# Increasing Crop Productivity When Water is Scarce – From Breeding to Field Management

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**Abstract**
To increase crop yield per unit of scarce water requires both better cultivars and better agronomy. The challenge is to manage the crop or improve its genetic makeup to: capture more of the water supply for use in transpiration; exchange transpired water for $CO_2$ more effectively in producing biomass; and convert more of the biomass into grain or other harvestable product. In the field, the upper limit of water productivity of well-managed disease-free water-limited cereal crops is typically 20 kg $ha^{-1}mm^{-1}$ (grain yield per water used). If the productivity is markedly less than this, it is likely that major stresses other than water are at work, such as weeds, diseases, poor nutrition, or inhospitable soil. If so, the greatest advances will come from dealing with these first. When water is the predominant limitation, there is scope for improving overall water productivity by better matching the development of the crop to the pattern of water supply, thereby reducing evaporative and other losses and fostering a good balance of water-use before and after flowering, which is needed to give a large harvest index. There is also scope for developing genotypes that are able to maintain adequate floret fertility despite any transient severe water deficits during floral development. Marker-assisted selection has helped in controlling some root diseases that limit water uptake, and in maintaining fertility in water-stressed maize. Apart from herbicide-resistance in crops, which helps reduce competition for water by weeds, there are no genetic transformations in the immediate offing that are likely to improve water productivity greatly.

**Media summary**
Improvements in water productivity will come from better agronomy and better genotypes tuned to each other so that the combination performs well in farmer's fields.

**Key Words**
Water balance, harvest index, floret fertility, water-use efficiency, water deficits

## Introduction
The ideas of drought resistance and drought tolerance are giving way in the agricultural world to the idea of water productivity ("more crop per drop"). This change is a great advance because the latter can be quantified, with units of amount of crop yield per volume of water supplied or used, say, kg $m^{-3}$ or kg $ha^{-1}$ $mm^{-1}$. Because it can be quantified it enables improvements to be charted, thereby encouraging faster progress.

Nevertheless, the idea of drought remains in widespread use – certainly in the mass media, and also among crop scientists. It comes with connotations of hardship, or, in poor agricultural communities, malnutrition or even famine. It is an idea that inevitably enters any discussion of the impact of the scarcity of water on food production. It is important therefore to be clear about what it means, for it means different things to different people depending on their time scale of interest (Table 1); debates can easily be at cross purposes.

Many explorations of water deficits by plant physiologists, biochemists and molecular biologists are rather more concerned with survival than production, as noted in Table 1. While it is true that a crop plant that does not survive severe water deficits will not produce any yield, the converse is rarely true. Thus the challenge provided by changing focus from "drought tolerance" to "water productivity" clarifies the targets of research, especially those carried out at time scales of hours to days. Some processes occurring at these time scales can strongly affect water-limited yields; others have little relevance, as I shall discuss later.

"Water productivity" can also mean different things to different people (see, for example, Kijne et al. 2003, Pereira et al. 2002). To an economist it might mean the monetary value of outputs divided by that of the necessary inputs. To a geographer or irrigation engineer, it might mean the value of crops produced in a catchment in relation to the water supply of that catchment. But the quintessence of the idea is that it is quantifiable. In this paper, I will concentrate primarily on improving water productivity on farm (with units of amount of crop yield per amount of water supplied or used), though with occasional reference to other aspects.

**Table 1. Drought: definitions and significance (adapted from Passioura 2002)**

| Practitioner | Time scale of interest | Meaning of drought | Significance |
|---|---|---|---|
| Meteorologist<br>Farmer<br>Insurer | Years to decades | Rare event (say, one of the ten driest seasons per century) | Risk management |
| Agronomist<br>Crop physiologist<br>Breeder | Weeks to months, Growing season | Yield strongly limited by water | Water productivity |
| Plant physiologist | Days | Pots not watered | Mild shock, Survival |
| Biochemist<br>Molecular biologist | Hours | Plants left to dry on lab bench | Severe shock, Survival |

*Water as a Limiting Resource*

This heading implies two questions:

- First, how can we tell, in specific instances, if it is water that is mainly limiting crop yield?
- Second, when water is the main limitation, how can we most effectively improve the yields that we currently obtain?

An answer to the first question is not always clear cut, for in farmers' fields there are typically multiple environmental influences on yield. But comparing actual yield with an expected one can nevertheless be revealing, and any large discrepancy is worth exploring.

Answering the second question is helped by dissecting it into three components (Passioura, 1977; Richards et al. 2002; Araus et al. 2002), namely, how can one manage a crop or improve its genetic makeup to:

- transpire more of the limiting water supply
- exchange transpired water for $CO_2$ more effectively in producing biomass, and,
- convert more of the biomass into grain or other harvestable product.

Although these three components often interact, they are sufficiently independent to make it worthwhile considering them one by one. There is a wide range of biochemical, physiological, agronomic and ecological processes that may affect water productivity and that variously influence these components, as discussed later.

*How to gauge if water is the predominant limitation to yield?*

There is a lot of available information on winter-cereal crop yields in relation to rainfed water supply in southern Australia, a climatically mediterranean environment. Fig.1, adapted from Angus and van Herwaarden (2001), compares simulated yields of well-managed rain-fed wheat with mean annual reported yields in the shire of Wagga Wagga in Australia, in relation to growing-season rainfall. The solid diagonal line depicts a transpiration efficiency of 20 kg $ha^{-1}mm^{-1}$, an upper limit that is rarely exceeded in farmers' fields (e.g. French and Schultz 1984, Cornish and Murray 1989) provided that estimates of available water in the soil at sowing are good and taken into account when assessing the seasonal water supply. The intercept of that line on the x-axis gives a rough estimate of the amount of water lost by direct evaporation from the soil (Hanks et al. 1969), which commonly varies by a factor of two, in specific cases, around the 110 mm average shown in the figure.

