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# Irrigation and Crop Improvement in Temperate and Tropical Environments

L. T. Evans

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# Irrigation and crop improvement in temperate and tropical environments

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There is a strong interaction between irrigation and crop improvement, irrigation creating new opportunities and challenges for plant breeders while depending on their progress for its full benefits to be realized. In temperate environments the primary emphasis is on raising yield potential, especially as irrigation enhances the use of agrichemical inputs. Efficiency of water and energy use through the modification of physiological processes and of sensitivity to stress at various stages of the life cycle is also sought. In tropical environments, breeding for greater yield potential and more comprehensive pest and disease resistance are still important. However, shortening the length of the life cycle, reducing its sensitivity to seasonal signals and increasing yield per day may be more important than raising yield per crop because of the scope for multiple cropping made possible by irrigation in the tropics in the absence of contraints by low temperatures.

## INTRODUCTION

A vast and rapidly growing literature is devoted to plant breeding for better adaptation to water stress, whereas virtually none has been explicitly concerned with plant breeding for irrigated conditions, the subject of this paper. To a degree, this latter objective is implicit in breeding programs for irrigated rice, such as those at the International Rice Research Institute (I.R.R.I.) in the Philippines, and in selection for high yield potential in other crops, but there is as great a need for discussion of the specific objectives of plant breeding for irrigated conditions as there is for those of water stress.

Irrigation both justifies and is justified by the enhanced use of agrichemicals, especially fertilizers, and this is in turn dependent on the availability of varieties which are responsive and high-yielding under those conditions. In this sense irrigation, improved varieties, and agrichemicals are interacting cofactors in agricultural development. Irrigation enhances the increase in crop yield, illustrated in figure 1*a* for rice yields in the Philippines. Over the ten-year period, modern varieties have been grown on almost as high a proportion of the rain-fed lowlands as under irrigation, but both fertilizer use and yield advance have been lower under lowland conditions (C. C. David, unpublished data). Increase in yield under upland conditions has been slight by comparison, as for rice in Colombia (Chandler 1979), and for dryland as compared with irrigated wheat in the U.S.A. Figure 1*b* illustrates the rise in the use of modern rice varieties in the Philippines and the parallel rise in the use of fertilizers on rice, made somewhat less smooth by the high fertilizer to rice-price ratios in 1970 and 1975–76. Investment in irrigation appears to have been encouraged by the rapid adoption of the modern variety-fertilizer package, illustrating the mutual interdependence of irrigation and plant breeding.

Plant-breeding objectives for irrigated crops in the tropics may be quite different from those

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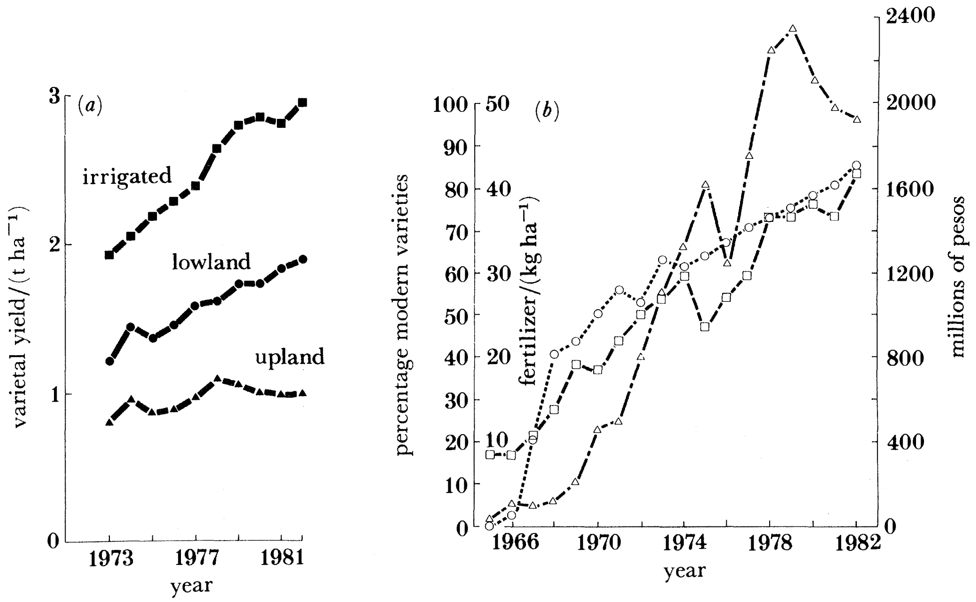

