 1972; Doorenbos and Pruitt, 1977).

A soil water deficit occurs when, as a result of loss of water by evapotranspiration, the water content of the soil falls below the drained upper limit (or field capacity). Plant water deficits occur when the plant transpires water faster than it can take up water from the soil, that is when demand exceeds supply. As a deficit develops in the soil or the plant, the energy status or potential of the remaining water decreases. For three decades leaf water potential (LWP) has been measured to characterise plant water status, and more recently to monitor crops for irrigation scheduling. LWP typically displays a diurnal cycle with lower values in the middle of the day and recovery at night. The low mid day values indicate a deficit when water cannot be supplied at the rate at which it is being transpired.

Until recently it was widely accepted that the effect of water supply on physiological processes in the plant was somehow mediated though plant water potential, and one of its components, turgor potential. During the last ten years a vigorous debate has developed over the mechanisms by which water supply controls plant growth and development. There is now serious doubt about the importance of plant water potential, and its physiological significance is not known (Passioura, 1988). The correlations found between water potential and plant activities such as stomatal conductance, photosynthesis and growth rate have not been proven as cause and effect. Turgor was thought to be the controlling mechanism for stomatal closure and cell expansion, though correlation between expansion rate and turgor were poor and the effects of turgor on cell expansion are transient and soon overridden.

Evidence is accumulating from several sources that plants react to drying soil with a fall in leaf growth rate and stomatal closure well before there is a detectable change in LWP, apparently in response to signals received from roots (Passioura *et al.*, 1993). Roots sense "difficult" soils conditions (drier or harder) and send inhibitory signals to leaves to slow down expansion and close stomata well before fall in shoot water status or the supply of water is affected (Passioura *et al.*,

1993). These are feedforward signals to which the plant responds by slowing growth in anticipation of future adverse conditions (Passioura and Stirzaker, 1993). These signals override water status of the shoot (Passioura *et al.*, 1993), and are possibly hormonal consisting of increased production of abscisic acid (ABA) or reduced production of cytokinin (Passioura and Stirzaker, 1993).

The existence of these roots signals throws light on the use of the term "signal" in Figure 2. Although much further research is needed to prove that the signals in Figure 2 exist and to unravel details of the mechanisms, these findings show how the signals might be sensed and transduced by the plant. Despite these root signals LWP and turgor are still important because turgor is essential for cell expansion. Turgor powers cell expansion but does not control it as turgor is often overridden by the signals from the roots.

Plants experience a deficit every day during the diurnal cycle of LWP but they are not necessarily stressed. In an agronomic context, stress can be defined as a deficit that leads to a reduction in the economic returns from of the crop by reducing yield or quality. Such a definition differs from stress in a physiological context where the issue may be whether a particular processes is affected or not, or in an ecological context where survival within or between generations is important.

This agronomic definition of stress is satisfactory as a concept, but is hard to define in terms of a specific soil or plant deficit, if LWP is used to define plant deficit. There is no unique soil water deficit that will cause an agronomic damaging plant deficit, because the plant water deficit is dependent supply and demand. Demand depends on atmospheric factors. Supply is not water content of soil *per se* but the rate at which water can move to the plant's roots, which is a function of soil water content and the root system. Thus the soil water content or deficit needed to cause a specific plant deficit is not constant, but depends on atmospheric conditions and the root system.

Furthermore, there is likewise no unique critical plant water deficit at which agronomic damage starts and stress occurs. There are several reasons for the lack of a unique plant threshold: (i) osmotic adjustment and cycling which maintains turgor when LWP falls (Cutler *et al.*, 1977; Radin *et al.*, 1986; Turner *et al.*, 1986); (ii) the many routes between deficit and yield or quality, to be discussed later; (iii) the issues raised by Passioura (1994) discussed three and four paragraphs earlier.

Although a good case could be made for abandoning the use of the term "water stress" on the grounds of ambiguity and confusion, it is so deeply entrenched amongst agronomists that its use is unavoidable. In environments with consistent evaporative demand, such as mediterranean or desert climates, it is possible to identify location-specific deficits in terms of LWP for stress. These deficits for stress are not universally applicable. In Australia for example evaporative demand is very variable within and between seasons. A soil based parameter, measured or simulated, may be a better indicator of stress. Even this is not foolproof as the same soil water content can give stress one day and not the next, depending on evaporative demand.

An alternative approach to defining stress is to use canopy temperature. Transpiration (T) is an evaporative cooling process for the plant. In the supply limiting phase of T in the drying cycle, when actual transpiration is less than the potential rate, evaporative cooling of foliage is less effective because the energy that is not dissipated in evaporation of water vapour heats plant tissues instead. The resultant rise in canopy temperature indicates water stress. The development of infrared thermometry has enabled canopy temperature to be readily measured in order to assess water stress (Jackson, 1982). The difference between canopy and air temperature alone is an inadequate measure of water stress. Other influences on the energy balance, particularly evaporative demand (measured by vapour pressure deficit), are included to account for differences among environments, resulting in a crop water stress index (CWSI) for cotton. Idso *et al.* (1981) has proposed an empirical CWSI and Jackson (1988) a theoretical version.

As an alternative to CWSI, the concept of the thermal kinetic window (TKW) has been proposed in order to provide a more mechanistic link between canopy temperature and crop growth and performance. The concept incorporates the effects of tissue temperature on species specific enzyme kinetics in the plant. The TKW is the canopy temperature range for optimal enzyme function and purports to integrate the effects of not only water stress but also ambient temperature

on crop growth and performance. Burke *et al.* (1988) determined that the specific TKW for cotton was 23.5 to 32°C, and reported a linear relationship between the time canopy temperature was within the TKW and dry matter production.

Further research into root signals may lead to defining stress in terms of soil conditions that elicit a signal, independent of current plant water status. However these also will be location- and soil-specific, not universal. A further limitation is that this behaviour is essentially conservative and in some situations it will be beneficial. A slowing down of shoot growth in response to soil water status could be deleterious in an irrigated crop by limiting yield potential and thus constitute stress, and beneficial in a rainfed crop by matching yield potential to anticipated water supplies.

### *The integration of water deficit effects at the plant level*

In order to have a more complete picture of the processes through which water deficits affects yield and WUE, the diagram in Figure 5 has been extended to include development and transpiration. The extended diagram is shown in Figure 6. Arrows have also been added to show routes through which deficits can reduce yield, creating a rudimentary but incomplete flow chart.

As cell division and differentiation are less sensitive than cell expansion (Hsiao *et al.*, 1976), morphogenesis continues as already described, unaffected by water deficit long after leaf growth and photosynthesis are affected. Cell division and differentiation take their place below stomatal resistance as the least sensitive of the first order of processes affected by water deficit.

Among the second order processes, rates of square and node production are dependent on cell division and differentiation and therefore relatively less sensitive than those above them. The observations already described of crops grown on stored water with a long drying cycle suggest square and node production are not affected until cell expansion finally stops and prevents the appearance of newly initiated organs.

The ranking in Figure 6 among leaf, stem and root growth is based on the intuitive assumption that when water is in short supply the organs closest to the source will take priority. Implicit in this assumption is the notion of a gradient of water potential between soil and leaf giving differences in turgor, as observed in cotton by Oosterhuis and Wullschleger (1987).

The role of turgor in determining relative sensitivity to water deficits of leaf, stem, root, and boll growth is debatable in the light of recent findings that roots signals can override turgor. Nevertheless as turgor is needed to power expansive growth, it still plays a role. Research is needed in cotton to determine the interaction of turgor and root signals in the sensitivity of leaf, stem, root, and boll growth to water deficits. This sensitivity may determine priority of growth amongst leaf, stems roots and bolls, which is an important issue for understanding and managing the balance between vegetative and reproductive growth.