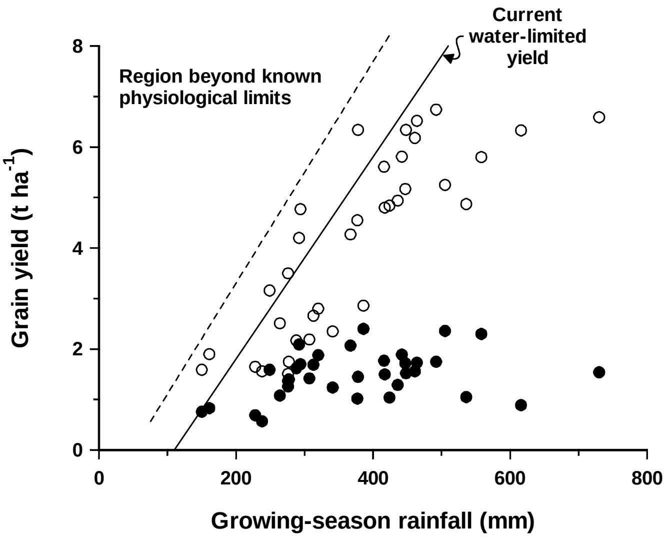


**Figure 1. Reported (●) and simulated (○) mean wheat yield in the shire of Wagga Wagga for 1949 to 1983 in relation to growing-season rainfall. The solid line depicts the upper bound of reported yields across a range of studies in southern Australia. It has a slope of 20 kg ha$^{-1}$mm$^{-1}$. The intercept of that line on the x-axis reflects the loss of water by direct evaporation from the soil. The region above the dashed line is outside known ecophysiological limits. Adapted from Angus and van Herwaarden (2001).**

The simulated points in Fig. 1 come from the SIMTAG model of Stapper and Harris (1989). The simulation assumed that the crops were well-managed and were without disease. They accord with the upper bound as determined in a wide range of field measurements, but show that some yields can be well below the line. The reason for such deviations is that the distribution of rain during the growing season can be unfavourable; for example, a preponderance of small falls of rain can lead to larger losses by direct evaporation from the soil (Sadras, 2003); or water deficits at flowering can lead to infertility even though the crop may have had good water supply at other times. Further, in regions prone to highly variable distributions of rainfall, such deviations can be large, especially in the subtropics where intense storms leading to much run-off are common (Hammer et al. 1993).

The most striking feature of Fig. 1 is that, except in the driest years, most of the field data fell well below not only the bounding line but also the cloud of simulated points. There are many reasons for this: weeds, disease, poor nutrition, frost, heat, and even waterlogging in the wetter years. But the horizontal distribution of these points suggests that water was not the main limiter of yield in most years, an observation similar to that of Rockström and Falkenmark (2002) for Sub-Saharan Africa. Subsequent to the range of years covered in Fig.1 there has been a large increase in yields in this shire such that many farmers are now achieving yields close to the upper bound (Angus 2001). Risk management has much to do with this change (Passioura 2002). In the earlier period, root diseases were rife, and thus exposed the crops to unexpectedly large water deficits because of the inability of the roots to effectively exploit water in the subsoil. Farmers therefore were cautious about applying enough fertiliser to produce large yields; they tended to aim for yields of 2 tonne ha$^{-1}$ which is typically the best that they achieved. Once they learned how to control root diseases, they had the confidence to aim for, and achieve, large yields, by increasing inputs such as nitrogen.

I have dwelt on this example because this type of analysis has proved to be an inspiration to farmers. It has provided them with a standard against which to compare their own crops, and although crude, it has stimulated them to improve their agronomic management. There seem to be few data available in other regions of the world for analysing farmers' yields in relation to water use or supply in this way. Such data are rare even from research stations, though Musick et al. (1994) provide a good example. The more common way of expressing water productivity is as the ratio of yield to water supply or total evapotranspiration. Kijne et al. (http://www.iwmi.cgiar.org/challenge-program/pdf/paper1.pdf ) and Hatfield et al. (2001) provide good compilations. While it is possible to analyse these ratios in individual cases to discern avenues for improvement, the functions that summarise many crops can be more revealing than the bare ratios, for they do establish an approximate upper bound, and they do reveal if many points are well below that bound, thus focussing attention on possible correctible causes that may be unrelated to water supply.

This empirical evidence accords with knowledge of the processes governing the net exchange by leaves between water and $CO_2$ leading to the production of biomass (often called transpiration efficiency (TE)), and by the fraction of that biomass that can be converted into harvestable yield – harvest index (HI), a dimensionless quantity usually defined as the ratio of grain yield to above-ground biomass. Transpiration efficiency depends on photosynthetic type (C3, C4, CAM) and on the evaporative demand of the environment (determined largely by solar radiation and humidity deficits). While the transpiration efficiencies of C4 plants are famously much larger than those of C3 plants at the level of gas exchange of leaves, the differences between the two in water productivity may be much smaller in the field, partly because of constraints that arise when scaling up (Gifford 1974) and partly because C4 crops are generally grown in hotter climates with larger evaporative demands (Fischer and Turner 1978).

As a general rule, well-managed, well-fed, disease-free cereal crops attain a maximum water productivity of about 2.0 kg of grain per cubic meter of transpired water (20 kg $ha^{-1}$ $mm^{-1}$). Comparable data for oilseeds and grain legumes are scarce, but generally these crops have smaller maximum water productivities, ranging from about 8 to 15 kg $ha^{-1}$ $mm^{-1}$ (Johnston et al. 2002; Loss et al. 1997; Zhang et al. 2000) . Because of the much greater energy cost of producing oil compared with carbohydrate, oilseeds have a maximum water productivity of about two thirds that of wheat (Hocking et al. 1997). Yields markedly less than these maxima are worth exploring for maladies other than low water supply.

