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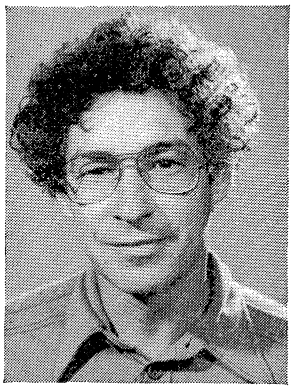
Forum

Grain Yield, Harvest Index, and Water Use of Wheat



J. B. Passioura

Many have argued that it is useful to view the yield of a cereal crop as the product of two factors, namely biological yield and harvest index (Donald and Hamblin 1976). When we are studying the yield of wheat grown with a limiting water supply, it may be useful to extend this analysis and view the yield as the product of three factors, namely (*a*) amount of usable water, (*b*) efficiency of water use, i.e. how much dry matter is produced per unit of water transpired, and (*c*) harvest index, i.e. how much grain is produced per unit of total dry matter. Assuming, as seems likely, that strong negative interactions between these factors are rare, increasing any one of them should usually increase yield. Is there much scope for such increases?

Amount of Usable Water

The amount of usable water depends on the rainfall, about which we can do nothing, on the water stored in the soil at sowing, which we can partly control by fallowing, on the water lost to weeds and by evaporation from the soil, which we can partly control by management, and on the effective depth of soil from which the roots will extract water.

Fallowing practice is well developed and probably cannot be improved to any considerable extent.

Evaporation from the soil depends on a complex interaction between weather, leaf area, leaf geometry and certain properties of the soil. It can be reduced by promoting rapid, even, development of leaf area by the crop (Ritchie 1974), but this may lead to a large early use of water, which, in turn, may be detrimental to harvest index (see below).

Roots, in some wheat-growing areas, usually penetrate as far as the wetting front and extract almost all the available water (Allen and George 1956; Fischer and Kohn 1966; Fawcett and Carter 1974), so we can make little improvement there. In other areas the roots do not usually penetrate as far as the wetting front, so that at maturity a substantial amount of available water remains at depth in the soil (Walter and Barley 1974; Schultz 1974). The point has often been made that if we could breed plants with vigorous root systems at depth, we may be able to increase yields substantially in certain environments. Sufficient genetic variability in deep rooting exists and can be exploited (Hurd 1974). However, in some areas, this deep water may not be as potentially useful as it at first appears. It may have taken several years to accumulate, and if so a deep-rooted crop could mine it only once. Little information is available on this point. The rate of local recharge of ground water would provide an upper limit to the sustained advantage which deep-rooted plants would have over shallow-rooted ones, but values for the wheat-growing areas are hard to find. Where the local recharge is large, however, breeding for deep roots would seem to be the most promising way of increasing the supply of usable water.

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Efficiency of Water Use

Efficiency of water use has proved hard to manipulate. The early promise of antitranspirants has not been fulfilled (Sinclair *et al.* 1975), and good husbandry seems to be the only sure route to high efficiency (Viets 1966). However, as is shown below, there is considerable variation between cultivars of wheat and hence explicit breeding for high efficiency may be worth trying.

Several cultivars of wheat were grown in a glasshouse in deep pots (1 m) containing 10 kg of loamy soil. (The cultural conditions were similar to those described by Passioura (1976*a*)). The plants were either (*a*) given 1000 g water per pot at sowing and harvested at death, or (*b*) given 1000 g per pot at sowing plus 100 g per week from the end of week 3 until anthesis, when they were harvested. The efficiencies for given cultivars varied little between the treatments, and the rankings of the cultivars were almost the same in the two treatments, so the results were pooled. The rankings were (*a*) Gabo, Gamenya, Ramona, Sonora, Penjamo (4.0 – 3.8 g shoot per kg water used), (*b*) Timgalen, Pitic, Chile 1B, Lerma Rojo (3.6–3.5 g per kg), and (*c*) Javelin, Olympic, Heron, Emblem (3.3–3.1 g per kg), with the varietal effects being significant at $P < 0.01$.

This large range in efficiency suggests that there is genetic variation in water-use efficiency of wheat cultivars, which it may be possible to exploit, although there was a fairly strong negative correlation between efficiency and time to anthesis ($r^2 = 0.47$; $P < 0.01$) in the above experiment which, if general, could complicate a breeding program. The reason for the variation in efficiency is obscure. There are grounds for suspecting that water-use efficiency may depend on specific leaf weight or on leaf thickness (Passioura 1976*b*), but in the above experiment there was no correlation of efficiency with specific leaf weight and only a weak correlation with leaf thickness ($r^2 = 0.19$; $P < 0.05$). The variation could be due to variation in root : shoot ratio, rather than in total dry weight per unit of water transpired, for the quoted efficiencies refer to shoot weight per unit of water transpired. If this is so, it makes the variation in efficiency no less valuable, and would be evidence that many cultivars have excessively large root systems; the amount of water extracted from the soil was virtually the same for all cultivars.