The ranking of the growth of bolls, once they are set, as the least sensitive of the second order processes is also based on turgor, and must be likewise treated with caution. Bolls are able to maintain a water potential 0.3 to 0.5 MPa higher than leaves (Stewart, 1986; Trolinder *et al.*, 1993; Van Iersel and Oosterhuis, 1993). Bolls are extremely resistant to water loss; they are xeromorphic organs with very few stomata (Brown, 1968; Wullschleger and Oosterhuis, 1990, 1991). Furthermore van Iersel *et al.* (1994) conclude that most water for bolls comes through the phloem and is not dependent on water potential gradients. As a result of maintaining a higher water potential and turgor, bolls maintain a greater potential for growth than vegetative organs, conferring on them a nutritional priority and giving them a competitive advantage for assimilates over vegetative growth. With large deficits bolls are able to continue growth after leaves stop. Boll growth continues to the end of the terminal drying cycle; bolls will grow as long as photosynthesis continues. Fibre elongation continues after stem elongation ceases (Grimes and Yamada, 1982). Under moderate deficits bolls are able to grow closer to their potential rates than leaves are to theirs, enabling a favourable balance to be maintained between reproductive and vegetative growth. At the wet end in Figure 2 the differential in water potential and turgor between bolls and vegetative organs is probably reduced or lost, thus diminishing the bolls' competitive advantage. This loss of competitive advantage would reduce the assimilate supply to the bolls and cause the shedding of

bolls in response to the wet conditions (the wet end "signal" in Fig. 2) leading to rank growth and allowing vegetative growth to take priority over reproductive growth.

A result of the differential sensitivity of leaf, stem, root and boll growth to water deficits is to influence short term partition of assimilates. Since leaf and stem growth are more sensitive, deficits reduce their demand relatively more than root and boll demand, and more than assimilate supply, so that more assimilates are available for boll and root growth. However in the long term there are feedback loops operative through Jordan's sequence that result in a smaller canopy with reduced canopy photosynthesis. These feedback loops ultimately correlate growth so that at harvest there is a constancy in partition (Constable and Hearn, 1981).

Boll shedding is included in Figure 6, but has not been linked to either the deficit or to canopy photosynthesis. This omission is not because water deficits do not affect boll shedding, but in recognition of the continuing debate about how water deficits induce shedding. The debate involves the role of nutrition and hormones in boll shedding and water deficits (Jordan, 1986; Krieg and Sung, 1986). It is incontrovertible that hormones control the abscission mechanism. The majority view (Guinn, 1982; Jordan, 1982; Bielora *et al.*, 1983) is that water deficits can directly trigger the hormone mechanism and cause shedding independently of carbohydrate nutrition. The discovery in other species of signals from roots in drying soil, possibly hormonal in nature, supports this view. Research on this topic is urgently needed in cotton. However there is no unequivocal evidence that the carbohydrate supply is not reduced as a link in the causal chain between deficit and abscission, leading to the view that all shedding in responses to water deficits is a result of a reduced carbohydrate supply to the bolls, which triggers the hormonal mechanism, which in turn causes the abscission layer to develop.

The many routes through which water deficits can affect yield highlight the danger of measuring one or two parameters, for example flower production or boll shedding, and assuming that these explain or account for all the effects of deficits on yield. As a water deficit develops leaf size is reduced before photosynthesis at leaf level. As a result, in the above sequence water deficits can reduce canopy photosynthesis through reduced LAI without photosynthesis at leaf level being affected.

Figure 6 shows two places where WUE can be assessed: (i) in the centre column of second order processes, from the ratio of the rates of photosynthesis and transpiration; (ii) at the right hand side, the ratio of yield to seasonal transpiration gives biological WUE or agronomic WUE. These ratios will be discussed later.

Height is included in Figure 6 because it is dependent on cell expansive growth and is readily measured. The differential in sensitivity to water deficit between height increase and node production enables the tendency towards rank growth to be monitored; if height is increasing too fast relative to node production, it means the crop is near the wet end of the range in Figure 2. The balance of growth is being tipped towards leaves and stems and away from fruit. Management of this is discussed later.

Radin and Mauney (1986) have shown that the common nitrogen x water interaction that affects yield (e.g. Hearn, 1979) is more complex than a simple interplay of limiting factors at an agronomic level (that is, if both are limiting yield, both must be increased to raise yield). Nitrogen and water interact at a physiological level. As noted, N deficiency uncouples stomatal conductance from turgor so that closure occurs at substantial positive turgor. At moderate soil temperatures in controlled environments, but not at higher soil temperatures in the field in Arizona, N deficiency reduces plant hydraulic conductivity by altering root cell membranes and by reducing the width of xylem vessels (Radin *et al.*, 1991). N deficiency also increased LWP (leaf water potential) in the field.

As a result of these effects, the combination of N deficiency and large water deficits increases WUE, which is probably further ancestral adaptation to an arid environment because desert soils are typically low in organic matter and N. Although these adaptations may increase drought resistance for survival in ancestral environments, they are of limited value in crop production in intensive systems, since they are outweighed by the deleterious effects of N deficiency. However these effects confer on cotton further flexibility inherited from wild ancestors to thrive or survive in the

boom or bust conditions that often characterise desert and semi-arid regions. This flexibility may help to explain why cotton is so well adapted to both high input irrigated production and low input rainfed production.

Radin *et al.* (1986) showed that diurnal osmotic cycling was absent in N-stressed plants and weak in water-stressed plants, and in plants with a heavy fruit load. They postulated cycling was evidence of a 'sink-limited' condition in the plant, and contrasted this behaviour of cotton with that of cereals in which cycling is maintained or increased by large water deficits, indicating sink development in cotton may be less sensitive to deficits than in cereals. Turner *et al.* (1986) observed a degree of osmotic adjustment in cotton similar to that in sorghum. Ackerson *et al.* (1977a) concluded that the drought tolerance mechanisms of cotton differ from those of sorghum because in cotton relative water content changes more per unit of LWP, and dawn values of LWP and turgor pressure are lower.

### *Genetic variation in response to water deficits*

Much research has been devoted to the genetic aspects of water relations with a view to identifying drought resistant germplasm as a step towards breeding varieties adapted to various water regimes. At Lubbock in Texas Quisenberry and his colleagues started with the premise that drought adaptations may have been lost and WUE neglected in the development of modern varieties (Ray *et al.*, 1974). This view is consistent with the descent of all modern varieties of *G. hirsutum* from upland cotton introduced into the USA over 200 years ago, and grown and subjected to selection pressure under high rainfall in the eastern states for over 100 years before production moved west into more arid areas (Hearn and Fitt, 1992).

Exotic (Mexican) photoperiodic non-flowering strains of *G. hirsutum* were screened and significant three fold variability was demonstrated for WUE (Quisenberry *et al.*, 1981). One strain with low leaf conductance was able to conserve water and maintain leaf water potential and turgidity for longer than another with high conductance (Quisenberry *et al.*, 1985). When flowering (day neutral) genes were introgressed into these strains, the population from the low leaf conductance strain outyielded the other by 26%. McMichael *et al.* (1985) reported that the low leaf conductance strain also had higher root axial conductance for water flow as a result of five vascular bundles instead of the usual four, but Oosterhuis and Wullschleger (1987) were unable to confirm this finding. In any case the axial component of resistance is substantially smaller than the radial component. McMichael and Quisenberry (1991) found that a larger water deficit increased root growth. The increase varied among these and related strains, with the low leaf conductance strain showing less response than the high conductance strain, suggesting that the increased root growth of the high conductance strain under stress could not compensate for the disadvantage of high conductance.