FIGURE 1. Aspects of rice production in the Philippines. (*a*) Changes in the yields of irrigated, lowland and upland rice (Philippines Bureau of Agricultural Economics, unpublished data). (*b*) Changes in the percentage of paddy area planted to modern varieties (○); fertilizer use (Kg N, P, K) per hectare of rice (□); and annual investment in irrigation in millions of pesos, 1981 price (△); all over the period 1965–82. (Adapted from David 1984.)

in temperate regions. Where only one crop cycle per year is possible, the maximization of yield per crop is a major objective, but in the tropics, where temperature and radiation permit year-round cropping with irrigation, yield per day may become more important than yield per crop, with profound effects on the life cycles and other characteristics sought in plant-breeding programmes.

Irrigation makes possible the growth of crop plants out of their usual season and environment as well as exposing them to changed pest, disease, and weed pressures. It may either remove or accentuate the need for plant breeders to select for tolerance to extreme temperatures and humidities. On the one hand, irrigation may allow the crop season to be shifted to minimize the effects of stress periods, for example, by avoiding extremes of heat or cold at meiosis or flowering. On the other hand, by extending the growing season and by allowing crops to be grown in arid environments, irrigation may expose them to extremes of heat or cold not previously encountered. Increased tolerance to cold at both the beginning and the end of the life cycle has been a major component in varietal improvement of rice in Japan (Tanaka *et al.* 1968; Samoto 1971). By contrast, rice growing in irrigated arid areas must endure temperatures substantially higher than the range to which it has previously been adapted, as must wheat in the Sudan (Gabar Ahmed 1977), in northern Australia and in many tropical areas where there is current interest in growing it under irrigation.

## ADAPTATION TO IRRIGATED CONDITIONS

For most crops, breeding for irrigated conditions has probably been equated with breeding for high-input, well-controlled conditions, and therefore for high yield potential. With high fertilizer use, strong short stems are needed to prevent lodging, and are possible if weed control

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protects the plants from being over-topped. With denser crops and higher humidities within the canopy some disease and pest problems are exacerbated, such as powdery mildew of wheat and tungro virus incidence in rice. Breeding for resistance to them or their vectors, as for tungro, therefore becomes more important with irrigation. Other diseases such as brown spot (incited by *Helminthosporium oryzae*) and rice blast (incited by *Pyricularia oryzae*) become less serious with irrigation, and varieties whose resistance is inadequate under dryland conditions may be sufficiently protected under irrigation. Also, the more varied and flexible crop rotations possible with irrigation can help in the control of diseases and weeds. Flooding eliminates many of the weeds that plague upland rice crops. Consequently, whereas upland varieties must be tall to compete with weeds, short stature can be, and has been, incorporated into varieties suitable for irrigation.

More specific varietal selection may be required to cope with some of the changes in soil conditions induced by irrigation. The most common changes of this kind are the salinization and alkalization associated with poor drainage, and resistance to salinity and alkalinity is often needed in older irrigation schemes. However, because of the patchiness of these conditions, Richards (1983) has argued that most of the yield comes from the least saline areas and that the best breeding strategy is to select for high yield on non-saline soils.

Other toxicities may also develop in heavily irrigated soils, for example, boron with some sources of water. Iron may also be in excess, whereas zinc may be deficient, as on the I.R.R.I. field station where plant breeders may have unconsciously selected high-yielding lines that are tolerant to these conditions.

