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Harvest index: a review of its use in plant breeding and crop physiology

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Summary

This review charts the use of the concept of harvest index in crop improvement and physiology, concentrating on the literature from the last 20 years. Evidence from abstract journals indicates that the term has been applied most to small grain cereal crops and pulses, in India, Western Europe and the USA, and that it has been less useful for maize and tuber crops. Standard methods of measuring harvest index, the associated problems of measurement and interpretation, and representative values for a range of world species are reviewed. The values for modern varieties of most intensively-cultivated grain crops fall within the range 0.4 to 0.6. Variation between varieties of the same species is illustrated by trends in the harvest indices of old, outclassed and recent varieties of temperate and mediterranean wheat and barley (compared under uniform conditions); this shows a progressive increase throughout the present century, although improvement has been much slower in Australia and Canada than in the UK. In most cases, the improvement in harvest index has been a consequence of increased grain population density coupled with stable individual grain weight. The high heritability of harvest index is explored by examining its (rather weak) response to variation in environmental factors (fertilisation, population density, application of growth regulators) in the absence of severe stress. A fuller perspective is gained by reviewing aspects of the harvest index of rice, maize and tropical pulses. With rice, attention must be paid to the fact that the adhering lemma and palea (not primarily part of economic yield) can make up 20% of grain weight; and there are important interactions among biomass, grain yield and season length. Maize differs from most small grain crops in that harvest index (in N. American varieties) was already high at the start of this century, and increases in yield potential have been largely the consequence of increased biomass production. The harvest index of many pulse species and varieties tends to be low because selection has been for some yield in all seasons. Extension of the harvest index concept to express the partitioning of mineral nutrients as well as dry matter (e.g. the nitrogen harvest index) has provided a range of responses whose implications for production and breeding remain to be explored. It is concluded that even though the principal cereal crops appear to be approaching the upper limit of harvest index, and future yield gains will have to be sought by increased biomass production, there will still be a need for the concept of harvest index as a tool in interpreting crop response to different environments and climatic change.

Key words: Harvest index, wheat, barley, rice, maize, pulses, chickpea, varieties, biomass, grain (economic) yield

Introduction

In plant ecology, the concept of 'reproductive effort' can be traced back to Darwin (e.g. Harper, 1967, 1977) if not further. It has been particularly useful in ecophysiological studies: for example, proportional increases in the allocation of dry matter to reproductive organs are a familiar aspect of the adaptation of higher plants to dry and cold environments (Fitter & Hay, 1987). Increase in the fraction of above-ground biomass partitioned to useful parts has also been a feature of the evolution, selection and breeding of higher-yielding crops. In the early stages of the domestication of cereals this was a consequence of simple selection for bigger ears and grains (associated with seed retention: Evans, 1993), but subsequent improvements were gained by setting a range of additional selection or breeding objectives (such as delayed crop senescence, shorter straw, disease resistance), under different combinations of temperature and photoperiod.

The central importance of 'reproductive effort' for crop yield was recognised early in this century by some plant breeders and crop scientists. In reviewing barley breeding in the UK, Beaven (1920) used the (misleading) term 'migration coefficient' to express the ratio of grain to straw at harvest, but most other breeders ignored his approach. Although physiologists touched on the significance of ear:shoot ratio (e.g. Watson & Norman, 1939), interest focused on leaf expansion, canopy photosynthesis and the physiology of the economically-important fraction of the crop (grain, tuber, root), rather than biomass. It was not until the early 1960s in Australia that Donald (1962, 1968), drawing on contemporary ideas about assimilate partitioning in the USSR, first coined the term 'harvest index' for the ratio of (wheat) grain yield to biological yield or biomass.

The adoption and use of the term harvest index by crop scientists can be charted by counting the number of abstracts per year in Field Crops Abstracts which contain "harvest index" as key words (Fig. 1). Although not strictly objective, this approach does show that harvest index appeared only rarely in the world literature until the late 1970s (around the time of publication of Donald & Hamblin's (1976) review), when it experienced a sharp and sustained increase in popularity amongst crop scientists. During the first 15 years of its life (1962–77), harvest index was employed mainly by Australian scientists, and it was strongly linked with Donald's concept of the ideotype as a blueprint for wheat breeding (Donald, 1962, 1968). As discussed in more detail in later sections of this review, use of the term has become more widespread in the last 15 years for four principal and interlinked reasons: the introduction of shorter-strawed cereal varieties (wheat, barley and rice) with higher harvest indices; increased interest in the yield and physiology of older cereal varieties; the shift in interest among crop physiologists towards the interception of solar radiation and biomass production as the ultimate determinants of crop yield (Gallagher & Biscoe 1978*a*; Hay & Walker, 1989); and the use of harvest index in interpreting the physiology of other seed crops (notably pulses in India, see below).

Analysis of the geographic origin of 314 abstracts over 31 years (1962–1992) reveals that 30.6% of the papers were published in India, followed by Western Europe (13.4%, including the UK), USA (12.4%; relatively low owing to the lack of interest amongst maize breeders and agronomists, see below), Australia (8.6%), Africa (3.2%) and Japan (3.2%). Use of the term has by no means been restricted to wheat and other cereals. The distribution of abstracts by crop was: wheat (19.1%), tropical and mediterranean legumes, excluding soybean (18.2%), rice (12.1%), oilseeds excluding soybean (8.6%), soybean (7.6%), maize (5.7%), root and tuber crops (4.1%).

The purpose of this review is to explore the application of the term harvest index to this wide range of environments and species since the major review of Donald & Hamblin (1976). The treatment deals first with temperate cereals, to establish the main concepts, and then surveys the application of the term to rice, maize and pulses.