Other physiological selection criteria have been evaluated. Maintenance of turgor by osmotic adjustment was rejected, as it was associated with reduced growth (Quisenberry *et al.*, 1984). Measurement of canopy temperature by infra-red thermometry showed that strains that had the warmest canopies under irrigation also had the lowest leaf conductances (i.e. were conserving water), and the greatest dry weights when not irrigated (Hatfield *et al.*, 1987). The point at which stomata closed was determined by a simple transpiration decline assessment and was correlated with growth under water stress (Quisenberry *et al.*, 1982). Timpa *et al.* (1986) and Wilson *et al.* (1987) have studied various biochemical criteria with inconclusive results. Karami *et al.* (1980) found that in response to water deficit photosynthesis, assimilate translocation and leaf turgor were reduced less in a superokra leaf genotype than in a normal leaf genotype.

Other workers, besides the Lubbock team, are using exotic stocks of cotton as a source of drought tolerant germplasm. Lemeshev (1987) is using Mexican (in common with the Lubbock team) and Brazilian stocks of *G. hirsutum*. *G. hirsutum* has been hybridised with *G. anomalum* (Makhmundov, 1985) and with *G. tomentosum* (Li and Hu, 1984) for drought resistance. Stewart (1989) reports that exotic germplasm is a source of good osmotic adjustment, without naming species.

In Brazil perennial cottons, which are drought resistant, were studied and compared with annual forms. Drought resistance was attributed to a larger root system and storage of assimilates in the root. Selection for root growth and starch content showed some genetic advance. (Silva, 1984; Souza and da Silva, 1987). However in a study of a number of genotypes Cook and el Zik (1992) found increased partition to the root system did not confer drought resistance. In fact they observed the reverse, that genotypes with a high root:shoot ratio at first flower shed more bolls in response to water stress, and consequently yielded less. In genotypes with a higher ratio, roots were a stronger sink before flowering, and this sink strength was apparently maintained during flowering, and during water stress, so that the bolls were disadvantaged as a sink in competing with the roots for assimilates, leading to reduced boll setting and yield. Kennedy *et al.* (1987) found that out of four varieties, two were more drought tolerant because their roots were able to grow better in an acid subsoil and extract more water. As well as these reports and that of McMichael and Quisenberry (1991) discussed in the previous paragraph, a number of other studies report genetic differences in root systems (Farbrother, 1960; Gutstein, 1969; Hearn, 1976b; Reddy *et al.*, 1989).

Cotton growing regions are frequently hot as well as arid. Radin's (1992) observation noted earlier suggesting that drought tolerance may be incompatible with heat tolerance needs further examination. While Radin *et al.* (1994) confirm that selection for yield in Pima cotton has resulted in genotypes with increased leaf conductance, increased evaporative cooling of the leaf and lower leaf temperature. While biological WUE has probably been reduced, the associated canopy cooling seems to promote boll setting and may actually increase agronomic WUE. These results suggest caution should be exercised in selecting for drought resistance on the basis of biological WUE.

Samiev *et al.* (1985, 1987) have studied the biochemistry and sub-cellular structure in drought tolerant irrigated varieties in Uzbekistan and found that tolerant varieties retain more water in their leaves, maintain chloroplast size, have better developed palisade parenchyma and maintain synthesis of certain proteins. Proline, which accumulates in stressed plants and aids recovery from stress, has been advocated as a selection criteria for stress tolerance (see Mussell and Staples, 1979). In India, Janagoudar (1983) and Singh and Sahay (1990) found more proline in drought tolerant varieties under stress but there is no report of its successful use as a selection criterion in cotton. Jagmail Sing *et al.* (1990) found small thick leaves associated with drought resistance.

Clearly there is much genetic variability in attributes associated with WUE and drought resistance. A number of counter-intuitive responses has been noted and more study is required of the physiological correlations, linkages and feedbacks involved. It is unlikely that a single attribute will confer drought resistance.

### **Application: the Agronomy of Water Relations**

#### *Yield responses*

When reviewing the effect of water deficits on yield of cotton fifteen years ago (Hearn, 1979), I noted the contradictory reports on the stage most sensitive to large deficits, particularly in relation to flowering. Recent reports suggests nothing has changed. For example, Reddell *et al.* (1987) found that "*The **early flower** period was found to be more sensitive to stress*", Orgaz *et al.* (1992) state that "*Cotton yield is most severely affected by severe stress during **peak flowering***" and de Kock *et al.* (1993) conclude that "*The most pronounced inhibiting effect stress had on yields was during boll development well **after the end of effective flowering***".

Such contradictions are not surprising in view of the multiplicity of routes through which deficits can affect yield (Fig. 6), and the wide range of environments in which cotton is produced, with differences particularly in the water holding capacity of soil and evaporative demand of the atmosphere. Comparing and evaluating such experiments is hampered by lack of universally accepted growth stages; the terms "early flower", "peak flowering" and "boll development" are too vague for scientific use. Use of day degrees or heat units to define stages is not the solution because the time needed to set the crop (boll setting) is not driven by temperature, being more strongly influenced by assimilate supply and pest control (Hearn, 1988). In discussing the most sensitive

stage we also need to distinguish between the situation where one irrigation is omitted from an otherwise fully irrigated crop, and one where a single irrigation is applied to an otherwise raingrown crop.

There are no grounds for dogmatically asserting, as is frequently done, that peak flowering is universally the most sensitive stage; in most cases it is, but several recent studies report that the boll filling stage is very, if not most, sensitive (Radin *et al.*, 1992; Plaut *et al.*, 1992; de Kock *et al.*, 1993). The results of all experiments are only valid in the context of the experiment and care is needed in extrapolating. Increased sensitivity during boll filling may be caused by deterioration and loss of function of the root system (Radin *et al.*, 1992), and by reduced osmotic adjustment resulting from increased competition for assimilates and consequent lack of osmotica (Radin *et al.*, 1986), both of which result from a heavy boll load, which usually occurs after peak flowering.

### *Water use efficiency (WUE)*

The term water use efficiency (WUE) is used in various ways. Two places have already been identified in Figure 6 where WUE can be measured giving different definitions:

1. the ratio of the rates of photosynthesis and transpiration gives the amount of CO<sub>2</sub> fixed per unit of water transpired over a short time span (one day or less). It is a daily or instantaneous value that describes gas exchange of a leaf or canopy, and is the physiological basis of WUE which is the subject of Gerik and Landivar's (these proceedings) contribution to this conference.
2. the ratio of biological or agronomic yield to seasonal transpiration gives biological WUE or agronomic WUE. This ratio is the amount of dry matter produced in a season per unit of water transpired. The amount of dry matter can be measured as root plus shoot, shoot only or agronomic yield.

Gas exchange WUE was discussed in detail at this conference by Gerik and Landivar (these proceedings). At this point it is sufficient to note that gas exchange WUE will influence seasonal WUE. Carbon dioxide and water vapour exchange are linked by sharing a common diffusive pathway through the stomata, and are both driven by solar radiation. On the basis of these gas exchange processes, the amount of CO<sub>2</sub> fixed per gram of water transpired is expected, and found, to be relatively constant. This constancy translates into a constant relationship for a species between total dry matter yield and T (transpiration) for the season, when adjusted for climatic differences of evaporative demand (Tanner and Sinclair, 1983; Hanks, 1983). The constancy and generality of this relationship within a species is the subject for on going debate (Ritchie, 1983). If harvest index is not affected then a linear relationship would be expected between T and economic yield. Constancy of harvest index is supported by data of Constable and Hearn (1981), who found a remarkable constancy in the partition of dry matter between fruit, leaf and stem over a wide range of conditions, despite well established effects of water and nitrogen on fruit retention (Hearn, 1975a,b).