Indirect selection for anatomical characteristics that enhance the internal transfer of oxygen via aerenchyma to the root system (I.R.R.I. 1978), as well as the 'snorkel' and 'gill' functions identified by Raskin & Kende (1983), may also have occurred, and for rooting habits adapted to irrigation. Even with only periodic irrigation there may be a need to select for root systems specifically suited to such conditions, for example, for greater tolerance of temporary water logging in cotton, and perhaps even to the different kinds of irrigation, whether furrow, trickle or overhead.

Similarly, with irrigation in arid areas of high irradiance the leading edges and surface of the crop canopy may suffer from water stress even though the root zone is well supplied, and specific selection for such conditions may be needed. Leaf rolling may be as advantageous to rice in these as it is in upland conditions, as may the many other mechanisms of adaptation to water stress (O'Toole & Chang 1979), especially when the supply of irrigation water is uncertain or not well programmed. Several important irrigated crops such as wheat and cotton are well adapted to semi-arid conditions but may need better adaptation to irrigation itself. However, even essentially wild arid-zone plants such as jojoba (*Simmondsia chinensis*) and guayule (*Parthenium argentatum*) have been successfully grown under irrigation (see, for example, Miyamoto *et al.* 1984).

## WATER USE AND ITS EFFICIENCY

More or less linear relations between accumulated growth and total evapotranspiration (e.t.) have been found with many crops (Hanks 1983). However, the slope of the relation varies greatly depending on the crop, its environment and its duration of growth, as may be seen in figure 2.

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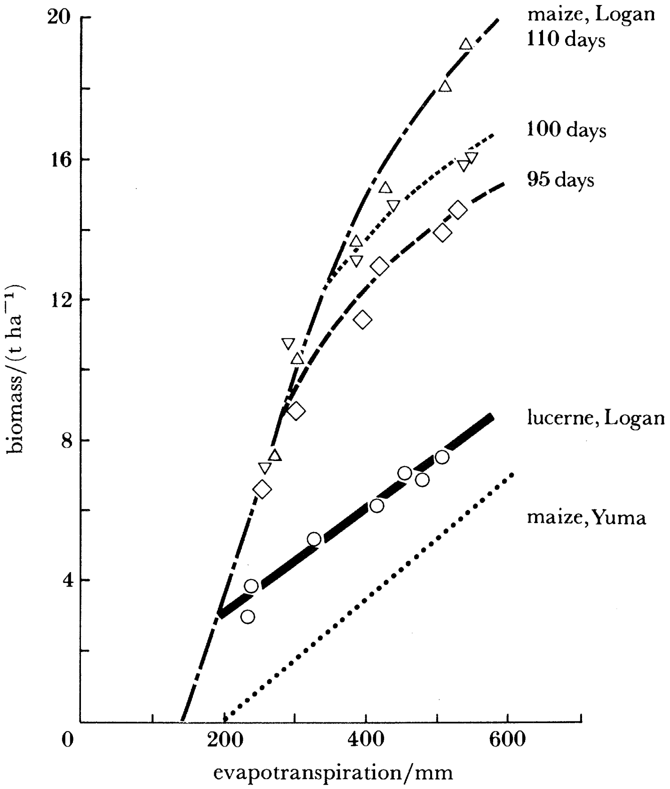

Figure 2. Relation between evapotranspiration and biomass for maize hybrids of different maturities and of lucerne crops at Logan in 1976 (Retta & Hanks 1980) and for maize at Yuma in 1975 (Hanks 1983).

Comparison of the crop dry-mass–e.t. relations for maize at Logan and Yuma illustrates the influence of environment. The great difference between species with the C3 and C4 pathways of photosynthesis is evident in the comparison between the dry-mass–e.t. relations for maize (C4) and lucerne (C3) grown at Logan in the same experiments. The curves for the three maize hybrids, differing in their time to maturity, illustrate the advantage of later maturing varieties at high e.t. values.

In view of the wide ranges in absolute yield and evapotranspiration, for the purposes of comparison and prediction much of the data in the literature is presented in terms of relative yield and relative e.t. This is unfortunate because such transformations may conceal the differences between varieties which are of interest to plant breeders. Hanks's (1983) presentation of the data on five varieties of spring wheat obtained by Rasmussen & Hanks (1978) is a case in point.