*Avenues for improving water-limited yield of rainfed crops*
While it is clear that water productivity will be low in crops beset by diseases, pests, or weeds, there are also more subtle aspects of crop management or the behaviour of various cultivars that can have large effects on productivity. Hatfield et al. (2001) have reviewed many aspects of soil and stubble management that influence the water balance of the soil by affecting infiltration and water storage in the soil, and evaporative losses from the soil surface. These combined effects can substantially affect how much water is available to a crop. There are, as well, many other agronomic effects on water productivity. Timeliness of sowing, evenness of establishment, use of herbicides, management of nutrients (Viets 1962 still makes interesting reading), the role of previous crops (Kirkegaard et al. this volume), in fact, anything that improves the general vigour of a crop can strongly affect water productivity, usually, though not always, for the better.

Remarkably many of these agronomic influences do not necessarily involve plant water relations per se. Rather they involve the judicious, timely, more complete and more effective use of the water supply: capturing more of it for transpiration, exchanging it for $CO_2$ more effectively to produce biomass, and optimising the development of the crop to ensure a large harvest index. The most important processes are summarised in Table 2, together with others of lesser importance, set against the scales of time and space at which they operate. The Table deals with crops that are free of disease, but may be subject to other stresses that influence the effective use of water. The estimates in the final column are necessarily very general, but reflect arguments presented below and elaborated in more detail in Passioura (2004).

*Capturing more of the water supply: reducing losses from soil evaporation, deep drainage and runoff.*
A rainfed crop's water supply comprises available water in the soil at the time of sowing plus rainfall during the growing season. The main losses are by direct evaporation from the soil surface and vertical drainage of water beyond the reach of the roots. Run-off from the soil surface may be substantial during heavy rain, but much of that run-off may become run-on in lower parts of a field, with little net loss from the field as a whole (Batchelor et al. 2002) unless infiltration rate is poor or rainfall is intense. Runoff during intense rainfall can be greatly reduced with a good (>50%) trash cover on the soil (Silburn and Glanville 2002).

For crops that rely on growing-season rainfall, much water can be lost by direct evaporation from the soil, especially if there are many small falls of rain (Sadras, 2003). Crops that rely largely on water stored in the soil at the time of sowing lose much less in this way while they are growing, though evaporative losses before sowing are typically large (Hatfield et al. 2001). Cabangon et al (2002) report especially large evaporative and other losses in rice fields in the few weeks it takes to prepare them for planting. The rate of development of leaf area by the young crop strongly affects this loss, for the larger the leaf area the greater is the proportion of evapotranspiration that passes through the leaves. Indeed, the marginal increase in evapotranspiration induced by additional leaf area can approach zero if the distribution of rain is such that the soil surface remains wet during much of the crop's vegetative phase, as is common in mediterranean environments, for the evaporative demand by the environment may be met no matter what the ratio of transpiration to direct evaporation (Shepherd et al. 1987).

**Table 2. The effects of processes at various scales on the effective use of water by crop plants in producing grain (adapted from Passioura 2004)**

| Issues, processes | Temporal scale | Spatial Scale | Likely influence on water productivity |
|---|---|---|---|
| Carbon fixation rate at constant stomatal conductance | seconds | chloroplast | moderate |
| Instantaneous exchange rate of carbon and water | minutes to hours | stomata | moderate |
| Boundary layer effects, orientation, rolling | seconds to hours | leaf | moderate |
| Desiccation tolerance | hours to days | whole plant | slight |
| Harvest index, matching phenology to water supply, impact of water deficits on fertility and on supply of assimilate to the grain | hours to days or weeks | floral organs | large |
| Trajectory of green leaf area through time; ratio of water use of plant to other evaporative losses (soil, weeds) and to drainage; effective depth of roots | weeks to months | canopy, root system | large |
| Lateral movement of water: run-on and run-off; spatial variability in soil properties and plant growth; carry-over effects of different crops between seasons; effectiveness of irrigation; on-farm storage | one to several growing seasons | field | large |

Rapid development of ground cover relies on good seedling establishment. Crusting of the surface in soils of poor structure, uneven sowing depth, and poor quality seed can all lead to large gaps in plant cover. Poor establishment is an especial problem with the semi-dwarf wheats that are used widely throughout the world and that contain the Rht1 or Rht2 dwarfing genes. These genes induce short coleoptiles that do not extend to the soil surface if the seed is sown more deeply than about 60 mm, as can happen in a rough seed bed. Alternative dwarfing genes that can provide the benefits of short stems without overly restricting the maximum length of the coleoptile are available. One such is Rht8 which in experimental breeding lines enables emergence from sowing depths as great as 120 mm but yet provides adequate dwarfing of the canopy (Rebetzke et al. 1999).

Even if emergence of seedlings is good, the rate of development of leaf area may be slow. Leaf growth is strongly affected by temperature of both air and soil, so sowing winter-growing crops early, when soil and air are still warm, leads to good canopy cover during late autumn and winter with consequently less evaporative losses from the soil surface. Changes in mechanised agriculture during the last twenty years have enabled farmers to sow their crops at more opportune times (Hatfield et al. 2001; Hobbs and Gupta 2003). These changes include: directly sowing seed into the soil without the need for prior ploughing; using large and fast machinery that can sow large areas quickly; using general herbicides for killing emerged weeds just before or during sowing; and using specific herbicides for controlling weeds once the crop has established, or more powerful general herbicides, such as glyphosate with genetically modified crops resistant to such herbicides. Repeated cultivation of the soil to control weeds and to make a fine seed bed, which damages soil structure and allows greater evaporative loss of water from the soil, is no longer needed. Such techniques greatly improve the timeliness of sowing and can thereby improve yields in water-limited environments where unreliable weather at the start of the growing season means that opportunities for sowing are best taken when they arise (Hobbs and Gupta 2003). Agronomic flexibility such as this requires a range of cultivars that are specifically suitable for early, mid, or late starts to the season (Anderson et al. 1996).