Figure 7 presents recent data of Orgaz *et al.* (1992) for cotton supplied with different amounts of irrigation water. The linear relationship for total dry matter is consistent with a constant relationship between yield and transpiration. The intercept with the X axis at 126 mm estimates the amount of soil evaporation (the E component of ET). There was also a linear relationship for seed cotton up to 700 mm ET, indicating a constant harvest index. The intercept with the X axis for seed cotton is 146 mm and the difference from the dry matter intercept is the amount of water transpired by the crop in the vegetative stage before boll filling. With ET greater than 700 mm, the harvest index decreased and the linear relationship between ET and seed cotton broke down (not shown in Fig. 7).

In Figure 7 the slopes for total dry matter and seed cotton are the biological and agronomic WUE of the plants, with values of 18.7 and 8.4 kg per ha per mm respectively. These values measure how efficiently plants are using the water that passes through them, but they are the WUE

of the *plants* not the *crop*, because one important component has been left out, soil evaporation (the E in ET), which is water that does not pass through the plant but is nevertheless debited to the supply available to the crop. Crop WUE is estimated by dividing yield by ET, thus including E. For the data of Figure 7, crop agronomic WUE peaks at 700 mm of ET with 6.6 kg seed cotton, or 2.7 kg lint, per ha per mm.

Table 3 compares the plant and crop WUE data from Figure 7 with similar data from other locations. Plant biological WUE shows a much smaller relative range (18.7 to 24.8 kg per ha per mm) compared with the threefold range for agronomic WUE (1.42 to 3.68 kg per ha per mm). Two of the six data sets, Howell *et al.* (1984) and Orgaz *et al.* (1992), deviate from a linear increase in agronomic yield at high values of ET. Grimes *et al.* (1969) reported a similar divergence. This non-linearity has several possible causes: deep drainage not being accounted for and included in ET; increased E with more frequent wetting of the soil; or reduced harvest index, possibly associated with incidence of pest or disease, when large amounts of water are applied during the season. The crop WUE values in Table 3 are the largest value recorded in each experiment and take into account soil evaporation (E) as described above. When there is little difference between crop and plant WUE, it is because E (the intercept of the yield-ET regression) is small.

Table 4 summarises crop agronomic WUE data from other studies, including comparisons of drip with furrow irrigation, full with deficit irrigation and narrow with standard rows. Drip irrigation increased WUE in only one case out of three, and the increase was the result of increased yield, not reduced ET. However when a wider range of experiments are considered later in examining drip irrigation in more detail it will be seen that drip saved water in most cases, and therefore increased WUE. Deficit irrigation increased WUE in two cases and slightly decreased it in another. Narrow row planting had a higher WUE because yield increased while ET was hardly affected. Taking Tables 3 and 4 together, there is three fold variation in WUE caused by a number of factors: variation in soil E and advection, limitation of yield by factors other than water and over-estimation of ET by failing to take deep drainage into account.

For irrigated crops engineering efficiency is another aspect to water use efficiency. Engineering efficiency accounts for conveyancing and application losses and is the percentage of the water pumped or diverted for irrigation used by the crop as ET. Engineering efficiency must be taken into account in evaluating the production obtained or expected from a given irrigation water supply, Surface methods of irrigation, which are mostly used for cotton, give an engineering efficiency of 30-75% (Hoffman *et al.*, 1990).

To summarise, it is essential to compare like with like, either plant WUE on the basis of T, crop WUE on the basis of ET and field WUE for irrigated crops on the basis of ET but taking into account engineering (application and conveyancing) efficiency.

All these recent WUE studies relate primarily to irrigated cotton. There are no recent studies of WUE for rainfed cotton, although Gerteis *et al.* (1988) included rainfed treatments in Texas and obtained 1.85 kg lint per ha per mm (Table 4). Previously Gutstein (1969) obtained crop WUE values for rainfed cotton grown on stored winter rainfall, ranging from 3.30 to 4.35 kg lint per ha per mm, which are equal to the best of irrigated cotton in Tables 3 and 4.

No data are readily available to determine the agronomic crop WUE achieved in commercial irrigated production around the world. In Australia on the basis of records of a number of irrigated cotton farms Cull and Robson (pers. comm.) reported 3.08 kg lint per ha per mm of ET. Assuming an engineering efficiency of 75% and a linear relationship between ET and agronomic yield, this represents a marginal production of 2.31 kg lint per mm of irrigation applied. This may be compared with an estimate the national marginal return of 1.44 kg lint per mm of irrigation applied made on the basis 1.6 million Ml of water used to irrigate cotton (Baker and Loder, 1993), a national irrigated production of 0.41 million tonnes of lint (Appendix) and an irrigated yield 2.26 times a rainfed yield (Appendix). In the ICAC (1993b) survey most of the countries with more than 50% of the cotton crop rainfed are tropical with distinct wet and dry seasons, where most of the rainfall not running off or draining deep would be available for ET. In these countries the average rainfall for the seven months of the cotton season in the year of the survey was 804 mm, ranging from 426 mm to 1170 mm. The efficiency with which the cotton crops in these countries used that

rainfall was estimated by dividing yield by rainfall. The result was an average of 0.57 kg lint per ha per mm of rain, ranging from a high of 1.1 in Queensland, Australia to a low of 0.15 in Uganda. Although the comparison must be done cautiously, when these data are compared with Tables 3 and 4, it appears that rainfall is not being used efficiently in most countries for cotton production. Lower WUE values are expected for rainfed cotton because of the irregular frequency of rain and periods with severe water deficits, and because inputs of fertiliser and pest management will be less on account of the greater risks.

### *Fibre quality*

Water relations affect fibre quality (Hearn, 1976a; Ramey, 1986). Severe water deficit reduces fibre length if it occurs when fibres are elongating in the early part of the boll period, and reduces fibre maturity (the amount of cellulose deposited in the wall) if it occurs during fibre secondary thickening in the latter part of the boll period. These effects on length and maturity are simple expressions of effects of water deficits on processes already described - cell expansion and assimilate supply and partition. These simple effects can be confounded by effects of water on the duration and timing of boll setting and maturation. For example in relation to fibre maturity a generous water supply can: (i) reduce maturity of fibre (cellulose deposition) in the first bolls by stimulating competition for assimilates from vegetative growth; (ii) increase maturity of fibre in the of mid-season bolls through simple supply effect, and (iii) increase the proportion of later season bolls maturing in cooler weather, with reduced fibre maturity (Hearn, 1976a). Intrinsic fibre fineness is largely determined genetically and effects of water deficits are minimal and are usually limited to slight increases in thickness. Unlike length and maturity, fibre strength is not a simple expression of growth processes and effects of water deficits are variable and unpredictable. Water stress can increase the occurrence of immature seeds causing neps.