An important consideration in relation to plant breeding for irrigation is the great difference in sensitivity to water stress between the various stages of the crop life cycle, which has been well documented for many crops. In general, yield is least sensitive to water stress during the early vegetative and late grain-filling stages, and most sensitive during meiosis and anthesis, for example, in wheat (Fischer 1973), rice (O'Toole 1982), maize (Shaw 1977; Musick & Dusek 1980) and sunflower (Stegman & Lemert 1981). This has important implications for the scheduling of irrigation, and also for plant breeding. No matter how reliable the scheduling of irrigation early and late in the season, its benefits may largely be dissipated unless relief from

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water stress at the flowering stage is assured; if it is not, the plant breeder must still select for drought resistance at that stage.

Many factors influence the efficiency of water use by crops. In the early stages of crop growth, evaporation may exceed transpiration until the leaf area equals the ground area, so that rapid leaf-area development to cover the ground is desirable for efficient e.t. as well as for weed control. Close matching of the crop life-cycle with the length of the growing season is also advantageous. Figure 2 suggests that the three maize hybrids had comparable water-use efficiencies at low e.t., but that the longer season hybrids were more efficient at high e.t. However, the yield data presented by Retta & Hanks (1980) suggest that intermediate maturity dates were optimal for grain yield at Logan in 1976, and this feature predominated in the estimation of grain yield per unit of evapotranspiration, which reached a maximum of 18 kg $ha^{-1}$ $mm^{-1}$ e.t. with a relative maturity of 104 days, compared with 12 and 10 $kgha^{-1}$ for maturities of 95 and 115 days respectively. Even with irrigation, therefore, the length of the life cycle remains important, although rather less crucial than with dryland crops.

With the maize hybrids used by Retta & Hanks (1980) there was a slight tendency for the harvest index to increase as e.t. rose. A similar trend is apparent with *Vicia faba* (Hebblewhite 1982), sunflower (Connor *et al.* 1985), and in all five wheat varieties examined by Rasmussen & Hanks (1978). It was quite marked in the experiments of Faci & Fereres (1980) with grain sorghum, where the harvest index rose from 0.3 at low e.t. to more than 0.5 at high e.t. It is also apparent in the relation between lint yield and biomass as influenced by evapotranspiration of narrow-row cotton crops (Howell *et al.* 1984). If such increases in harvest index with increased e.t. prove to be general, selection for high harvest index could enhance yield and water-use efficiency for grain production under abundant irrigation (cf. Fischer & Kertesz 1976).

Taken overall, the evidence suggests that there are substantial differences between the varieties of a crop in the efficiency of water use for grain production, but relatively small differences for biomass production. Comparisons among varieties of either maize or lucerne for crop biomass have generally not exposed much difference at low levels of e.t. (Retta & Hanks 1980; Hanks 1983). Quite marked differences were found by Rasmussen & Hanks (1978) between five wheat varieties but, as with the maize hybrids, these were associated with differences in time to flowering. However, Farquhar & Richards (1984) have recently demonstrated varietal differences in the efficiency of water use by wheat through measurement of their $^{13}C:^{12}C$ discrimination ratios, and such differences may be as valuable under irrigation as in breeding for drought stress.

## YIELD POTENTIAL

In temperate areas where only one crop can be grown each year, greater yield potential per crop is a major goal of plant breeding for irrigation. Much of the irrigation in these regions is for conjunctive use with rainfall to minimize water stress and to maximize the response to agrichemical inputs.

Irrigated cropping is usually accompanied by increased fertilizer use. Table 1 indicates a four- to eightfold increase in fertilizer application rates for irrigated crops in India. Countries with a heavy reliance on irrigated agriculture, such as Egypt, are amongst the highest users of fertilizer per hectare of arable land, along with the Common Market countries.