Nutritional status of the young crop, especially nitrogen, can markedly affect rate of development of leaf area and thence evaporative losses from the soil, as illustrated in Fig.2 for a mediterranean environment.

Seasonal evaporation from the soil surface ranged from about 60 to 160 mm, as determined using the technique of Cooper et al. (1983). The corresponding overall water productivity of grain yield/transpiration ranged, with increasing nitrogen supply, from 11 to 20 kg $ha^{-1}mm^{-1}$, a similar, though larger, response to that found by Zhang et al. (1998). Water productivity is not necessarily higher at luxurious nitrogen supply, though, because of the possibility that the crop may use too much water during its vegetative phase and run out of water during grain filling, as discussed later.

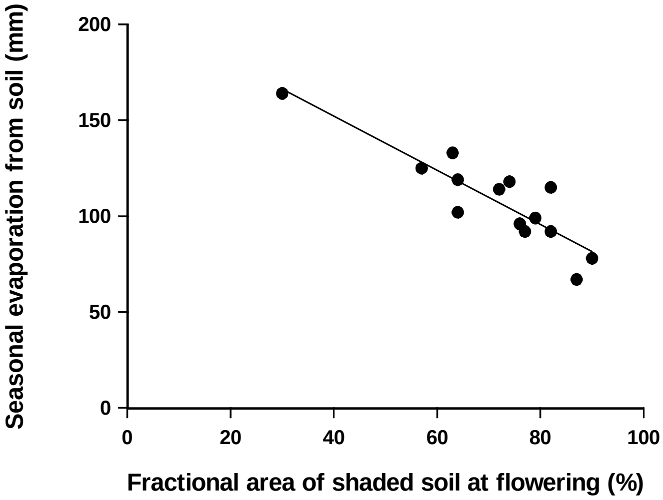


**Fig. 2. Evaporative loss of water from soil under wheat canopies of different size. The size of the canopy was varied by varying nitrogen fertiliser. (Adapted from van Herwaarden and Passioura, 2001).**

These major agronomic effects are matched by equally strong genetic ones. Richards et al. (2002) describe how selecting for large early leaves can produce breeding lines of wheat that develop leaf area twice as fast as standard cultivars in common use. These lines not only reduce evaporative losses, but also inhibit the growth of weeds (Lemerle et al. 2001). Because of the danger that such genotypes may lead to excessive vegetative growth that results in too little available water during grain filling (see later), it is important that any rapid development of the main stem that provides good early ground cover is not accompanied by too many tillers. The incorporation of a gene for inhibiting tiller development may prevent mid-season canopy development getting out of hand (Richards et al. 2002), and ensure that resources are not used in producing unproductive tillers.

*Reducing losses of water by deep drainage*

Water lost by drainage beyond the reach of crop roots is usually much less than that lost by direct evaporation from the soil, except in very sandy soils. Nevertheless it can be very important in foregone yield (Angus and van Herwaarden 2001). It is hard to measure, but is likely, in a semi-arid environment, to vary from zero to 100 mm per year depending on soil, management, and season (Dunin et al. 2001).

Capturing water that may otherwise drain can greatly boost yield. If roots do access it, they usually do so late in the season, after anthesis, when the products of the photosynthesis go almost entirely towards filling the grain, with little respiratory or other losses. Angus and van Herwaarden (2001) estimate that the marginal return from capturing such water is 33 kg $ha^{-1}mm^{-1}$, much greater than the overall value of 20 kg $ha^{-1}mm^{-1}$ shown in Figure 1. Thus, capturing 30 mm of this water could be translated into an increased yield of about 1 tonne $ha^{-1}$, a very substantial increase in water-limited environments in which average yields may be less than 2 tonne $ha^{-1}$. Further, this water is often rich in mineral nitrogen, leached from the topsoil earlier in the season when the plants were too young with root systems too small to use it (Angus, 2001). This nitrogen can boost the quality and possibly the amount of the developing grain if it keeps the nitrogen content of the leaves high.

Active deep roots help reduce drainage losses, but many soils in semi-arid areas are beset by subsoils that are inhospitable to roots for one or more of the following reasons: saline, sodic, too hard, too alkaline, too acid, too high in boron or too low in zinc and other nutrients that roots need locally for their adequate growth. Naturally occurring salinity at the bottom of the rooting zone may be common (Rengasamy 2002). Many crops may fail to send roots deeper than about 50 cm in such soils despite water penetrating to a metre or more in average to wet seasons. Plant breeding has made little impact on such problems, with the notable exception of tolerance to high boron (Paull et al. 1991).

Roots typically penetrate inhospitable subsoils through biopores, large extended pores made and repeatedly recolonised by successive generations of roots. These pores differ chemically and microbiologically as well as physically from the surrounding soil matrix (Pierret et al. 1999). They act as conduits from which lateral roots can explore the adjacent soil matrix. Given the environmental complexity of the subsoil, breeding crop plants whose roots can better exploit it will be difficult. Creating and maintaining a network of accessible biopores by agronomic means may be more feasible (McCallum et al. 2004).

Crops that are vigorous when young tend to extract more water from the subsoil, presumably because their roots grow deeper (Angus et al. 2001). There are substantial effects of cropping history – the sequence of earlier crop species – on the abilities of following crops to extract water from the subsoil, which may be through effects on early vigour but may also be due to other still unknown mechanisms (Kirkegaard et al. this volume, Angus et al. 2001). Premature senescence, in the sense that leaves senesce despite some water still being available in the soil, may be common. The "stay green" character, most studied in sorghum but also in other crops, prevents early senescence. In sorghum at least it seems to arise from positive feedback in nitrogen uptake: plants that maintain nitrogen in their leaves during grain filling (and hence stay green) fix more carbon, which in turn enables roots to continue extracting soil nitrogen, so that the system is self-reinforcing (Borrell et al. 2001).