### *Management of water resources*

Management decisions are made at policy, strategic and tactical levels. A decision made at one level will flow down to influence a decision made at a lower level. Policy decisions are national or regional and often involve political as well as technical factors. Political factors may be over-riding and are beyond the scope of this paper. For irrigated cropping, policy decisions are required regarding how much water can be drawn from a river or reservoir or pumped from an aquifer, and must consider water required for other uses including industry, wetlands and lakes. The economic benefit of water used for cotton production must be assessed and balanced against other water uses. Decisions have to be made whether to charge users the full economic cost of water or whether to subsidise, how to ration the water and how to police water use. For raingrown crops in the tropics the influence of climate on optimum sowing date through water requirements for growth and dry weather for harvest has to be balanced with the needs of pest and disease management in determining statutory sowing periods and uprooting dates. These decisions made at a political level have a big impact on strategic decision making.

Strategic management decisions are made at the level of the farming enterprise. Where irrigation water supplies are limited the axiomatic aim of management should be to optimise use of those limited supplies. How frequently this aim is accepted and achieved is not known. Judging from the scientific literature and the farming press, maximising yield or returns per hectare are still the more usual aims. Of course for rain-grown cotton, maximising returns per hectare will in any case also maximise returns from the limited rainfall.

Much technology has been developed to aid the management of water resources in cotton production, either addressing or employing the principles discussed. However technology is no better than the people using it and its use will not guarantee sound management! Technology can be conveniently discussed as hardware and software for strategic and tactical purposes. The term "software" is used in a broad sense to include, not only computer based decision support systems, but also any procedure to document crop or environmental data and make management decisions.

Discussion will be limited to technology for conserving water and increasing WUE. In most cases there is no way of knowing to what extent a technology has been adopted in practice. Widespread adoption does not necessarily mean a technology is the most appropriate, nor failure to adopt that it is inappropriate.

#### Strategic management of water resources: hardware - water conservation

Use of tied ridges constructed manually has always been a feature of African production to reduce runoff (Prentice, 1972). In the USA, where the practice is known as basin listing or furrow diking, after a period of unpopularity associated with operational problems, there is renewed interest following the development of improved technology (Unger and Stewart, 1983). Various stubble retention and minimum till system also have a role in minimising losses of water from rainfall (Chopart, 1987; Unger and Stewart, 1983). Plastic sheet is widely used in China and Spain and has been advocated in California to reduce loss of water by soil evaporation in the spring, as well as warming the soil (Raman *et al.*, 1990; Chen and Guo, 1991; Fereres and Goldhammer, 1991; Mateos, L., pers. comm.).

#### Strategic management of water resources: hardware - water application

During the last 25 years various systems have been developed and applied to irrigated cotton production: centre pivot, lateral move, its extension to low energy precision application (LEPA), and drip systems. The aim of such systems has been not only to save water, but also to save labour with varying degrees of automation. Laser levelling can improve the efficiency of surface application methods; on heavy soils in Australia engineering efficiency of furrow irrigation can reach 75% (Cull *et al.*, 1986). Surface irrigation has also been improved by surge or cable irrigation (Kay, 1990) in which the discharge is automatically reduced to match the decreasing infiltration rate.

In order to put this technology into perspective, it is useful to look at the recent ICAC (1993b) survey in Table 5. Globally, 94% of cotton irrigation is done with traditional surface methods (flood or furrow). Israel is listed separately as it stands in stark contrast to the rest of the world in the adoption of drip and sprinkler irrigation for cotton. Stanhill (1993) has recently reported the impact of these developments in Israel. Over the last thirty years the amount of water applied to all crops has been almost halved from 850 to 470 mm per year, while the yield per mm has almost been trebled, from 1.2 to 3.3 kg per ha per mm. J. Spenser and I. Spharim (pers. comm.) in a poster at this conference argue that there is scope for even further improvement in efficiency of water use in Israel.

Apart from Israel, drip has hardly made any impact on the irrigation of cotton, although there has been a lot of research, with contributions to this conference from Hutmacher *et al.* (these proceedings) in the USA and Dippenaar *et al.* (these proceedings) in South Africa. Table 6 summarises recent reports; drip irrigation saved water in 7 cases out of 9, and increased yield in 5 cases out of 9. Savings in water result from reduced conveyancing and application losses, reduced soil evaporation (E component of ET) and reduced deep drainage. Yields are enhanced by: (i) improving water status of shallow soils (see papers cited by Radin *et al.*, 1992), (ii) improving plant water status when root function is impaired during fruiting (Radin *et al.*, 1992) or when osmotic adjustment is diminished (Radin *et al.*, 1986), (iii) improving partitioning between root, shoot and fruit (Ben-Porath and Baker, 1990), and (iv) changing hormonal relations (Carmi and Shalhevet, 1983).

Most differences in response to drip irrigation arise from differences in soil conditions. In Australia, furrow irrigation is very efficient with little scope for improvement on laser levelled heavy clay Vertisols with a low saturated hydraulic conductivity that almost eliminates losses from deep drainage. On lighter soils there is scope to reduce loss of water by deep percolation. On shallow soils of low water holding capacity there is scope to raise yields with drip irrigation; the potential of marginal soils of variable depth can be raised to that of better soils. There is potential

for drip, particular on lighter texture soils. Cost is the main constraint. Drip irrigation has contributed to the remarkable achievements in Israel with a 50% increase in yield with 50% less water (Stanhill, 1993), and having to pay a full economic cost for water is a major contributory factor. As water costs rise, and drip costs fall there may be wider adoption. Low cost, low pressure drip systems are being developed (Miller, 1990).

Recent observations in Uzbekistan highlight the role of the price of water (Hearn, 1993). On one farm 224 ha of drip irrigated cotton used only one third of the amount of water used by furrow irrigation (3.3 vs 10 Ml per ha). Yields were maintained but not increased. The saving in water was of no economic benefit to the farm as water was not rationed, and the project was therefore not considered successful.

### Strategic management of water resources: software

Hutchinson *et al.* (1958) pioneered this approach with the use of a simple water balance model to analyse yield variation within and between seasons in Uganda. They used the model to optimise sowing date for rainfed cotton by fitting the seasonal pattern of water requirement to the probable rainfall pattern. We ought to be able to do it much better today with computers, and it is disappointing to note the absence of papers at this conference on the strategic use of software for risk analysis and exploration of management options for rainfed cotton and use of limited supplies of irrigation water. There are several crop models which could be used for this purpose. Simulation is a powerful tool for exploring the management options available with limited irrigation water supplies.

In Australia, for example, the OZCOT model (Hearn, 1994) has been used with long term weather data to evaluate strategies for irrigated and rainfed cotton production (Hearn, 1990, 1992). The extremely variable rainfall in the cotton production areas of Australia means that not only is rainfall for rainfed production unreliable but so also are irrigation water supplies for supplementing the unreliable rainfall. In the driest years 9 or 10 Ml of irrigation water per ha are needed to irrigate the crop fully, assuming reasonable application efficiency; in the wettest years irrigation is hardly needed. In a year when his supply is reduced, a farmer can plant either a smaller area, allowing 10 Ml per ha to be sure of being able to fully irrigate the crop in a dry year, or a larger area with fewer Ml per ha. The risk of failing to break even associated with such strategies, and the strategy most likely to maximise returns per Ml can be assessed by simulation (Hearn, 1992). The strategy under Australian conditions that maximises returns per Ml and minimises the risk of failing to break even is to: (i) sum all sources of irrigation water, including that allocated from the public reservoir, the expected free flow and any held in storage at the beginning of the season; (ii) plant an area that gives 5 or 6 Ml of irrigation water per ha; (iii) start irrigating at the normal time and continue at the normal frequency until the supply is exhausted. In a wet year the supply will last for the whole season. In a dry year the supply will run out before the end of the season, but the interval between irrigations should not be lengthened as the crop will encounter the dry end signal and switch prematurely from vegetative to reproductive growth. Because this switch cannot be reversed, the crop will then be unable to take advantage of any subsequent rainfall that might occur to develop and set a larger crop.