Heavier fertilizer applications are needed to maximize the increase in yield made possible

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Table 1. Fertilizer use on irrigated and non-irrigated crops in India 1970–1971

| crop | percentage of crop area irrigated | fertilizer/(kg ha$^{-1}$) rain-fed | fertilizer/(kg ha$^{-1}$) irrigated |
|---|---|---|---|
| sugar cane | 72 | 38 | 160 |
| wheat | 54 | 10 | 80 |
| rice | 39 | 13 | 89 |
| cotton | 17 | 12 | 86 |

(Source: G. M. Desai 1982).

by irrigation and greater evapotranspiration, while irrigation is often needed to maximize the yield increase made possible by fertilizers. Increase in the optimum level of nitrogenous fertilizer application with increased irrgation has been shown for maize by Stutler *et al.* (1981) and Eck (1984), and for wheat by Shimshi & Kafkafi (1978). Higher N levels not only increase yield but also increase the ratio of $CO_2$ assimilation to transpiration (Evans 1983), and therefore the efficiency of water use.

With irrigation and greater fertilizer use, greater use of herbicides, pesticides and other inputs becomes justified, and total energy input per hectare rises substantially, as has been shown for maize in the U.S.A. by Pimentel *et al.* (1973) and Smil *et al.* (1983). Their data are used in figure 3 to illustrate the relation between harvested and input energy for U.S. maize production at 4–5 year intervals. The greater efficiency implied by the analysis of Smil *et al.* largely reflects their taking account of improvements in fertilizer manufacture. For those maize crops that are irrigated, irrigation pumping is the largest energy term in the crop budget, and the proportion irrigated is rising rapidly. But the most interesting feature of these analyses is the absence of any indication of an approaching asymptote, presumably because each agronomic or agrochemical innovation rescues the U.S. maize crop from diminishing returns to the inputs of energy. Quite apart from the sequence of agronomic innovations, such a response has also required the breeding of a sequence of hybrids of higher yield potential and better adapted to more intensive agronomic conditions, such as closer spacing (Russell 1974; Duvick 1977).

The physiological basis of increased yield potential has been discussed elsewhere (Evans 1984) and need only be summarized here with special reference to irrigation. It is clear from work with many crops that, so far, greater yield potential has not come from increased rates of photosynthesis or growth. This conclusion applies not only to dryland crops but also to irrigated crop plants such as rice (Tanaka *et al.* 1968; Cook & Evans 1983*b*; Evans *et al.* 1984). Greater yield potential has come, rather, from changes in the overall duration and balance between phases of the crop life-cycle associated with irrigation and other inputs, and from an increased harvest index.

Selection for this latter feature is made possible by the increased level of agronomic support provided to irrigated crops. Many investigations have shown the root:shoot ratio to increase with soil moisture stress (Fischer & Turner 1978). With lowland rice, for example, root length density in the upper layers of soil increased as water supply decreased (O'Toole 1982). Rice varieties adapted to upland conditions characteristically have a higher root:shoot ratio and more, thicker and deeper roots than lowland varieties. For example, Yoshida & Hasegawa (1982) found root:shoot ratios ranging from more than 110 mg g$^{-1}$ in upland varieties to less than 50 mg g$^{-1}$ in modern varieties for irrigation. With irrigation, therefore, it is possible

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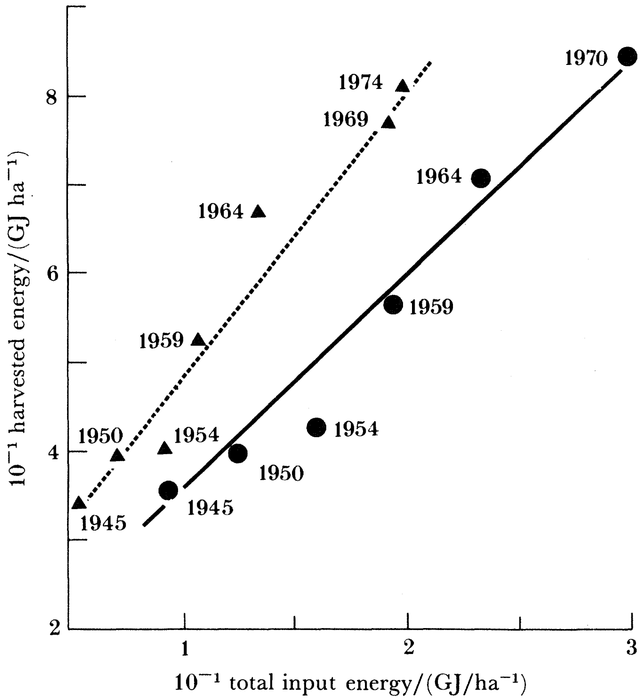