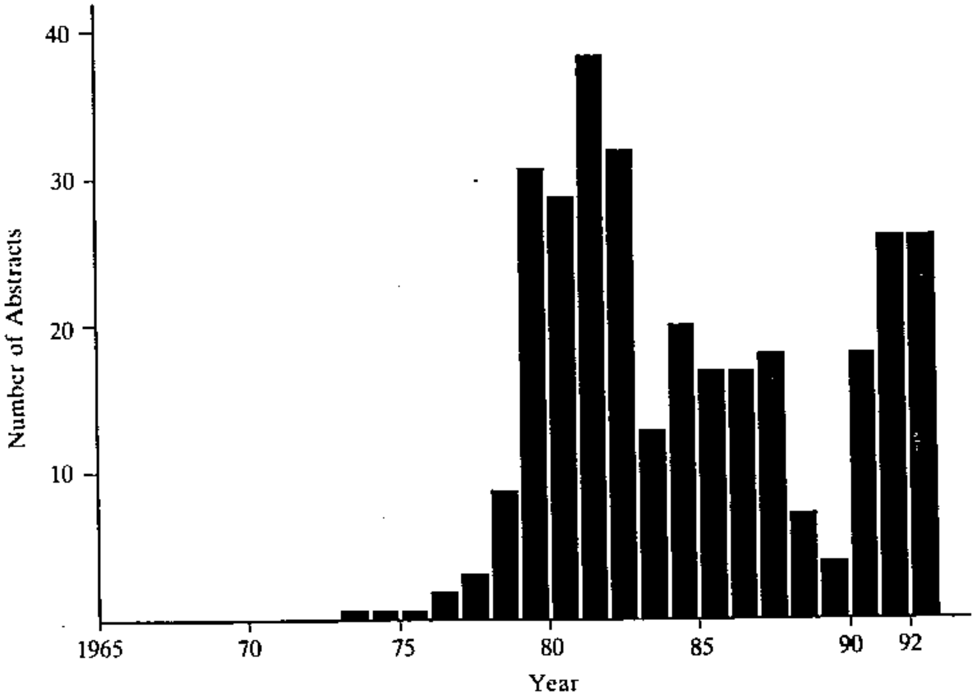

Fig. 1. The annual frequency of papers abstracted in *Field Crops Abstracts* containing 'harvest index' as key words.

Measurement

Donald (1962) first defined harvest index as the economic (grain) yield of a wheat crop expressed as a decimal fraction of *total* biological yield, but he clearly meant *total above-ground* dry matter production (Donald & Hamblin, 1976). The definition was made in the course of a wide-ranging address to plant breeders, and no attempt was made either to recommend procedures for measuring harvest index, or to point out the hazards encountered in applying them.

Over the years since 1962, different field approaches have evolved, but there now appears to be broad agreement, at least for annual seed crops, that the crop sample for harvest index determination should be cut at maturity by hand at ground level, dried to constant weight, threshed, and the resulting grain weighed (Donald & Hamblin, 1976; Innes, Blackwell, Austin & Ford, 1981). A variant of this approach involves the pulling up of the crop sample in the field followed by trimming to ground level in the laboratory (e.g. Ford, Austin, Gregory & Morgan, 1984).

These procedures minimise losses, for example of senescent leaves and chaff, and ensure that the same proportion of the plant is harvested (no variation in stubble length, Holliday & Williams, 1969). Standardisation of cutting height at ground level is also necessary to avoid bias in comparisons of cultivars of differing height, although leaving a stubble of 10 cm would, in comparisons of tall and semi-dwarf cereals of the same harvest index, lead to differences of no more than 5%. Most of the data on seed crops reviewed in the rest of this paper (e.g. Table 1) originated from experiments where protocols of this kind were followed; the many papers in which the method of measurement is not described, are largely ignored.

This pragmatic approach can lead to at least three major difficulties in interpreting results. First, it overestimates the proportion of plant dry matter production partitioned to economic

Table 1. *Representative values of harvest index for selected crop species (Measured by applying standard methods to high yielding crops of modern varieties mainly in the 1980s)*

Species	Type	Area	Harvest index	Source
Triticum aestivum, wheat	Winter	UK	0.43–0.54	McLaren, 1981 Darby, Widdowson & Hewitt, 1984 Austin *et al.*, 1989
		USA	0.31–0.51	Gent & Kiyomoto, 1989
	Spring	Canada	0.38–0.41	Hucl & Baker, 1987
		Australia	0.37–0.47	Stapper & Fisher, 1990
Hordeum vulgare, barley	Winter	UK	0.43–0.57	Ellis & Russell, 1984
	Spring	UK	0.55–0.63	Ellis & Russell, 1984
		Canada	0.33–0.49	Foster *et al.*, 1991 Ma & Smith, 1992
Triticale		UK	0.45–0.47	Ford *et al.*, 1984
Oryza sativa, rice	wetland	Philippines	0.55–0.62*	Anon., 1978
		India	0.35–0.59	Sahu *et al.*, 1980
Zea mays, maize	hybrid	Nigeria	0.36–0.46	Remison & Fajemisin, 1982
		USA	0.42–0.49	Deloughery & Crookston, 1979
		Canada	0.47–0.57	Place & Brown, 1987
Glycine max, soybean		USA	0.35–0.53	Schapaugh & Wilcox, 1980
Cicer arietinum, chickpea	desi, Winter-sown	Australia	0.28–0.36	Siddique, Sedgeley & Marshall, 1984
Vigna unguiculata, cowpea	determinate	USA	0.44–0.64	Fernandez & Miller, 1985
	indeterminate		0.15–0.29	
Brassica napus, oilseed rape	Winter	Germany	0.22–0.38	Huhn, Grosse & Leon, 1991
Manihot esculenta, cassava		India	0.30–0.65	Ramanujam, 1985
Solanum tuberosum, potato	maincrop	Canada	0.47–0.62	Knowles & Botar, 1992

* Values for 'rough rice' before dehulling.

yield because of the losses of dry matter (tissue shedding and respiration) between anthesis and maturity (Donald & Hamblin, 1976; Holliday & Williams, 1969), which vary markedly between species; for example, pulse crops tend to have undergone complete defoliation by maturity (Khanna-Chopra & Sinha, 1987) whereas cereals tend to retain senescent leaves. Secondly, in the case of indeterminate seed crops, including some economically-important grain legumes, the measured harvest index depends strongly upon the date of harvest.

Perhaps more seriously, the approach ignores the possibility of substantial variation in the partitioning of assimilates to below-ground organs (Siddique, Belford & Tennant, 1990). Most of the available measurements, from a limited range of cereal varieties (e.g. winter wheat in England; Gregory, McGowan, Biscoe & Hunter, 1978; Barraclough, 1984), indicate that around 10% of crop biomass is below-ground at anthesis, although Siddique *et al.* (1990) recorded values up to 39% in Australia. Akita (1989) uses a correction factor of 5% to allow for rice roots at harvest. In this context, some authors prefer to use two terms: *actual* harvest index (measured as described above, following Donald's (1962) original concept), and *apparent* harvest index (determined as a proportion of *total* dry matter including roots) (e.g. Schapaugh & Wilcox, 1980; Walker & Fioritto, 1984). These terms are misleading, and not in common use.