Prospects for rainfed cotton in various regions of Australia have been evaluated by estimating mean yield, yield percentiles, risk of failing to break even, risk of insufficient rain to sow, and the latest safe sowing date (Hearn, 1990). This approach is particularly valuable for comparing a region in which there is experience of cotton production with an unknown one. Simulation can be used to show whether, on the basis of the historical rainfall pattern, the unknown region has a higher or lower yield potential, is more or less variable, has a longer or shorter season and is early or later. S.A. Routley and G.A. Constable (pers. comm.) are extending this approach by employing GIS (geographic information systems) technology.

### Tactical management of water resources

Tactical management of water resources involves irrigation scheduling and use of growth regulants. Hardware and software developed initially for research have been used for crop monitoring. In most cases the hardware is of limited use without accompanying software.

Irrigation scheduling involves determining when to water and, when appropriate, how much water to apply. Hardware used consists of a neutron probe to measure soil water, a pressure chamber to measure LWP (leaf water potential) and an infra-red thermometer to measure canopy temperature. Software available ranges from rules of thumb, such as days elapsed since the last irrigation, adjusted for rainfall (Hearn, 1980) or appearance of crop, to plant and water balance models and the crop water stress index (CWSI). Examples of computer-based software are AZSCHED described at this conference by Clark *et al.* (these proceedings) for Arizona, *hydroLOGIC* (Wells and Marsden, 1989) based on the OZCOT model and CALEX (Plant *et al.*, 1992). These packages require weather data as input; neutron probe data are optional.

The neutron probe is widely used in Australia to measure soil water content for scheduling of cotton irrigation (Cull, 1980). The optional software package (Cull and Finch, 1994) computes the current rate of soil water depletion and extrapolates it to the refill point (the soil water content at which to irrigate) in order to predict the date of the next irrigation. An advantage of the neutron probe over other scheduling methods is that it can identify abnormalities in the profile, such as compact layers, that affect not only scheduling but soil management (Cull, 1983). A further advantage is accurate measurement of seasonal water use, and storage of the data for calculation of the WUE of crops as reported by Cull and Robson (pers. comm.) at this conference.

Turner (1990) advocates plant-based measurement for all situations. As discussed earlier, environments with consistent evaporative demand, such as California or Israel, have location-specific plant water deficits for stress (Grimes and Yamada, 1982). Consequently LWP, measured with a pressure chamber can be successfully used to schedule irrigations (Grimes and el Zik, 1990; Plaut *et al.*, 1992).

The use of canopy temperature measurements has been proposed for irrigation scheduling. In spite of much research to measure canopy temperatures using infra-red thermometry, and to interpret them using either the CWSI or the TKW, very few tests of their actual use for scheduling have been reported. CWSI was tested by Garrot *et al.* (1990) and the TKW by Wanjura *et al.* (1990). Stockle and Dugas (1992) report shortcomings of canopy temperature measurements for irrigation scheduling. This technology has not been widely adopted yet, but its use to monitor crops from aircraft, as opposed to hand held guns, holds promise because a whole field can be measured instead of a limited sample, as is the case with all other manual monitoring techniques.

For reasons explained earlier, a water supply that is liberal relative to evaporative demand puts the crop too near the wet end of Figure 2 and causes rank growth in which the balance has been tipped in favour of vegetative growth relative to reproductive growth. Rank growth is therefore undesirable. The vigour index developed by T.A. Kerby (pers. comm.) and described at this conference indicates the balance between vegetative and reproductive growth, and the risk of rank growth. The index is based on the differential sensitivity to water deficit of height increase and node production, noted in Figure 6. If the risk of rank growth has been detected, it can be countered in both irrigated and rainfed crops by applying the growth regulant mepiquat chloride (PIX) (T.A. Kerby, pers. comm.; Edmisten, these proceedings; G.A. Constable, pers. comm.). In the past the conventional way to avoid rank growth in irrigated crops was to stress them by delaying the early irrigations. In future better adapted varieties may be available that are less sensitive to the wet end signal!

## Varieties

Much research devoted to searching for drought tolerant germplasm in order to maximise WUE was described earlier in this review. Although these studies have greatly enhanced our understanding of the genetic and physiological factors involved in adaptation to water deficits, as far as is known, no commercial varieties have yet been released. We have already noted that it is unlikely that a single attribute, such as biological WUE, will confer drought resistance because of

physiological correlations and linkages among the traits. Passioura *et al.* (1993) comment that an attribute, such as proline accumulation or osmotic adaptation, is unlikely to have much bearing on yield under limited water, if cannot be readily related to one of the three components of a scheme consisting of the amount of water transpired, the plant biological WUE and the harvest index.

Namken *et al.* (1974) proposed early maturity as a strategy of increasing WUE in water limited environments. This strategy is successful when the crop is grown on a limited amount of stored water in the Yemen or Israel (Hearn, 1966; Gutstein, 1969), or for rainfed crops in India where the season is short but early rainfall is reliable (Katarki, 1982; Bhatt and Nathan, 1984). On the other hand Quisenberry and Roark (1976) and Bourland (1989) report that later maturing varieties performed better with limited water. Cook and el Zik (1993) found no correlation between earliness and yield amongst six diverse genotypes under drought conditions. In Australia full season varieties bred for irrigation are also the best varieties for rainfed and limited water crops (Pyke, Thomson and Reid, 1990), a finding that suggests that adaptation to pests and soils may be more important than adaptation to drought conditions. In a three year study of 12 advanced breeding lines of varying maturity, early lines did not perform better than late lines under limited water supplies; there was a hint that they did not perform as well (Hearn, unpublished data). Quisenberry *et al.* (1980) also report selections made in an optimum environment also performed well in a stress environment.

In considering drought tolerance and maturity types, a thermal short season needs to be distinguished from a drought-induced short season. Early maturing genotypes are suitable for a thermal short season. A drought induced short season needs the maximum reproductive flexibility found in later maturing genotypes. A strategy of matching the fruiting pattern to the water supply pattern (Hutchinson, 1959; Hearn, 1976b) requires full expression of the indeterminate habit. It is concluded that where rainfall is irregular and liable to arrive late, late maturing varieties with full expression of the reproductive flexibility of the indeterminate habit are able to take advantage of rain when it eventually arrives.

An aspect of varietal adaptation that has not been explicitly addressed is the rank growth syndrome described previously. It is a related set of responses, including excessive vegetative growth, to low water deficits, high nitrogen levels and high, but not extreme, temperatures. Some varieties are more prone than others to rank growth. It is currently managed with pre-emptive application of the growth regulant mepiquat chloride (PIX), which inhibits excessive gibberellin production, implying that an hormonal imbalance is being corrected, suggests incomplete genotypic adaptation to the environmental conditions that are associated with the syndrome. Further breeding might achieve better adaptation resulting in reduced levels of endogenous gibberellins in response to conditions that induce rank growth.

### Environmental impact

Three major environmental issues involve the water relations of cotton: (i) degradation of wet lands and lakes, (ii) contamination of ground water, and (iii) salinity and rising water tables. Irrigation is the sole cause of the first and has a major impact on the other two. None is uniquely a cotton problem, nor therefore is the research needed nor the management options available specific to cotton.