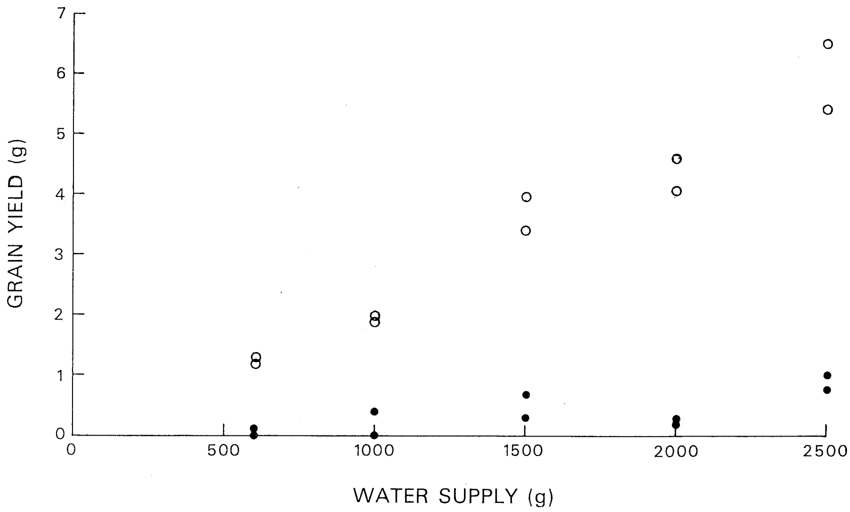


Fig. 1. Grain yield as a function of total water supply for individual Gabo wheat plants grown in pots. (● water supplied *in toto* at sowing; O water metered out).

Harvest Index

In a given environment the total dry matter produced by water-limited wheat depends on the total amount of water used (de Wit 1958). Grain yield, however, depends rather more on the water used after anthesis than on the total used (de Wit 1958; Nix 1976; Passioura 1976*a*). Therefore, we might expect the harvest index to depend on the proportion of the total water supply which is used after anthesis (provided there have been no catastrophic effects on grain set).

Fig. 1 shows the yields of individual plants of Gabo wheat, grown in pots as described above, except that the total water supply of each plant varied from 600 to 2500 g and the plants either had all their water given to them at sowing, or they had only one-third at sowing, with the remainder being metered out to them slowly over a period of 10 weeks from the end of week 3. The figure shows a poor relationship between grain yield and total water supply. No plant that got all its water at sowing outyielded any plant that had its water metered out, even though, in the extreme, plants of the former group used four times as much water as those in the latter.

Fig. 2 shows, for the same experiment, harvest index plotted against the percentage of water used after anthesis. Here the data are much more coherent: irrespective of the total water supply, the harvest index was large when about 30% of the water supply was used after anthesis, but was small when less than 10% was so used. That this relationship is not peculiar to Gabo is illustrated in Fig. 3, which shows data for four cultivars, grown in pots as described above, and with their water supply metered out in different ways so as to vary the proportion used after anthesis.

If the dependence of harvest index on the percentage of water used after anthesis applies in the field as well as in the glasshouse,

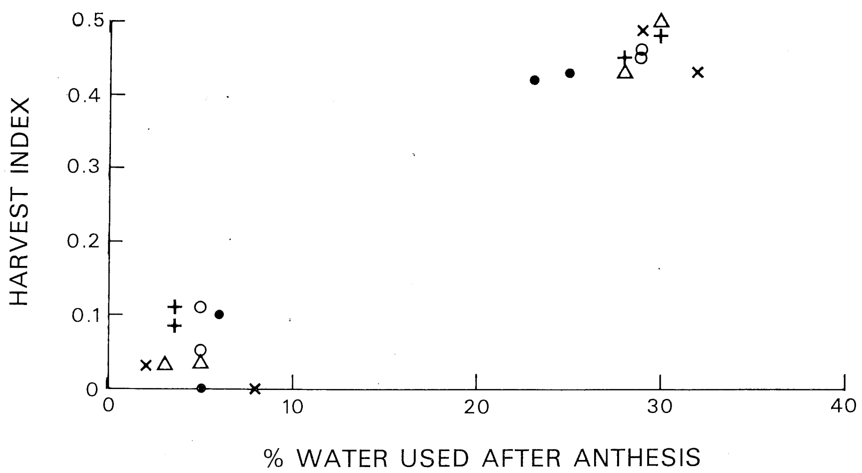


Fig. 2. Harvest index as a function of the percentage of the total water supply which the plants in Fig. 1 used after anthesis. The different symbols designate different total water supplies as follows: ×, 600 g; ●, 1000 g; O, 1500 g; Δ, 2000 g; +, 2500 g.

it gives us an opportunity to increase yield. When a crop is relying heavily on current rainfall, the only room for manoeuvre is by influencing the timing of anthesis. Much successful attention has been given to this and many present cultivars are a good compromise between being early enough to be able to fill their grains before running into severe summer drought, and late enough to avoid major frost damage at anthesis, yet having sufficient time to develop a reasonable number of grains per unit area. But if the crop is relying heavily on a limited supply of stored water, and if, as often happens, that store is almost exhausted by anthesis, there is still additional room to manoeuvre. For if we could slow down the rate at which the roots extract water from the subsoil, we would increase the amount of available water remaining in the soil at anthesis, and this should result in an increased yield.