Although most workers now adhere to the measurement protocol outlined above, methods of *sampling* crops for harvest index determination vary from the random harvesting of single plants, through row lengths to crop areas from less than 1 to several m^2. Statistically-sound sampling is very important because of variation both between and within plants and field areas. In particular, there is increasing evidence from cereals, and other seed crops, of relationships between the harvest index of individual stems/branches and their hierarchical position (e.g. Table 2); in each study cited, the harvest index of the mainstem was higher than that of subsidiary branches, although Darwinkel (1980) found a more complex pattern. Recently, Huhn (1990*a,b*, 1991) has established a thorough theoretical foundation for field sampling for harvest index.

Although the term harvest index has been applied usefully to a range of species, other than annual seed crops, yielding economic products such as edible tubers or sugar-containing stems (Evans, 1993), standardised methods have yet to be established. Tuberous crops, and the potato in particular, pose several difficulties in addition to the problems of harvesting below ground. The harvest index of a potato crop increases progressively from tuber initiation onwards (Hay & Walker, 1989); however, if the crop is permitted to progress to maturity, much of the above-ground dry matter is lost to senescence (rather than by translocation to the tubers), leading to high and unrealistic values (Ezekiel, 1990; Osaki *et al.*, 1991 measured values as high as 0.92). Clearly, the harvest index of a potato crop depends critically upon the date of sampling. This may be less important in short-season crops where the haulm is still green at harvest (e.g. Knowles & Botar, 1992), but there remain difficulties in making comparisons between geographic areas.

Other difficulties can be caused by measuring harvest index in terms of fresh weight (for example, under water stress the haulm and tubers can be subject to differing degrees of water loss), and interpretation of results is complicated by the observation that harvest index is strongly influenced by the physiological age of the seed tubers (Knowles & Botar, 1992). By contrast, the harvest index of cassava, a perennial tuberous crop, appears to be a most useful crop characteristic because it remains stable from 6–8 wk after establishment onwards (e.g. Ramanujam, 1985). In spite of this, Boerboom (1978) advocated an alternative index of dry-matter partitioning: the increment of storage root increase per unit of whole plant increase.

The concept of harvest index has also been applied successfully to tree crops, by concentrating on yields of stem wood or of fruit as a proportion of annual dry matter production (Cannell & Jackson, 1985). For example values as high as 0.7 can be achieved using apple hedgerow systems and dwarfing rootstocks (Jackson, 1985). However, attempts to use other, non-destructive, measurements as indices of crop harvest index have, as yet,

Table 2. *Harvest indices of plants, mainstems and subsidiary stems*

Species	Whole plant	Individual stems	Source
Wheat	0.44–0.48	0.45–0.51 (mainstem) 0.40–0.46 (tillers)	McLaren, 1981
Barley	0.36–0.40	0.36–0.53 (mainstem) 0.18–0.48 (tillers)	Ma & Smith, 1992
Chickpea	0.28–0.36	0.29–0.44 (mainstem) 0.10–0.38 (branches)	Siddique *et al.*, 1984

proved unsuccessful (e.g. proportion of water transpired after anthesis in cereals: Sadras & Connor, 1991).

Comparisons amongst species

Harvest indices of modern varieties of a range of crop species grown under conditions favouring high yield, in a number of countries, are presented in Table 1. In general, irrespective of time of sowing (winter/spring), the highest values are achieved by temperate small-grain cereal crops, which appear to have reached a plateau within the range 0.5 to 0.65 (see below). Modern rice cultivars grown in fertile soils in humid zones can show similar values, but wheat, barley and rice have lower harvest indices (down to 0.3) when grown in areas of lower yield potential (e.g. drier areas of Australia, India). The relatively few values which are available for maize worldwide fall within a similar range (0.35 to 0.6).

Building on the ideas of Penning de Vries, Brunsting & var Laar (1974), Sinha, Bhargava & Goel (1982) predicted that the harvest indices of oilseeds and grain legumes would tend to be lower than those of cereals because of the high energy costs of synthesising seed lipids and proteins: this is not borne out by the high values recorded for soybean and cowpea cropped intensively in the USA (Table 1). However, the few available values for oilseed rape do tend to be low, and grain legumes can show low or very low harvest indices under less favourable conditions (e.g. chickpea in Australia) or where indeterminate types are grown. Furthermore, harvest indices for grain legumes may, in general, be boosted by the fact that most are deciduous by maturity. Even though the harvest indices of tuberous crops depend strongly upon date of harvest, the values in Table 1 are broadly in line with those of cereal crops. Kawano (1990) documents some harvest indices of species grown in mixtures.

Comparisons amongst varieties: historical trends in varieties of temperate cereals

Variation in harvest index amongst varieties of a given species, grown under identical conditions can be illustrated by a series of recent studies of old, outdated and modern varieties of wheat and barley (in England, Canada and Australia; Fig. 2). In the comparisons carried out in England, the crops were supported by netting to ensure that the older varieties did not lodge and were able to express the full influence of high levels of nitrogen fertilisation, and in all experiments disease incidence was low. In each study, even though improvement in harvest index *per se* had not been an objective of the national breeding programme (Hay & Walker, 1989; Hay, 1993*b*), a progressive increase in this character since 1900 was demonstrated.

Increase in harvest index has been most rapid and most regular in wheats and barleys bred for temperate zones, whereas, in the generally less favourable environments of Canada and Australia, improvement has been slower and more erratic. For example, the trend shown by Australian wheat cultivars (Fig. 2) has been interpreted as a stepwise increase associated with the introduction of Gabo in 1945 and cultivars with Rht genes in the 1970s (Perry & D'Antuono, 1989). The values recorded in Canada and Australia are significantly lower than in temperate Europe because grain filling is generally cut short by water stress; thus the mean individual grain weights from the wheat experiments shown in Fig. 2 were 29.0 (Australia), 34.4 (Canada) and 41.6 mg (England). Perry & D'Antuono (1989) estimate that if the grain weights of their modern Australian cultivars were 45 mg, with no change in crop biomass, then the harvest index would reach 0.64. Overall, breeding in this century