In summary, there is substantial variation in the ability of crop roots to capture water that may otherwise drain beyond reach. This variation arises mostly from agronomic effects, including little understood results of cropping history and season. There must be genetic variation in the ability of crop roots to exploit subsoils, but as yet there are no obvious traits that breeders could realistically select for. Capturing this water can have environmental benefits as well as improving yield. In semi-arid environments especially, which are prone to have saline subsoils, water lost to deep drainage may mobilise salt and bring it to the surface lower in the landscape, there to cause dryland salinity. In more humid environments, the water may carry nutrients or other agricultural chemicals to discharge areas there to generate algal blooms and other toxicities.

*Improving the exchange of water for $CO_2$ by leaves*

The transpiration efficiency of leaves, i.e. the amount of carbon fixed per unit of water transpired, depends on both evaporative demand by the environment and the $CO_2$ concentration within the leaves (Tanner and Sinclair 1983; Condon et al. 2002). For a given evaporative demand and stomatal conductance, the lower is the concentration of $CO_2$ within a leaf the larger is the transpiration efficiency and the less is the discrimination against the heavy stable isotope of carbon, $^{13}C$, during photosynthesis. These two relationships together provide an effective tool, based on isotopic analysis of plant tissue, for estimating average internal $CO_2$ concentration within leaves, and thence the intrinsic transpiration efficiency (Farquhar and Richards 1984). Fig. 3 shows the yield advantage of breeding lines of wheat selected for intrinsically higher transpiration efficiency. As expected, this trait has greater impact the lower is the rainfall. These lines have culminated in the release of two cultivars in Australia, "Drysdale" and "Rees", which promise to increase water-limited yields in dry years by about 10% above those of the widely sown cultivars from which they were derived. Thus, in terms of Fig.1, it promises to increase the slope of the lower end of the water-limited line by up to 10%.

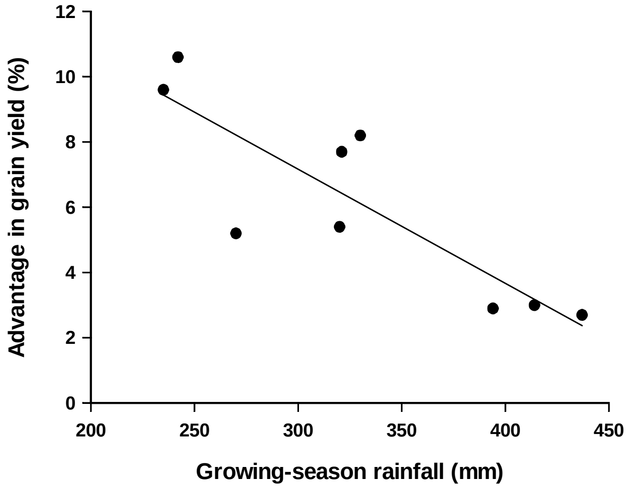


**Figure 3. The advantage in grain yield of lines of wheat selected for low discrimination against $^{13}C$ during photosynthesis (i.e. high intrinsic transpiration efficiency) over those selected for high discrimination, as a function of growing-season rainfall. Adapted from Rebetzke et al. (2002).**

*Converting biomass into grain*

The timing of flowering is the most important trait that plant breeders select for when targeting water-limited environments. For example, winter-growing crops that flower too early may not have built enough biomass to set and fill a large number of seeds, and may also be prone to frost damage at flowering. Those that flower too late, while they may have set a large number of grains per unit area and thereby have a large yield potential, may fail to fill their grain adequately because they have too little water left in the soil and may be exposed to the heat and aridity of late spring and early summer (Richards 1991).

Fig. 4 illustrates these points for wheat. There is an optimal flowering time at which there is an appropriate balance between water used during canopy development and water used during grain filling. Crops that flower before the optimal time may achieve large harvest indices unless damaged by frost, but do not produce enough biomass to set a large enough number of seeds to generate a good yield potential (Fischer, 1979). Those that flower too late are at risk of severe water deficits that can lead to sterility, and may have too little water left to allow for adequate post-flowering photosynthesis or time to mobilise stores of carbohydrate accumulated before flowering and transfer them to the grain.

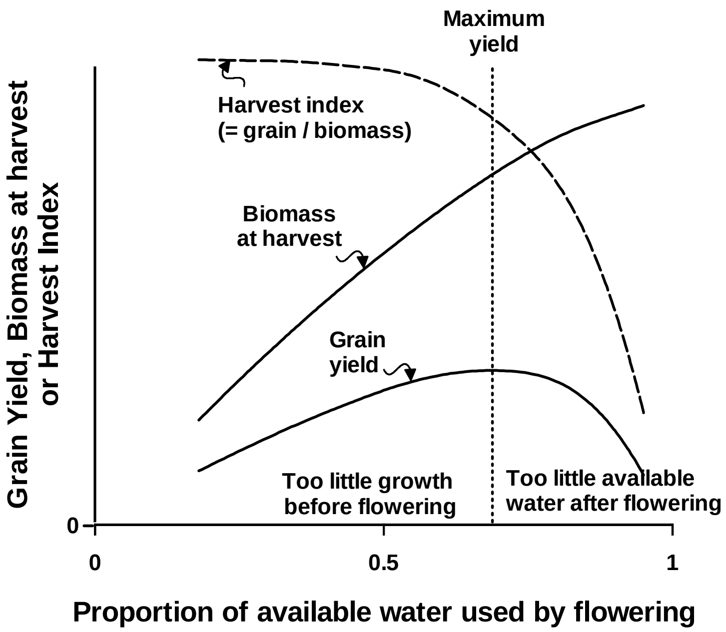


**Fig 4. Schematic graph of grain yield of wheat, biomass at harvest, and harvest index, in relation to proportion of the available water supply used by flowering. The scale of the y-axis is arbitrary, though the maximal harvest index is typically 0.5. Copyright © CSIRO 2002. Reproduced from Functional Plant Biology 29,537-546 (Passioura, 2002) by permission of CSIRO Publishing.**