### Environmental impact - degradation of wetlands and lakes

Diversion of water from a river for irrigation deprives ecosystems downstream of water, resulting in their degradation. It is an issue in Australia and a major issue in Central Asia where there has been a massive reduction in the area of the Aral Sea (Musaev, 1993; Perara, 1993). In the course of debate, cotton production is frequently targeted, for example "*The cotton industry has a voracious appetite for water*" (Dr Peter Crabbe, Australian Broadcasting Commission TV Documentary "Running the Rivers", October, 1993). To put this into perspective, we have already noted that the global cotton growing industry only occupies 7.3% of the world's irrigated land, and

uses an even smaller fraction of the water resources. In Australia cotton uses only 14% of the irrigation water but produces 35% of the export revenue generated by irrigation (Meyer, 1992; Baker and Loder, 1993). These facts should be taken into account in the debate and in the allocation of water resources to cotton production. Dudley (1993) has proposed an innovative market model to resolve competition for water resources. It is largely a political question outside the ambit of cotton research. But if water supplies are restricted as a result of political action, increasing WUE becomes of even greater importance.

#### Environmental impact - contamination of ground water and rivers

Cotton production carries a significant risk for contaminating ground water and rivers with nutrients, salt and pesticides, because it is often a heavy user of agricultural chemicals (Bowmer, 1993). Irrigation in excess of ET (evapotranspiration) requirements, and leaching for salinity management (see next section) increase the risk to ground water by leaching. More efficient irrigation to minimise water use will reduce the former risk; again WUE is of prime importance. Leaching for salinity management should be accompanied by provision of drainage. Engineering solutions for dealing with drainage water are discussed in the next section. The risk to water courses is related to discharge of runoff and drainage water into water courses. For irrigated production the risk of runoff can be reduced by engineering work (Barrett *et al.*, 1991).

#### Environmental impact - salinity

Salinity is inevitably a potential threat to all irrigated land where water lost by ET equals or exceeds that gained in rainfall and irrigation. It has caused the demise of irrigation systems, and the civilisations dependent upon them, in past millennia. All irrigation water, even of the best quality, contains some salts which accumulate in the soil unless leached. In humid regions rainfall usually leaches salts added by irrigation. In arid regions the threat becomes a reality. No data could be found of the extent to which cotton production specifically is affected or threatened by salinity. Shalhevet and Kamburov (1976) report that more than half the irrigated area in 24 major irrigation countries is affected by salinity. In the western United States crop production is limited on 25% of irrigated land (Hoffman *et al.*, 1983). Without exception, all the countries identified on the map in Figure 1 in the broad Afro-Euro-Asian belt of irrigated cotton, and those with similar climate in the west of North and South America, report salinity problems. These are all the cotton producing countries with desert and mediterranean climates where the crop is fully irrigated without rainfall.

The effect of saline soil or saline irrigation water is to reduce the osmotic potential of soil water (i.e increase the negative potential) and reduce its availability to the crop. In many crops salinity also has a toxic effect but cotton is able to exclude the sodium ion. Its effect on crop growth is therefore similar to severe water deficit. Shalhevet and Hsiao (1986) have compared the effects of salt and water stress on cotton and found that salt stress had less effect on plant functions than water stress at similar potentials.

Cotton is one of the most salt-tolerant crops; only barley is marginally more tolerant (Hoffman *et al.*, 1983). Herein lies a danger - because of this tolerance salinity may be allowed to get worse before action is taken. This tolerance is an ancestral adaptation to arid environments where salinity hazard is greater, and to the coastal littoral where *G. hirsutum* originated. Varietal differences in tolerance to salinity have been reported (Fowler, 1986) and varieties with increased salt tolerance have been bred in Uzbekistan. However such varieties will only gain time for a few years until salt levels increase further, unless a steady state is reached.

Where salinity is an inevitable hazard the primary curative and preventative solution is to ensure a net downward flow of water through the root zone by applying additional irrigation, and adequate drainage to remove the excess where there is a risk of raising the water table. These are primarily engineering issues beyond the scope of this review, though the extra water needed for leaching will reduce the field WUE. A concomitant problem is disposal of the saline drainage water. Return to rivers and water courses creates more environmental problems. The options are

discharge into the ocean (e.g. Pakistan, McCready, 1987), evaporation basins (e.g. Australia, Smith, 1987) which involves sacrificing land, or recycling of the saline water to irrigate tolerant crops.

Recycling of saline drainage water is only one aspect of the body of research into the use of saline water for irrigation of cotton. In Israel Shalhevet (1984), in Central Asia Afanas'ev *et al.* (1991) and in California Rhoades (1983) and Bradford and Letty (1992) have confirmed the feasibility. There are several options for conjunctive use of good and saline water (i) good water on sensitive crops, saline water on tolerant crops, (ii) blending, (iii) applying good and saline water alternately and (iv) applying good water for part of the season, preferably the early part when crops are most sensitive, and saline for the rest.

Rising water tables associated with irrigation exacerbate the salinity problem by causing secondary salinisation. Rising water tables are in turn exacerbated by the need periodically to apply irrigation over and above the ET requirement in order to leach salts out of the profile. The risk of rising water tables can be reduced with improved technology, reviewed above, to schedule and apply water in order to avoid excessive irrigation. This will minimise through drainage to the water table and improve WUE

Drip irrigation, and similar fully articulated precision systems that deliver water direct to the soil at frequent intervals, have a number of advantages for salinity management. Precise application of small controlled quantities of water greatly reduces drainage, particularly on light-textured soils where surface irrigation methods cause much through drainage. Because soil salinity reduces the availability of soil water, drip irrigation provides an easy means of keeping soil water within the narrow available limits because frequent irrigation is possible (Anon., 1983; Shalhevet, 1984; Mantell *et al.*, 1985). For the same reasons, drip irrigation has advantages for saline water, either alone or for conjunctive use of fresh and saline water are being explored. Drip irrigation may reduce but not obviate the need for periodic leaching.

Impermeable soils, such as the Vertisols of the Sudan Gezira and Australia, are a special case. Because of very low saturated hydraulic conductivities, leaching is very limited (Farbrother, 1972; Cull, 1979) and may be inadequate. In both cases water quality is good. A simulation study in Australia with the SODICS model (Thorburn *et al.*, 1990) suggested that salinity will become a problem after 30 years of irrigation (Jessop *et al.*, 1993). Some cotton growing areas are approaching 30 years of irrigated cropping but no evidence can be found of increasing salt concentration in the topsoil. Likewise in the Gezira, no salinity problems have yet been attributed to irrigated cotton production after 80 years. The high intensity of rainfall in the short wet season of the Gezira and the occasional floods on the Australian Vertisols may be sufficient to leach salt below the root zone. In Australia there is evidence of accumulation of salt below 0.5m peaking at 1.5m (McGarry *et al.*, 1989; Triantafilis and McBratney, 1991). It has been suggested that in the Gezira sufficient salts are removed in crops harvested is to prevent accumulation in the soil, though no evidence was presented (Russell, 1973).

Drip irrigation has great potential for reducing the risk of all three categories of environmental impact described. Urban domestic wastes (Bielorai *et al.*, 1984; Oron and Malach, 1987; Papadopoulos and Stylianou, 1988) and saline drainage water can be used in drip irrigation, recycling otherwise unusable water and reduce requirements for fresh water. Charging full cost of public water would be unpopular with cotton growers, but an effective economic incentive to reduce the risk of environmental impact.

### Water logging

In addition to the rank growth syndrome, another effect of excessive water is water logging. Because of its xerophytic ancestry, cotton is not well adapted to water logging which in some environments is unavoidable and as deleterious as water stress. This review does not attempt to cover this aspect of water relations, and the reader is referred to Hodgson (1982). There is scope to improve the plant's poor adaptation to water logging by using biotechnology to enhancing the expression of the genes responsible for production of the enzyme alcohol dehydrogenase which enable the plant to survive anaerobic conditions (Millar and Dennis, 1990).