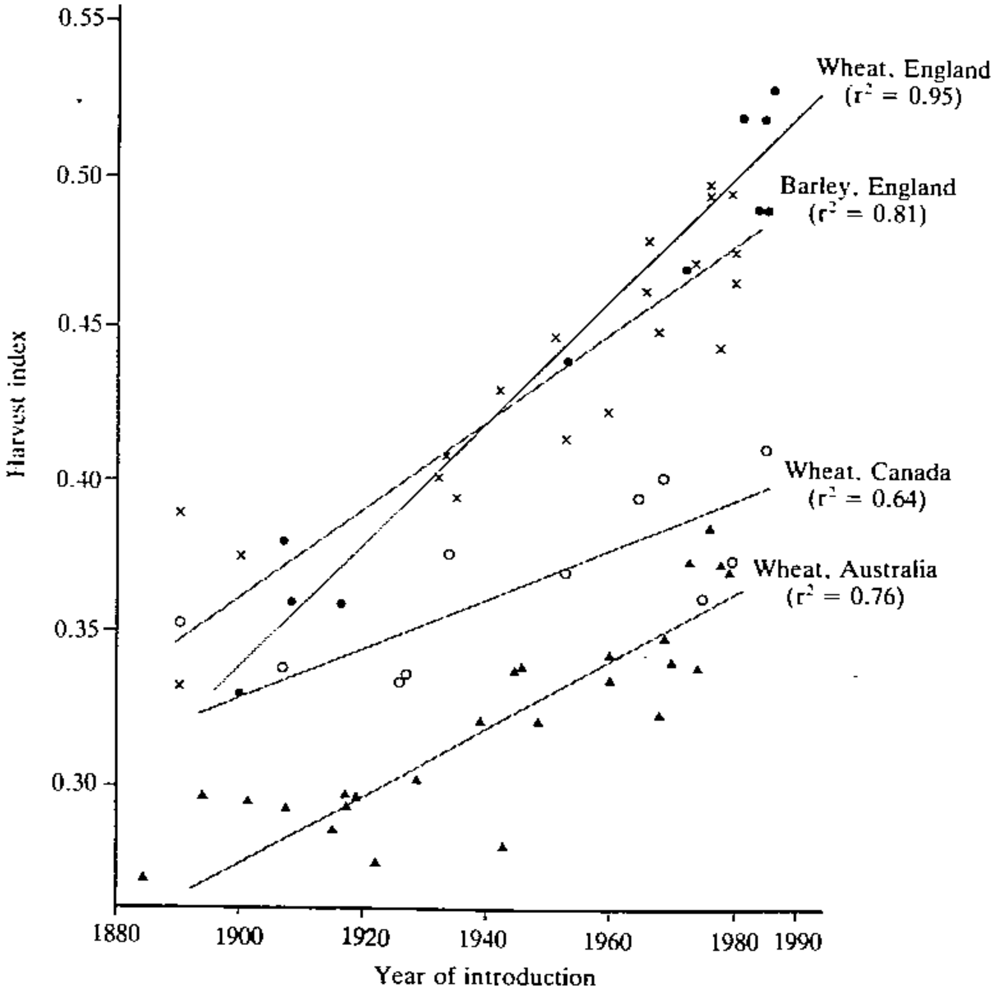

Fig. 2. Relationships between harvest index and date of introduction of wheat varieties in England (●), Canada (○) and Australia (▲) and of barley varieties in England (×). Data from field experiments in which all varieties were grown under the same conditions (Austin *et al.*, 1989; Hucl & Baker, 1987; Perry & D'Antuono, 1989; Riggs *et al.*, 1981). The slopes of the regression lines indicate that the time required for harvest index to increase by 0.1 was 51 years (wheat, England), 74 years (barley, England), 160 years (wheat, Canada) or 97 years (wheat, Australia).

has tended to increase the divergence in harvest index between crops growing in northern Europe and those in Canada/Australia (Fig. 2).

Physiological basis of trends in the harvest index of wheat and barley

Throughout most of the twentieth century, the primary breeding objective for cereals, particularly in temperate zones, has been to overcome lodging, so that the crop can benefit from greater applications of fertiliser nitrogen. Thus there have been progressive increases in stem strength/stiffness and decreases in stem length which have intensified since the 1960s with the incorporation of dwarfing genes, such as the Rht genes from Japanese Norin 10 wheat (e.g. Austin *et al.*, 1980).

Associated effects on the yield and physiology of cereal crops grown according to modern cropping systems can be illustrated by the data on barley varieties in England presented in Figs 2 and 3 (Riggs *et al.*, 1981). Reduction in straw length from 140 cm (Plumage, introduced