Plant breeders have produced a range of cultivars that flower close to the optimal time in a given environment. This optimum is necessarily an average, for depending on the pattern of rainfall during the growing season earlier flowering crops may do better in one season, and later flowering ones may do better in another. As an average there is little room for further genetic improvement, though breeders have been producing slower maturing cultivars that can be sown earlier in the season while still flowering at the optimal time (Anderson *et al*. 1996). Such cultivars allow farmers to capitalise on the flexibility in sowing time that their modern machinery and agronomic techniques enable, as mentioned earlier; they may also have environmental benefits in that their deeper roots may capture more water and nutrients that might otherwise escape towards the groundwater. Global warming may, over the next few decades, alter the optimal time of flowering, but breeders are so concerned with getting the phenology right that they may well make the necessary adjustments without being strongly aware that they are doing so.

Nutrient management also strongly affects the pattern of water use by a crop. Too much nitrogen, whether from fertiliser or from excessive mineralisation of soil organic matter, can result in crops that are too vigorous and that use too much water before flowering; they set a large number of seeds but are unable to produce enough carbohydrate to fill these adequately, neither from photosynthesis after flowering nor from carbohydrate stored before flowering and available for retranslocation (van Herwaarden et al. 1998; Angus and van Herwaarden 2001). The crop senesces prematurely, resulting in a low yield of often poor quality grain. Farmers can get around this potential problem by applying nitrogen fertiliser tactically, in mid-season, once they have a better idea of how much water their crops are likely to get, rather than applying large amounts at sowing.

*Effects of drought on fertility*

Water deficits during specific stages of floral development can severely damage seed set, through pollen sterility or abortion of embryos, or can prematurely end grain filling. Low water potentials during pollen mother cell meiosis can induce severe pollen sterility and thence low yields in the cereals even though subsequent conditions might be good. Because the water status of the floral tissue is maintained despite the low water potential of the leaves (Westgate et al. 1996), it is likely that a sporicide, perhaps ABA (Morgan and King 1984), travels from the vegetative tissue to the reproductive.

Low water potentials around the time of anthesis are especially damaging in rice and maize. In rice, panicles may fail to emerge fully, spikelets lose water readily and lemma and palea may die, and anthers may fail to dehisce (Saini and Westgate 2000). Maize is prone to severe embryo abortion. Such abortion can be largely prevented by infusing stem internodes with sucrose solutions that essentially replace the assimilate that would have been produced by photosynthesis had the plants not been water-stressed (Boyle et al. 1991). However, it is not the lack of assimilate alone that is the problem. There is also a metabolic disruption of carbohydrate metabolism in the ovary, especially of acid invertase, which prevents the embryos from developing (Zinselmeier et al. 1995).

Water deficits in maize can also bring about a mismatch in the timing of anthesis and silking, such that silking is delayed until after the pollen has been shed, leading to lack of fertilisation. Bolaños and Edmeades (1993) showed that the anthesis-silking interval (ASI) accounted for a remarkable 76% of variation in grain yield across a range of cultivars and watering regimes, with yield reductions of almost 10% per day increase in ASI. The genetics of this effect are simple enough to have enabled the development of hybrids with markedly better yields during drought (Ribaut et al. 2004) .

These various effects of water deficits on fertility can lead to severe, sometimes complete, loss of yield in droughted grain crops. While total loss is rare, it is likely that drought-induced infertility can unnecessarily reduce yields in seasons in which there is a reasonable water supply but in which severe transient water deficits occur at these especially sensitive times. Unravelling the processes involved is a promising way of laying a foundation for genetically improving grain yields in such droughts.

*Mobilising pre-anthesis reserves during grain-filling*

Crops that suffer water deficits during grain filling may produce a large biomass but be unable to match that with a good harvest index. Excessive vegetative growth, especially if induced by an oversupply of mineral nitrogen, can make the effects of water deficits worse by using too much water before flowering (Fig. 4). The result is that the crop senesces prematurely and its yield falls with excessive nitrogen supply.

Van Herwaarden et al. (1998) have argued that an oversupply of nitrogen worsens this imbalance in water use by reducing the amount of storage carbohydrates available for retranslocation to the grain. There is a negative correlation between nitrogen level and storage carbohydrate, not necessarily related to water deficits (Batten et al. 1993), with the implication that excess nitrogen results in the investment of photosynthate into structural rather than storage carbohydrate when stimulating excessive vegetative growth. Whether there is enough useful genetic variation for breeders to use, in the ability to store mobilisable carbohydrate in the stems before flowering, remains moot.

*Getting the most out of irrigation*

As water for irrigated agriculture becomes scarcer, it is likely that it will increasingly be used supplementally – that is, full irrigation will be replaced by deficit irrigations targeted to periods without rain that coincide with especially sensitive stages of a crop's life. Pereira et al. (2002) review the possibilities as well as outlining general good irrigation practice. Ideally, supplemental irrigation means using limited irrigation water so that it gives the greatest marginal return over a larger area than would be possible with full irrigation. While there is some appreciation of when crop yield can be most damaged by water deficits, for example, during meiosis of pollen mother cells or around anthesis (Saini and Westgate 2000), much agronomic research will be needed to tune such an irrigation technique to local conditions, so that irrigations are made at the best times or in the best way. A simple technique for deciding when to stop an irrigation rather then when to start it offers promise of markedly reducing over irrigation by resource-poor farmers (Stirzaker 2003). Irrigating alternate furrows is another technique that looks promising (Kang et al. 2000).