FIGURE 3. The relation between total input energy and harvested energy for the U.S. maize crop at 4–5 year intervals, derived from analyses by (●) Pimentel *et al.* (1973) and (▲) Smil *et al.* (1983).

to select for a reduced investment in root growth, thereby freeing assimilates for greater investment in the inflorescences and grains. Likewise, root:shoot ratios decline as nutrient levels rise, e.g. in rice (Cook & Evans 1983*a*), again allowing the plant breeder to select for greater investment in the grain, and raising the harvest index. Osmotic adaptation is an important mechanism in drought resistance and, during water stress, plants may maintain a large pool of soluble carbohydrates in the leaves, for example, in sorghum (McCree *et al.* 1984). When freed by irrigation from the likelihood of such stresses, selection for the mobilization of these resources into inflorescences and grains poses no hazards. Similarly, with effective weed-control measures, stem height and leaf size can be reduced by selection, again freeing assimilates for alternative use.

These examples indicate how selection for increased yield potential, through a rise in the harvest index, is made possible by irrigation and by associated agronomic practices, even in the absence of any increase in rates of photosynthesis and growth.

However, now that the harvest index exceeds 50 % in high-yielding varieties of several crops, the scope for further increase will be limited, and ways to increase crop photosynthesis and growth must be sought. Genetic variation in the net $CO_2$ exchange rate per unit leaf area (n.c.e.) exists in most crop plants, but higher n.c.e. rates are frequently associated with smaller leaves, and these in turn with correlative changes in other organs (Evans 1984). To take full advantage of irrigation and high-input agriculture, however, there is a trend towards denser crops of shorter stature and smaller, more upright leaves. This is illustrated by the changes that have occurred in varieties of lowland rice grown in the Philippines over the last 70 years (Evans *et al.* 1984). With more upright leaves there is greater light transmission through the canopy,

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and the extinction coefficient for modern rice varities is about 0.3 compared with 0.6 in the older varieties. We did not find any increase in crop growth rate associated with these changes, but at high densities this may become apparent.

## IRRIGATION IN THE TROPICS

Our work on trends among varieties of rice grown widely in the Philippines during this century highlighted two changes that may be of more significance for irrigation in the tropics than increase in yield potential per crop. The first was the pronounced increase in grain production rates per day in recent varieties. All rates were relatively low because of the sparse planting density needed to protect the old varieties, but they increased more or less in proportion to the shortening of the crop life cycle from 210 to 100 days. Thus, a quite radical reduction in the time to maturity has been achieved without much loss of yield potential per crop. The shortening of the life cycle has been mainly a shortening of the period from sowing to panicle initiation. Under low-input conditions this period had to be long to allow the plants time to accumulate N and other nutrients from infertile soils, but with irrigation and fertilizers this phase of the life cycle can be greatly accelerated, and recent I.R.R.I. varieties are characterized by a reduced juvenile stage. With irrigation and good agronomic support, and with the growing use of direct seeding, it should be possible to abbreviate this stage still further without much loss in yield potential per crop and with further gains in grain yield per day. The reason why multiple cropping with shorter duration varieties is the better strategy to follow in the tropics is because high temperatures reduce the duration of the reproductive and grain-filling stages and therefore limit the yield per crop (Sofield *et al.* 1977; Chowdhury & Wardlaw 1978).

The other major change among the Philippine rice varieties, from day-length sensitivity to relative insensitivity, was associated with irrigation and was not apparent among the upland varieties (Evans *et al.* 1984). The older lowland varieties were adapted to the seasonal rainfall patterns, not flowering until near the end of the wet season. They were strict short-day plants. But as off-season irrigation became more widespread, varieties able to flower in longer days were needed. The modern irrigated varieties have a relatively weak flowering response to day length, but this was initially coupled with a longer juvenile stage which was presumably selected for unconsciously, along with high yield potential. That is now the target for further reduction in breeding for greater grain yield per day and more intensive multiple cropping.