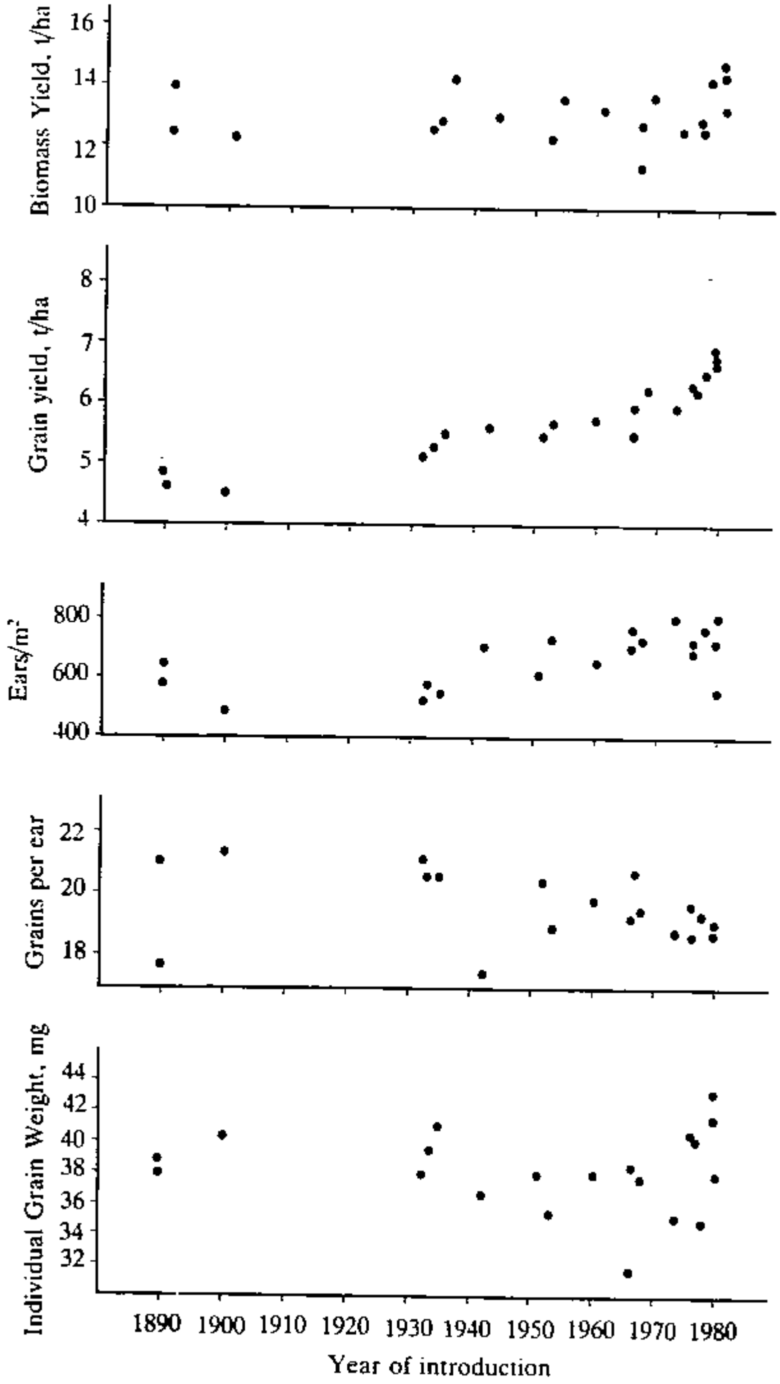

Fig. 3. Components of grain yield of spring barley varieties, introduced to the UK between 1890 and 1980, grown under uniform conditions (Riggs *et al.*, 1981).

in 1900) to around 75 cm (Triumph, 1980) had little effect on crop biomass; indeed the widely-grown (in Scotland) but now outclassed malting cultivar Golden Promise (1966) yielded significantly *less* biomass than varieties introduced before 1900. The progressive increase in grain yield potential (4.5 – 7 t/ha at 15% m.c.) between 1900 and 1980 was, therefore, almost entirely accounted for by the increase in harvest index from 0.36 to 0.48 (Table 3). This confirmed the original observations of van Dobben (1962) in relation to Dutch wheat cultivars, and the same trend has been recorded for wheat in the UK (Austin

Table 3. *Correlation coefficients between grain yield and its components*

Crop	Grain yield *vs* biomass	Grain yield *vs* harvest index	Source
Spring barley, England	0.47	0.83	Riggs *et al.*, 1981
Spring wheat, Canada	0.72	0.62	Hucl & Baker, 1987
Spring wheat, Australia	0.79	0.96	Perry & D'Antuono, 1989
Wheat, India	0.42	0.85	Jain & Kulshrestha, 1976
Rice, Thailand			
High yielding	0.07	0.66	Kawano, 1990
Low yielding	0.89	0.22	

(Note that care should be taken with these values since grain yield is not independent of harvest index)

et al., 1980; Austin, Ford & Morgan, 1989; Tables 3 and 4; including studies at low fertility, Austin, Ford, Morgan & Yeoman, 1993).

Similar findings have been recorded in India and Australia (Table 3), although Perry & D'Antuono (1989) demonstrated that up to 20% of the increase in wheat yield potential in Western Australia could be accounted for by increased biomass, the remainder by harvest index. By contrast, Hucl & Baker (1987) showed that increased potential for biomass production in Canada had been the major component in the increased potential grain yield of Canadian wheat cultivars during this century.

In the context of the near-constant crop biomass recorded in most wheat and barley studies, notably in temperate zones, the observed progressive increase in harvest index with date of introduction is an expression of the increased ability of the spike to compete with the stem for assimilates. Over the last 20 years, competition between stem and ear has been studied in detail by comparing wheat varieties or lines with or without Norin 10 dwarfing genes (Gale, 1979; Gale & Youssefian, 1985); the most rigorous of these investigations have used isogenic or near-isogenic lines (Fischer & Stockman, 1986; Siddique, Kirby & Perry, 1989).

Higher competitiveness of the ears (or reduced competitiveness of the stems) of shorter wheats has been detected as early as the terminal spikelet stage (Siddique *et al.*, 1989) and is clearly established by the time of anthesis (Brooking & Kirby, 1981; Fischer & Stockman, 1986). This superiority does not seem to have a strong influence on spikelet or floret initiation, but results in the survival of higher numbers of florets, per spikelet and per ear, to give grains (Gale, 1979; Brooking & Kirby, 1981; Fischer & Stockman, 1986; Hay &

Table 4. *Components of yield of varieties of winter wheat of varying age grown under uniform conditions at Cambridge 1984–1986 (adapted from Austin* et al., *1989)*

Year of introduction	Biomass yield tDm ha^{-1}	Grain yield tDm ha^{-1}	Harvest index	Ears m^{-2}	Grains per ear	Wt per 1000 grains g
1830–1907 (4 varieties)	15.00	5.05	0.34	393	32.2	50.9
1908–1916 (2 varieties)	15.41	5.57	0.36	406	34.5	49.8
1953–1972 (2 varieties)	14.84	6.69	0.45	402	33.4	59.7
1981–1986 (5 varieties)	15.88	8.05	0.51	447	42.0	51.5

Kirby, 1991). In most investigations, the resulting higher numbers of grains per ear have been associated with more modest increases in ear population density, although Bremner & Davidson (1978) reported the opposite. For example, Austin *et al.* (1989) found that modern wheats had 14% more ears per unit area and 30% more grains per ear than older, taller varieties (Table 4). Thus the higher harvest indices of modern wheat varieties are a consequence of higher grain population densities, coupled with relatively stable individual grain weights (Table 4; Bremner & Davidson, 1978; Hay & Walker, 1989).

The more limited evidence which is available for barley indicates that the parallel improvement in harvest index (Fig. 2) is a consequence of increased ear population density rather than number of grains per ear (e.g. Fig. 3). This may reflect the fact that, in contrast to wheat, each barley spikelet carries a single fertile floret.

Austin (1980) argued that since non-reproductive tissues are necessary to support the ear physically, to display photosynthetic organs, and to provide water, photosynthate and other supplies to the expanding grains, there must be an upper limit to the harvest index of seed crops. He examined the serious implications of increases in the harvest index of temperate cereals above about 0.62, a value which has subsequently been widely accepted as the upper limit, although some measurements have already reached this value (e.g. Table 1; Crowley, Jones & Foley, 1993).