There are also broader issues. Spatial variability in soil properties are common, and may mean, for example, that shallow patches of soil, or ones in which roots are unable to penetrate deeply for other reasons, will need to be treated differently from ones in which roots can penetrate deeply. Perhaps of most importance is learning how to manage the risk associated with using deficit irrigation where irrigation supplies are unreliable (English et al. 2002). This applies especially where very limited supplemental irrigation is available and could be used to sow a crop at the usually optimal time even though the seasonal rains have not arrived (Oweis and Hachum 2003).

Lowland rice, the most profligate of all crops in water use, poses a great challenge in reducing water use because of its extreme sensitivity to water deficits. Nevertheless there are innovative management practices that could reduce its water consumption (Tuong and Bouman 2003). Reducing the preparation time before sowing or transplanting, when empty fields are being flooded and therefore using a lot of water, can save much water (Cabangon et al. 2002). "Aerobic" techniques, in which rice is grown without continuous flooding, possibly on raised beds, also use less water, though with them come reduced yields. Further, there are complications arising from weed control in unflooded rice, and possibly deleterious changes in the emissions of greenhouse gases, methane going down, but nitrogen oxides going up.

*Farming systems and agricultural landscapes*

Water productivity depends not only on how a crop is managed during its life, but also on how it is fitted in to the management of a farm as a whole, both spatially and through time. Further, the management of water use by crops may generate offsite effects that lead to dryland salinity or eutrophication or other pollution of discharge areas. The role of tillage has been changing and is likely to keep on changing as the advantages of direct-drilling techniques become more widely appreciated, not only for improving crop performance but also for protecting the soil. Some specific examples follow.

The use of bare fallows in semi-arid agriculture, to store water during one potential cropping season for use in the next, has been common. Where land is plentiful this practice reduces the risk of crop failure, perhaps not so much from the stored water, for the effectiveness with which that is stored is low, but because of the accumulation of mineral nitrogen and the reduction of inoculum of soil-borne diseases. The practice also exposes the soil to erosion, and can allow much water to drain beyond the reach of the crop roots, there to mobilise salt that may then appear lower in the landscape. Recent studies have shown that continuous cropping can increase water productivity over a series of crops and can repair the damage caused by the frequent cultivation of the bare fallows (Schillinger et al. 1999; Li et al. 2000). Continuous or, rather, opportunistic cropping can both increase average water-limited yields and also reduce risk, for instead of a fixed pattern of fallow and crop, a crop can be chosen tactically, to suit conditions at the start

of the growing season, and to be fertilized accordingly as the season develops (Sadras et al. 2003). The addition of extra organic matter to the soil with continuous cropping, even if only from the roots, and the protection of that organic matter by the lack of disturbance, can improve the water relations of the soil thereby enabling even better crops; an upward spiral of productivity can ensue.
Appropriate choice of crop sequence can improve water productivity by helping control diseases and weeds. Punctuating a series of cereal crops by oilseeds or grain legumes can increase the yields of the subsequent cereal crops (Kirkegaard et al. this volume). The role of canola as a "break" crop in southern Australia has been especially notable (Passioura 2002). The development of winter-growing chickpeas in the Mediterranean region may serve a similar role (Singh et al. 1997).

Tillage practices in the extensive rice-wheat cropping systems of Asia are also changing (Hobbs and Gupta 2003). Surface seeding, in which the wheat seed is broadcast directly on to the saturated soil left by the rice crop, or zero tillage techniques, enable more timely establishment of the wheat crop. The use of raised beds, stimulated by work at CIMMYT, can greatly improve water productivity (Wang et al. 2004). With these changes have come the need to avoid the traditional puddling of rice soils, which while it may reduce drainage losses, is not necessarily needed to attain high yields (Hobbs and Gupta 2003).

Finally, in semiarid agricultural landscapes, which typically contain much salt in the regolith, it is important to control the flows of water that escape the roots of annual crops. It is these flows that largely contribute to the increases in salinized land outside irrigation areas. Replacing bare fallows with crops will substantially reduce, but not eliminate, the loss. The escaped water drains slowly towards the watertable, and while it remains within the top few metres may be accessible to the roots of deep-rooted perennial agricultural plants such as lucerne grown for two to three years (Black et al. 1981; Latta et al. 2001; Ridley et al. 2001). Integrating a phase of deep-rooted plants into a cropping system is, however, challenging.

*Opportunities for molecular plant breeding to improve water productivity*
The foregoing discussion describes how breeding and agronomy are closely intertwined in improving water productivity of rainfed crops. While plant breeders have many agronomically important traits under control, for example flowering time and height, others, especially ones relating to the performance of roots, have been difficult to handle. Marker-assisted selection (MAS) is becoming increasingly useful. There are about 50 markers listed on the Plantstress website (http://www.plantstress.com/biotech/index.asp?Flag=1 ) that bear on the water economy of crops, including many dealing with root traits, but few appear to seriously interest breeders. Eagles et al. (2001) list about 20 markers in use in Australian wheat breeding programs. Most concern leaf diseases and grain quality. Apart from the leaf diseases, the control of which improves water productivity in both water-deficient and water-sufficient environments, several concern root diseases, which more directly affect water productivity. Table 3 lists several markers discussed by Eagles et al. (2001) and adds some more recent ones that are being used in breeding programs. Of these markers, the most important one so far is that for CCN resistance in wheat, which has contributed to the selection of several new cultivars. In maize, markers for ASI have proved useful in improving fertility in water-stressed crops.