Thus, in several respects the plant-breeding goals for irrigated crops are moving in opposite directions in temperate and tropical areas.

## IS BREEDING FOR IRRIGATION DYSGENIC UNDER DRYLAND CONDITIONS?

In more temperate regions particularly, plant breeding for irrigation has been largely equated with breeding for high inputs and yield potential, as well as for relative insensitivity to environmental signals such as day length. Given the prominence of these objectives in international plant-breeding programmes for rice and wheat, we need to consider whether they have adverse effects on performance in less favoured environments.

Opinions on this question are sharply divided between two schools of thought. Some plant breeders expect comprehensive breeding programmes to produce lines which are superior across a wide range of environments, and in this expectation they favour selection under high-input

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conditions because these magnify the differences between lines, facilitating selection and allowing faster progress to be made. Others, by contrast, are sceptical of universal superiority and emphasize the advantages of selection for local adaptation, based on the view that what is advantageous in one environment may be disadvantageous in another. To some extent these different approaches also reflect differences in the breadth of the gene pool, in the scale of the crossing programme and in the stage already reached in a breeding programme.

Figure 4 illustrates the performance of some individual lines of rice and wheat when rated against site mean yield for many lines, used as an index of environmental stress by Finlay & Wilkinson (1963) and Eberhardt & Russell (1966). In their work, and in the examples in figure 4, moisture stress or the duration of the period of water availability were the dominant environmental variables. Such figures are usually read from left to right, a steep slope being taken to indicate responsiveness to more favourable conditions, but Fischer & Maurer (1978) have taken yield potential as the starting point and used the relative fall in yield as an index of susceptibility to drought.

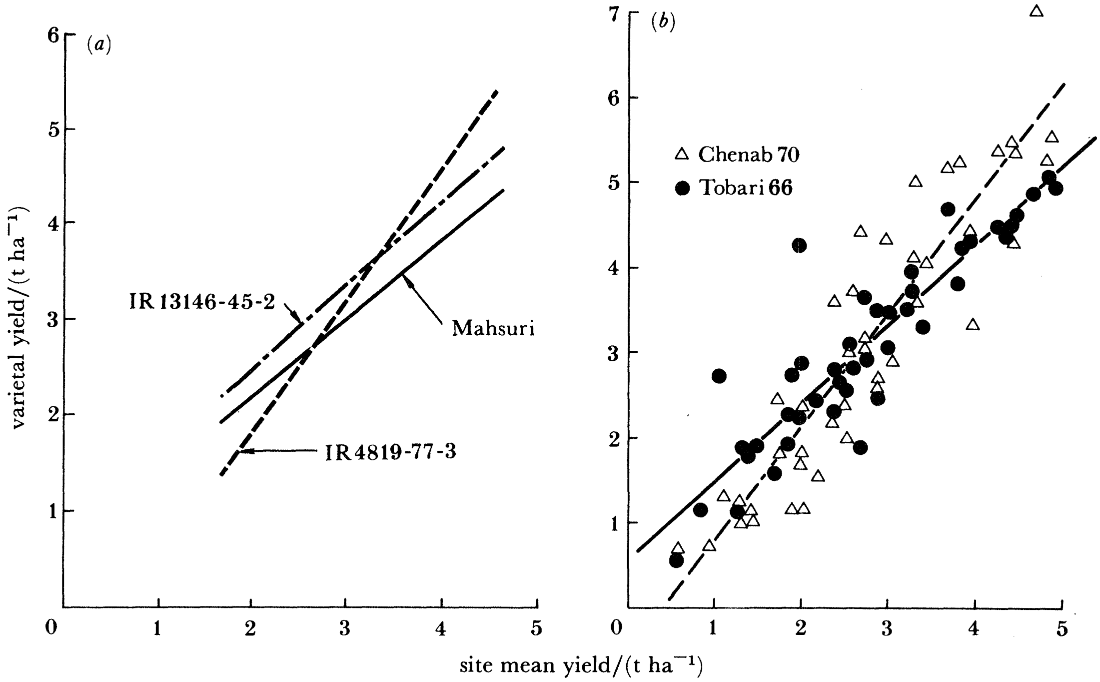

FIGURE 4. The relation between grain yield of several lines and average yield for many lines in variety trials with (*a*) rice (regressions only, from Seshu 1985); (*b*) wheat (CIMMYT trials, Fischer 1981).