The influence of the environment on the harvest index of wheat and barley: stability and heritability

As a ratio of grain to biomass yield, the harvest index of cereal crops can be affected by any factor which influences the two components of yield to different extents. For example, the grain yield of modern wheat cultivars in the UK does not respond to rates of application of nitrogen fertiliser beyond 125 to 150 kg N ha^{-1} (perhaps up to 200 kg N ha^{-1} on soils with very low nitrogen reserves), whereas biomass can continue to increase beyond these rates (Hay & Walker, 1989). Use of super-optimal rates of nitrogen application tends, therefore, to cause small but significant reductions in harvest index (e.g. Austin *et al.*, 1993), although variation in application up to the optimum rate generally has little effect (e.g. Ellen & Spiertz, 1980; Thorne *et al.*, 1988; Table 5). There is some evidence to suggest that the harvest index of older cereal cultivars may be more sensitive to the level of soil fertility (Austin *et al.*, 1993), but no indication, from a range of investigations, that the *timing* of nitrogen application can affect harvest index (McLaren, 1981; Darwinkel, 1983; Peltonen, 1992).

Increased plant population density, by favouring biomass production over grain (Hay & Walker, 1989), also tends to result in lower harvest indices (Richards, 1988), but within the normal range of commercial crop densities, such reductions rarely exceed 10% of the optimum value (McLaren, 1981; Darwinkel, 1978; Table 5). The relatively few investigations of the effect of sowing date on harvest index have tended to show little effect (e.g. Ellis & Russell, 1984; Thorne *et al.*, 1988), although in areas where early or late sowing can lead to exposure to stress, much larger effects can be expected (e.g. variation from 0.23 to 0.42 in wheat crops exposed to frost or lodging in New South Wales; Stapper & Fischer, 1990). There is continuing interest in the influence of commercial growth regulators on harvest index (e.g. Foster, Reid & Taylor, 1991; Ma & Smith, 1992) but, again, the effects on harvest index tend to be modest (Hay & Walker, 1989). Some inappropriate combinations of application rate and timing can lead to very low values (e.g. down to 0.17 for spring barley treated with Ethephon at flag-leaf appearance; Ma & Smith, 1992).

Where cereal crops are exposed to severe stresses (water, temperature, flooding, disease),

Table 5. *The effect of nitrogen fertilisation and plant population density on the harvest index of two winter wheat cultivars growing in the Netherlands 1980/81 (from Ellen, 1990). Cultivar and plant population density effects are significant at* $P < 0.01$. *The nitrogen effects are not significant.*

Cultivar	Harvest index at 40 kg N ha^{-1}	80 kg N ha^{-1}	120 kg N ha^{-1}
Arminda (80 kg seed ha^{-1})	0.44	0.46	0.46
(160 kg seed ha^{-1})	0.44	0.44	0.43
Okapi (80 kg seed ha^{-1})	0.43	0.43	0.42
(160 kg seed ha^{-1})	0.40	0.40	0.42

especially those which cut short grain filling, very low harvest indices can be expected (e.g. for virus disease, Comeau & Barnett, 1979). For example, in pot experiments carried out in Australia, the values for wheat cultivars fell from around 0.45 to less than 0.1 under severe water stress (Passioura, 1977), whereas in an irrigated glasshouse experiment, also in Australia, Davidson & Birch (1978) recorded significant, but more modest, reductions (0.49 to 0.36). Nevertheless, in field experiments in England, harvest index proved to be relatively unaffected by plant water status: by varying the position of crop shelters which intercepted rain, Day *et al.* (1978) were able to reduce biomass production of spring barley crops by 50% without affecting harvest index. Even under the extreme drought of 1976 in England, relatively high harvest indices were maintained (0.37 to 0.40; Gallagher, Biscoe & Hunter, 1976).

In summary, within a given climatic zone, harvest index has been found to be a stable feature of wheat and barley cultivars, in the absence of severe stress or abnormal chemical treatments (Gallagher & Biscoe, 1978*b*). "Thus, with modern varieties, changes in harvest index tend to be small and so the weather predominantly influences grain yield by its effects on total dry matter production" (Biscoe & Willington, 1984). This is confirmed by the relatively few measurements of heritability of harvest index that are available. Using a set of 47 wheat genotypes adapted to temperate environments, Austin, Ford, Edrich & Blackwell (1977) measured a heritability of 60% (higher than grain yield at 48%), whereas Chaudhary, Luthra & Singh (1977) recorded an exceptionally high value of 97% from a study of 30 Indian varieties. Although, in their review of 'selection for partitioning', Snyder & Carlson (1984) confirm the high heritability of harvest index, they do quote values as low as 20% for oats.

Other species

Rice

The potential grain yield of irrigated rice cultivars under intensive production has risen sharply over the last 30 years, with the selection of shorter-season, day-neutral types which carry resistance to the relevant pests and diseases, and with, as for wheat and barley, the incorporation of dwarfing genes from older japonica varieties (e.g. Dee-geo-woo-gen), which permit the use of higher rates of nitrogen fertilisation (Akita, 1989; Evans, 1993; Khush, 1993; Swaminathan, 1993). This improvement has been associated with an increase in harvest index from around 0.3 to 0.5. However, these values are expressed in terms of 'rough rice' without removal of the husk or hull (lemma and palea) which are very substantial in rice, making up about 20% of rough grain weight; accordingly the modern value of 0.5 must be reduced to 0.4 for comparison with wheat (Akita, 1989). Other, less productive, cropping systems tend to give lower grain yields and harvest indices, with the extreme being represented by deepwater rice (harvest index down to 0.1: Banerji & Das Gupta, 1984).

For irrigated rice, there is an important interrelationship among biomass, crop duration and grain yield. Reduction in the duration of the crop (which is determined by the interaction between the genotype and the environment: temperature, photoperiod, extent and timing of stress) is associated with lower crop biomass because less radiation is intercepted. However, it is also associated with increased harvest index (Khush, 1993), and the effects tend to be compensatory; for example, in comparisons of a range of traditional and modern International Rice Research Institute (IRRI) cultivars, grain yield was constant at season lengths above 110 days (Akita, 1989). This explains the common observation that the grain yield of high-yielding rice crops is not correlated with biomass yield (Table 3: Murty & Sahu, 1977), although under low fertility biomass can become limiting (Kawano, 1990).