## Conclusions

Modern cultivated cotton species have inherited from their wild relatives attributes that enable them to survive long periods of drought and develop rapidly when water is available, enabling the crop to make full use of variable rainfall or respond well to irrigation. These attributes are the indeterminate habit and the relative sensitivity of physiological processes to water deficits. The former confers a flexible morphological and reproductive development and the latter determines priorities for assimilates. Ancestral sensitivity to the putative wet and dry "signals" from the environment imposes special constraints on management of the cotton crop in relation to water. Research is needed to see if signals from roots in drying soils found in other crops occur in cotton, and to determine their role in the response of the crop to water deficits, particularly boll shedding, priorities for growth, and the balance of vegetative and reproductive growth.

In order to maximise returns from limited rainfall and irrigation water supplies, research and management should concentrate on improving WUE in its various aspects. Opportunities exist to improve WUE with:

- new irrigation technology, or better use of existing technology, in order to reduce application, conveyancing and drainage losses and reduce the E component of ET;
- use of hardware and software to monitor crop progress for tactical optimisation of irrigation scheduling;
- identify by using simulation software, and then adopt, robust management strategies for irrigated and rainfed crops that will minimise risk and use maximise return from limited irrigation supplies and rainfall;
- soil surface management technology to retain rainfall and reduce runoff and soil evaporation;
- pursuit of genetic improvement of agronomic WUE by improved gas exchange and/or partition of assimilates.

If we are successful in raising WUE we will reap the benefits of higher returns from a limiting resource, with the added potential to reduce contamination of rivers and groundwater and reduce the risk of salinisation.

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# APPENDIX

## Estimation of irrigated and rainfed areas and production

The area, production and yield of cotton in each country for the seasons 1990-91, 1991-92, 1992-93 were obtained from ICAC (1993a). The mean area, production and yield for the period was calculated for each country. The percentage of the area irrigated was obtained from ICAC (1993b) and Bell and Gillham (1989) for 41 out of 53 countries. The remaining countries, which accounted for only 4% of the world area and 2% of production, were assumed to be rainfed on the basis of general knowledge. The mean areas of rainfed and irrigated cotton were calculated for each country.

The mean yield for each country was regressed on the percentage of the area irrigated with the following result:

$$\text{Yield} = 361 + 4.54 * \text{percentage} \quad (1)$$

From this it is inferred the the average yield with and without irrigation is 815 and 361 kg per ha respectively, thus

$$Y_i = 2.26 * Y_r \quad (2)$$

where  $Y_i$  is irrigated yield and  $Y_r$  is rainfed yield. Furthermore total production for a country can be expressed thus

$$\text{Production} = A_i * Y_i + A_r * Y_r \quad (3)$$

where  $Y_i$  and  $Y_r$  are define previously, and  $A_i$  is irrigated area and  $A_r$  is rainfed area. Substituting from Equation 2 in Equation 3 gives

$$\text{Production} = A_i * 2.26 * Y_r + A_r * Y_r$$

which can be rearranged to give

$$Y_r = \text{Production} / ((A_i * 2.26) + A_r) \quad (4)$$

Equation 4 was used to estimate the rainfed yield for each country which had both rainfed and irrigated production. The irrigated yield was then estimated from Equation 2. The validity of this procedure depends on the reasonableness of the assumption that the relationship between rainfed and irrigated yields in Equation 1 can be applied to all countries where there is both irrigated and rainfed production.

The results are given in the following table, in which countries are grouped into broad climatic regions.

Table 1. Comparison of strategies of wild species to survive arid conditions described by Fryxell (1986) with drought resistance classified by May & Milthorpe (1962).

Fryxell 1986	May & Milthorpe (1962)
Life cycle adaptation	Drought escape
Xeromorphic adaptation	Drought tolerance with high water potential
Habitat adaptation	Drought tolerance with low water potential

Table 2. Photosynthesis and water deficits.

	Initial LWP* MPa	Final LWP MPa	Final photosynthesis % of initial
Ackerson <i>et al.</i> 1977a	-1.0	-3.0	25
Turner <i>et al.</i> 1986	-1.9	-3.5	30
Puech-Suanez <i>et al.</i> 1989	-1.3	-3.2	8

\* LWP at which photosynthesis started to decline

Table 3. Plant WUE, based on regression of yield on ET, and maximum crop WUE from several studies. Units are kg per ha per mm.

Author	Location		Plant WUE		Crop WUE
			Total dry matter	Lint	Lint
Sammis 1981	California	Sprinkler		3.14	2.49
	New Mexico	Sprinkler		1.42	1.53
Howell <i>et al.</i> 1984	California	Furrow	24.8	2.79	1.94
Meiri <i>et al.</i> 1992	Israel	Sprinkler & drip	21.2	3.68	3.67
Orgaz <i>et al.</i> 1992	Spain	Sprinkler	18.7	3.36	2.65
Plaut <i>et al.</i> 1992	Israel	MSIS		3.58	3.76

Table 4. Crop agronomic WUE from various studies (Kg/lint/ha).

<i>Method of irrigation</i>			furrow	drip	
Hodgson <i>et al.</i> 1990			2.27	2.21	
Mateos <i>et al.</i> 1991			2.48	2.56	
Radin <i>et al.</i> 1992			1.32	1.96	
<i>Irrigation deficit</i>			full	deficit	rain
Khade <i>et al.</i> 1984	India	furrow	1.25	1.36 to 1.79	
Gerteis <i>et al.</i> 1988	Texas HP		2.15	2.00	1.85
Mateos <i>et al.</i> 1991	Spain	drip	2.56	3.02	
<i>Row width</i>			1.0m	0.67m	0.33m
Gerteis <i>et al.</i> 1988	Texas	clay loam	2.15	2.7	2.5
		loamy fine sand	1.75	2.4	2.75

Table 5. Irrigation methods: ICAC (1993b) survey.

	World	Israel
Flood	65%	-
Furrow	29%	14%
Sprinkler	5.6%	25%
Drip	0.22%	60%
Other	0.19%	1%

Table 6. Response to drip irrigation.

Was water saved?	Was yield increased?	Author	Country	Comment
no	no	Hodgson <i>et al.</i> 1990	Australia	deficit irrigation
		Mateos <i>et al.</i> 1991	Spain	full irrigation
yes	no	Howell <i>et al.</i> 1987	California	
		DeTar <i>et al.</i> 1992	California	good soil
yes	yes	Plaut 1983	Israel	
		Mateos <i>et al.</i> 1991	Spain	deficit irrigation
		Radin <i>et al.</i> 1992	Arizona	
		Henegler 1988	Texas	
		DeTar <i>et al.</i> 1992	California	poor soil

Figure 1. World areas of irrigated and rainfed cotton.

Figure 2. Specific adaptive responses of cotton to the environmental water regime.

Figure 3. Effect of the amount of stored water on rooting depth (Hearn, 1979).

Figure 4. The effect of stored water on size of fruiting structure; solid circle are harvested bolls, open circles are shed fruit; redrawn from Rijks (1965).

Figure 5. Sensitivity and sequence in water stress 1: the processes involved in dry matter production.

Figure 6. Sensitivity and sequence in water stress 2: development, transpiration and economic yield.

Figure 7. Yields as a Function of Seasonal ET; drawn from data of Orgaz *et al.* (1992).