When a crop is relying heavily on stored water, the topsoil is usually dry, the development of nodal roots is poor, and the seminal roots predominate in extracting water from the subsoil (Passioura 1974). There is a substantial resistance to the longitudinal flow of water in the seminal axes because almost all the water collected in the subsoil by the lateral roots has to be transported through the dry topsoil to the transpiring shoots through only one small vessel in each axis. Ways in which this resistance may be increased in order to reduce the rate of early extraction of subsoil water have been discussed elsewhere (Passioura 1972, 1974).

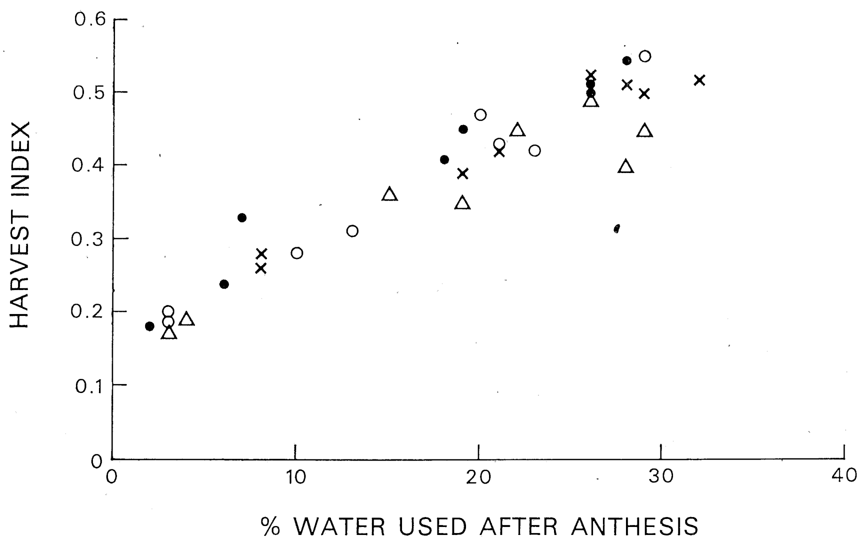
This stratagem of increasing the hydraulic resistance of the seminal root system has the attraction that while it may improve yield in a poor season, it should not affect the crop's ability to respond to good seasons. For if the topsoil were frequently moist, the nodal roots would develop well and amply supply the crop.

Interactions between Water Use, Efficiency, and Harvest Index

It is useful to analyse yield in terms of these factors only if strong negative interactions between the factors are rare or can be avoided. The pot experiments described above showed no unfavourable interactions: harvest index was independent of total water use (Fig. 2); and so was efficiency which, for a given cultivar, was the same whether the plants had a fixed supply of 1000 g water or were watered at a constant rate until anthesis when their total water use was considerably greater; in the experiment from which Fig. 3 was derived, efficiency had a small positive correlation with harvest index.

Thus there seem to be no inherent reasons for negative interactions. In the field, however, there could conceivably be sufficiently strong negative interactions that an increase in one particular factor might decrease yield. For example, if we were to breed deep-rootedness

Fig. 3. Harvest index as a function of the percentage of the total water supply of 1800 g per plant which individual plants of different cultivars used after anthesis. (×, Gabo; ●, Pitic; O, Emblem; Δ, Heron).



into a cultivar that does reasonably well when growing on a limited supply of stored water, we might increase the total supply of available water by a small margin, but run the risk that the plants would use the extra water so fast they they would run out before anthesis; they may normally rely on the sparseness of their deep roots to meter out the water contained in the subsoil. Or, again, if we have a cultivar that does reasonably well when it is growing on a very large supply of stored water, restricting the early use of that water may indeed increase harvest index by increasing the proportion of the water used after anthesis, but the total water use may be so reduced that the net effect is to decrease yield. A third example, mentioned previously, is that of a crop which develops its leaf area rapidly and evenly. Such a crop may increase its supply of usable water by decreasing evaporative losses from the soil, but in so doing it may necessarily squander stored water early in its life, to the detriment of its harvest index.

These three examples have in common a marginal improvement in one factor when one of the other factors seems to be rather more sensitively limiting. By concentrating on improving the factor that seems to most sensitively limit yield in a given environment, we should be able to avoid such interactions. Thus where drought dominates the performance of wheat, as it does in most Australian wheat-growing areas, the improvement, through breeding or management, of one or more of the factors discussed above, might well result in increased yields.

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