The same interrelationship explains why, in zones of India where two rice crops per year are common, the harvest index of the crop grown during the dry (shorter) season is higher than that of the longer wet season (e.g. Sahu & Murty, 1978; Sahu, Murty & Vinay Rai, 1980; Sinha, 1993). As with wheat, variation in other aspects of crop management (plant population density, time and method of planting, nitrogen fertilisation) within moderate limits has only a modest effect on rice harvest index (e.g. in India: Sahu *et al.*, 1980; Venkateswarlu & Prasad, 1982; Palit, Kundu, Mandal & Sircar, 1976; Reddy & Reddy, 1986; Prasad, 1981; see also Anon., 1978).

Variation in the harvest index of rice between cultivars and environments is largely the result of differences in grain population density; in turn, these are the consequence of differences in tiller fertility, and/or in the initiation and survival of spikelets (with single florets), rather than substantial variation in individual grain weight (Murty & Sahu, 1977; Sahu & Murty, 1978; Akita, 1989). Most of the improved cultivars for irrigated cultivation in Asia have been developed for transplanting to the paddy field as seedlings, at spacings of 10 to 20 cm. In contrast to temperate cereals which are sown at high plant population densities, there has been positive selection for vigorously-tillering rice types, and most modern cultivars produce up to 25 tillers per plant, of which only 15 to 16 carry panicles (Khush, 1933; Swaminathan, 1993). Thus, although the harvest index of most recent cultivars falls below a notional limit of 0.65 (or around 0.52 for dehulled grain), there is still considerable scope for yield improvement through increased tiller fertility (and higher plant population density). Breeding efforts could be directed at developing cultivars for direct seeding at higher density, producing three or four panicles per plant, as in temperate cereals: the breeding objective here would be to increase panicle size (Jennings, 1964).

Maize

Maize is probably unique among major world crops in that the harvest index of many commercial varieties was already quite high in the first decades of this century. Thus the open pollinated types used in the USA up to the 1920s had values of around 0.45 (Fig. 4; Russell, 1991, 1993). In North America, selection of hybrids adapted to intensive cultivation (high population density; high soil fertility; pest and disease control) has resulted in very substantial increases in grain yield potential (Fig. 4), mainly caused by increased biomass production rather than increased harvest index, which has remained relatively stable (e.g. Fig. 4). Indeed harvest index does not feature in published maize ideotypes (e.g. Mock & Pearce, 1975); however, since selection has largely been for tolerance of high density, the maintenance of high harvest index has been an implicit breeding objective.

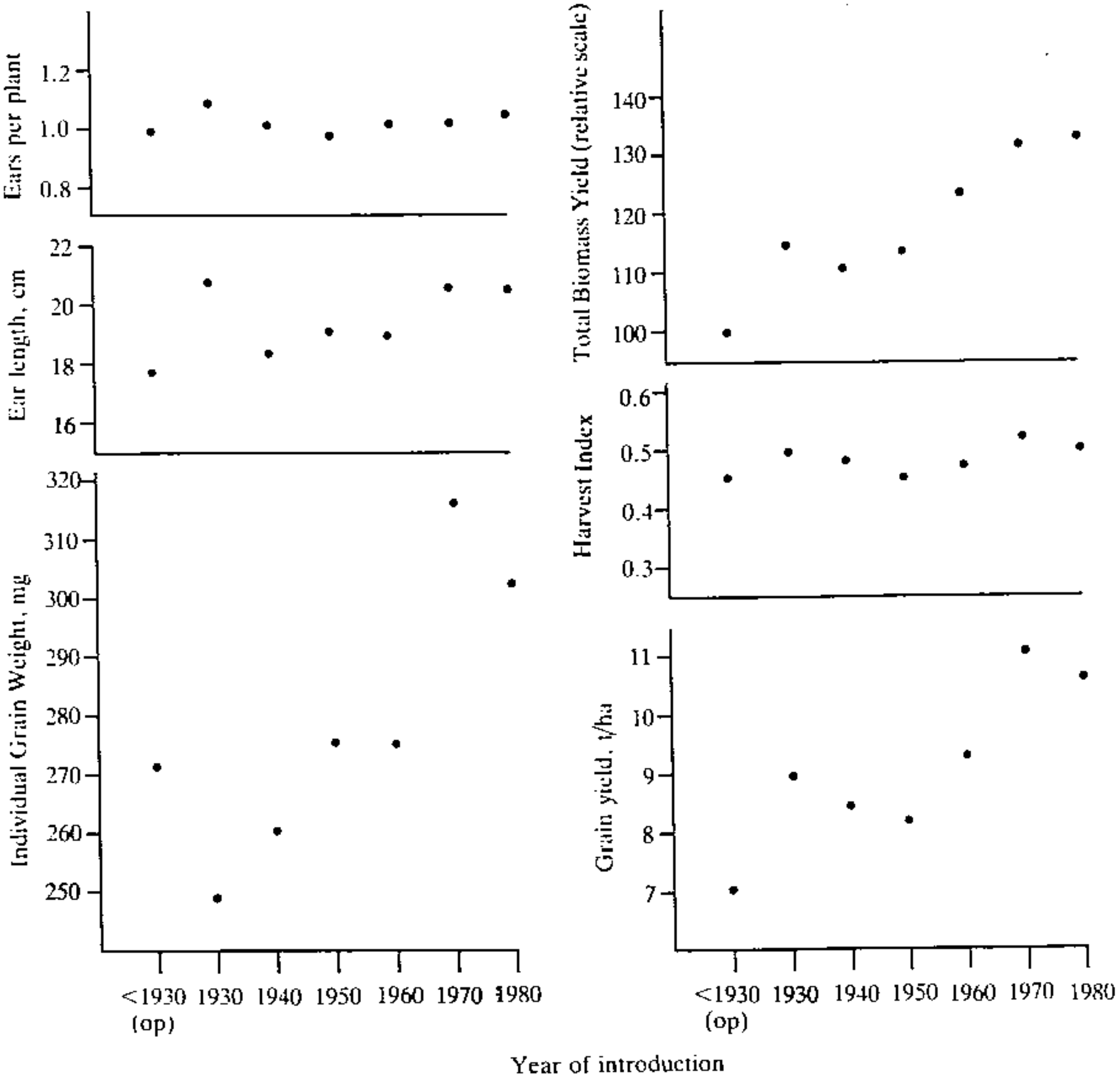

Fig. 4. Yield and its components for maize varieties, introduced into the USA between 1930 and 1980, grown under uniform conditions (Russell, 1991) (op refers to early, open-pollinated varieties).