The regressions in figure 4*a* include an example of a line (IR 13146–45–2) which is superior to the older, broadly adapted variety Mahsuri across the whole range of rain-fed lowland rice environments. Far more common, however is the response by the other line (IR 4819–77–3), superior to Mahsuri in the better environments but poorer in the adverse ones. Moreover, the statistical nature of these regressions, evident in figure 4*b*, should not be forgotten. After comparing many lines of rain-fed lowland rice at many sites, Seshu (1985) found (i) many sites where no entry in the yield nurseries was superior to Mahsuri; (ii) low correlations between rankings for yield at many of the lowland sites; and (iii) no significant correlation between rankings from the

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trials at I.R.R.I. under irrigation and those elsewhere. Selection under irrigation may be a useful guide to performance only under the most favourable lowland rain-fed conditions.

With wheat, Fischer & Wood (1979) found, in fact, that drought susceptibility increased with non-drought yield, and crossovers in varietal rankings of the kind indicated in figure 4 for both rice and wheat are quite common across sites varying in the extent of water stress. With wheat the advantage may also shift from the semi-dwarf habit under irrigation to taller varieties under moderately severe water stress (Fischer & Maurer 1978). Crossovers in rankings have also been found with maize (Fischer *et al.* 1982), sorghum (Seetharama *et al.* 1982), and many other crops.

These few examples suffice to indicate that selection under irrigation for high yield potential may, at the very least, provide no indication of performance under water stress, and may even be dysgenic. However, given the great and increasing extent of irrigated agriculture, varieties selected under irrigation may succeed over extremely wide areas, as indicated by the use of IR-36 rice on 11 Mha and of the progeny of one CIMMYT wheat cross over a comparable area. By its very nature, irrigation removes some of the most site-specific limitations to crop yield, with the result that relative performance by genotypes is more closely correlated across irrigated than across rain-fed sites. Breeding programmes for irrigated conditions may therefore have wide impact, and are well suited to international effort.

## CONCLUSIONS

Irrigation encourages the greater use of fertilizers and other agrichemicals, and the breeding of varieties of greater yield potential to take advantage of these inputs. Indeed, without such plant breeding, the full benefits of irrigation may be lost.

With irrigation, combined with fertilizers and better control of pests, diseases and weeds, plants may be selected for reduced investment in roots, stems, leaves and reserves, thus freeing assimilates for greater investment in inflorescence development and grain growth. But the price of such selection can be poorer performance under stress conditions, for example, if irrigation fails at the critical reproductive stage in the crop life-cycle. With irrigation, moreover, plants may be grown under environmental conditions more extreme, especially in terms of high temperatures, than those to which they are adapted.

So far there is no indication that selection for higher yield potential has increased the rates of photosynthesis or crop growth, but ways to do so must be sought if past increases in yield potential are to continue. Greater efficiency in water use may become a goal of plant breeding for irrigation as well as for drought stress, given that both irrigation water and the energy for pumping it may become more expensive in future. But as with photosynthetic efficiency, gains in water-use efficiency have to be weighed against the biological costs. At least in tropical conditions, they will also have to be considered in relation to grain yield per day as well as grain yield per crop.

Moreover, as irrigated agriculture becomes more intensive, and as human populations come to depend increasingly on continuous cropping in the tropics, plant breeding for irrigation may be forced to pay more and more attention to the long-term impacts of continuous cropping. This is already apparent in the need to build in resistance to a widening range of pests and diseases, but tolerance of deficiencies, toxicities and other adverse conditions may also be required increasingly in the future.

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