**Table 3. Use in breeding programs of markers that may influence water productivity**

| Trait | Significance | Reference |
|---|---|---|
| Resistance to cereal cyst nematode (CCN) | Competent root system | Ogbannaya et al (2001) |
| Boron tolerance | Competent root system | Jefferies et al. (2000) |
| Root lesion nematode | Competent root system | Williams et al. (2002) |
| Anthesis-silking interval (ASI) | Enables overlap of anthesis and silking in water-limited maize | Ribaut et al. (2004) |
| Rht1, Rht2, dwarfing genes | Select against to avoid short coleoptiles | Spielmeyer and Ellis (2002) |
| Rht8 dwarfing gene | Dwarfs shoot but not coleoptiles | Ahmad and Sorrels (2002) |
| tin, tiller inhibiting gene | Inhibits excess production of tillers in wheat | RA Richards (pers. comm) |

*Genetic transformation of crops to improve water productivity*
Apart from herbicide-resistant crops, which enable excellent control of weeds, there are no immediate prospects for producing GM crops that could greatly improve water productivity. There are hundreds of patents that claim inventions that may improve "drought tolerance" (as appear in CAMBIA's agriculturally-oriented patent database at http://www.cambiaip.org/cgi-bin/cipr/TT2/simple.cgi. ) But it is hard to discern any of these likely to influence water productivity in the field. Almost all are concerned with metabolic or stress-induced genes having doubtful functional significance at the level of a field-grown crop whose production is limited by water (cf. Table 2).

Desiccation tolerance, the ability of plants to survive severe water deficits, has been a popular target. However, even if substantial improvement in survival could be made, it is likely to have little effect in the field. The problem is that droughts that are severe enough to kill crop plants are not commonly relieved by good rains during the particular growing season. It would make sense to do a climatological analysis of a target region before investing major resources pursuing desiccation tolerance. Using a well-tuned crop simulation model driven by a long run of weather data would soon reveal how often genuine desiccation tolerance would be useful.

While there are genes available that confer desiccation tolerance in transformed plants (Haake et al. 2002) there remains doubt about whether this "tolerance" is simply due to the transformed plant growing more slowly or having smaller stomatal conductance than the wild type, thereby using water more slowly, and thereby not experiencing as severe water-deficits, despite having received no water for the same length of time (Blum, http://www.plantstress.com/biotech/index.asp?Flag=1 ). Evidently, assays need to be done more carefully, with the involvement of people experienced in exploring plant water relations. Indeed, progress in this general field is likely to remain slow unless teams are created which have the collective expertise not only to scale up from gene expression to the performance of plants in the field, but also to identify real problems in field-grown plants that may be amenable to effective genetic manipulation. The great prize of C4 photosynthesis in rice, while feasible, and although the requirements are well understood at biochemical, structural and physiological levels, is still a long way off (Mitchell and Sheehy 2000).

There are three areas that may prove useful before long. Carbohydrate metabolism in water-stressed maize at flowering, as noted earlier, can strongly affect embryo development. The work of Helentjaris et al. (2002) on invertase activity may prove to be effective in preventing severe embryo abortion during periods of water stress at flowering; it is soundly based on much physiological and biochemical analysis of floral development in water-stressed maize. Another example is the discovery of the CBF family of transcription factors (Thomashow et al. 1999) which markedly improve freezing tolerance in Arabidopsis. An important possible application of this invention, though not mentioned in the patent, is in protecting flowers from damage by freezing. Greater tolerance of freezing would enable breeders of crops with a winter-spring growing season to aim for earlier flowering, which would then give the crops a longer period of grain-filling in mild conditions before the heat and aridity of late spring and summer arrives. The third example is that of aluminium tolerance, now that a gene has been cloned that can enable roots of sensitive plants to grow in acid soils that commonly contain high levels of soluble aluminium (Sasaki et al. 2004).

*The way ahead?*
Improvements in water productivity will most likely come, approximately equally, from better agronomy and better cultivars, with improvements in one stimulating improvements in the other. That is what has happened in the past, and there is no strong reason to expect that the pattern will change. Developing expectations about what water-limited yield might reasonably be, given the growing season's weather and other conditions, has proved to be an important stimulus to the way farmers' think about how they manage their crops. Analysing major discrepancies between actual and expected water-limited yields can reveal other major limitations such as inadequate nutrition, hitherto unrecognised root diseases, inadequate rooting depth (compaction, inhospitable subsoil), inappropriate choice of cultivar, poor establishment, or inadequate infiltration. If such limitations do become evident, then dealing with them where possible is likely to bring the largest and fastest rewards.

One of the reasons for there being large differences in many regions between potential and actual yields is that farmers' management of their crops is often constrained by their perception and handling of risk. Aiming for high yields is risky, for to do so requires large inputs, especially of fertiliser. Even if economic analysis predicts higher average returns, farmers may, understandably, still not be prepared to take the risk of the occasional complete crop failure that may be devastating to them. Thus, the interaction between risk management and crop management may strongly influence how farmers can go about improving the water productivity of their crops. The participation of farmers in trying out new agronomic techniques in early stages of development is therefore essential.

While crop breeders' historical success in improving yield potential has at the same time improved water productivity except perhaps when water is extremely scarce, there are also many specific opportunities to improve the water economy of crops by better tuning the development of a crop, both vegetative and floral, to particular environments – to be able to take tactical advantage of variable weather to sow at the right time to capitalise on opportunities for good establishment. As well there are reasonably well understood biochemical and physiological behaviours that may be amenable to selection, possibly even transformation, for ensuring that water-stressed crops do not lose more fertility than necessary or be unable to transport stored assimilate to the grain. Premature senescence, especially when there is still available water in the subsoil which the crops fail to exploit, is a problem that may soon become soluble now that the "stay green" trait is becoming better understood.

The hope that plants can be transformed by one or at most a few genes to grow well with very scarce water, that is, to produce crops that occupy the top left quarter of Figure 1, is in my view misplaced. It seems to arise from a belief that plants that can revive after desiccation will also be able to grow despite being desiccated. They can't. Functional genomics may have much to offer in the coming decades in relation to improving water productivity, but only when embedded in well-understood biochemical, physiological, and agronomic contexts. The best immediate prospects come from well-understood single gene traits that affect the competence of roots, and therefore their ability to take up water, for example tolerance to the high levels of soluble aluminium that usually accompany soils of low pH.

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