Since the number of ears per plant (at comparable densities) has not varied significantly over this period, the absolute (as opposed to the proportional) increase in grain yield potential is a result of increased individual grain weight coupled with more modest increases in ear dimensions (an index of number of grains per ear) (Fig. 4; Russell, 1991, 1993). As with other crops, the harvest index of maize crops is relatively stable unless they are exposed to severe stress; for example, Deloughery & Crookston (1979) have explored how high population density and water stress can interact to give very low, and even zero, harvest indices.

A more limited range of observations from other climatic zones indicates that, on a world scale, harvest index of maize may be more variable than in North America (Jain, Mukherjee, Singh & Agrawal, 1976; Mostert & Marais, 1982; Remison & Fajemisin, 1982; Hammes, Steynberg, Beyers & Kriel, 1986).

Pulses

Much of this review has concentrated upon major world crops which have undergone considerable improvement during this century. Where a substantial fraction of the potential biomass yield of a crop can consistently be produced by well-adapted cultivars under conventional husbandry, harvest index becomes a very important determinant of economic yield (Snyder & Carlson, 1984) (e.g. the high and stable values for soybean cultivars in the USA; Spaeth, Randall, Sinclair & Vendeland, 1984).

By contrast many of the pulses grown traditionally in mediterranean and dry tropical zones have undergone little improvement, and selection has been for varieties and types which give some yield even in the most extreme seasons (e.g. Silim & Saxena, 1993*b*). In general such varieties tend to be low yielding, to show little response to fertilisation and irrigation, and they may have relatively low harvest indices. Thus Singh, Saxena & Sahu (1980) report values of 0.23 to 0.47 for mung bean (*Vigna radiata*), 0.17 to 0.30 for urd bean (*Vigna mungo*) and 0.17 to 0.29 for pigeon pea (*Cajanus cajan*) in India. Even under intensive cultivation in the USA, values as low as 0.18 have been recorded for cowpea (*Vigna unguiculata*) (Fernandez & Miller, 1985). As indicated earlier, even such low values may be misleadingly high, as a consequence of complete loss of leaf and petiole tissues (constituting 20–30% of plant dry matter; Khanna-Chopra & Sinha, 1987) by harvest; furthermore, in indeterminate crops, the balance between vegetative and reproductive development can vary considerably according to the degree and timing of stress.

In many respects, chickpea (*Cicer arietinum*) is a good example of such a crop. Although grain yields as high as 6.5 t/ha have been recorded (Singh, 1987), and trial yields of 4 t/ha are not uncommon (Khanna-Chopra & Sinha, 1987), the average world yield is around 600 kg/ha (Singh, 1987). There is little sign of improvement of world yields, partly because in poorer countries chickpeas have been replaced on better soils by "green revolution" cereal varieties, and partly because of the attractiveness of the chickpea crop to pests and diseases.

Chickpeas are indeterminate, but in most of the drier areas of their range in India and the Mediterranean Basin, the duration of the crop is cut very short by drought; season length is commonly less than 100 days. Selection under such conditions has led to varieties in which grain yield is normally dependent upon biomass which, in turn, is determined by season length (e.g. Muehlbauer & Singh, 1987; Silim & Saxena, 1993*a*); harvest index varies considerably amongst varieties (e.g. 0.21 to 0.38 amongst improved varieties growing under the same conditions in India; Lal (1976)) and has been shown to have a (broad sense) heritability which is lower than that of grain yield (43% compared with 50%; Raju, Mehra & Bahl, 1978), rather than higher, as in wheat (Austin *et al.*, 1977). Improvement of the chickpea crop, therefore, must be by increasing the magnitude and stability of both biomass yield and harvest index.

Further development of the harvest index concept

The original concept of harvest index, which was developed to help focus wheat breeding in Australia, has been extended, with varying degrees of success, to a wide range of seed, tuber, fruit and stem crops. It has also been used to quantify the economic yields of primary and secondary metabolic products (e.g. sucrose in sugarcane and sugarbeet, Evans, 1993; triglyceride oils in oil palms, Corley & Lee, 1992; terpenes in volatile oil crops, Hay, 1993*a*).

However, perhaps the most productive extension of the concept has been to the partitioning of nutrients, rather than dry matter. In particular, the nitrogen harvest index of seed crops (ratio of nitrogen in grain to the total nitrogen content of the plant biomass:

Austin *et al.*, 1977) has proved to be a powerful tool in the interpretation of crop nitrogen relationships; it is almost invariably higher than harvest index, indicating a strong preferential accumulation of nitrogen in the grain.

In an early application of the concept, Austin *et al.* (1980) demonstrated that, although wheat breeding in the UK had resulted in increased harvest index, the nitrogen harvest index had been little affected; they proposed that the total yield of nitrogen per unit area of crop tended to be higher using modern cultivars and growing systems but that this was offset to a considerable extent by a downward trend in the concentration of nitrogen in the grain. Findings of this kind have stimulated a considerable, and continued, interest in the recovery and distribution of fertiliser nitrogen. Concentrating on the most recent work, Fischer (1993) used an extensive field experiment in New South Wales to show that variation in the amount and timing of fertilisation can cause nitrogen harvest indices to change from 0.64 to 0.86. Meanwhile, working on historic wheat yields at Rothamsted, Rooney & Leigh (1993) have shown that Austin's conclusions were premature; for wheat cultivars bred in the UK, nitrogen harvest index (0.51 – 0.89) has shown a steady improvement over the last 50 years, maintaining an advantage over harvest index of around 0.2 units. The highest values in this investigation indicate that modern cultivars are capable of concentrating up to 89% of total plant nitrogen in the grain at harvest. It will be important to reconcile these findings with the conclusion of Scott, Foulkes & Sylvester-Bradley (1994) that the most modern wheat cultivars grown in the UK show a decreased ability to transfer soil nitrogen to the grains.

The future

Much has been made of the retrospective use of harvest index in the interpretation of trends in crop improvement (e.g. Hay, 1993*b*). In relation to the intensive cropping of wheat, barley and rice, there is now a widespread realisation that the harvest index of modern cultivars is probably nearing its maximum potential value, and that increased yield potential can be secured only by increasing biomass, as has been the case for maize (e.g. Fig. 4) and forage grasses (e.g. Wilson & Robson, 1981). Indeed the most recent cultivars of these three crop species (wheat, barley and rice) do tend to show an upward trend in biomass production (Fig. 3; Akita, 1989; Boukerrou & Rasmusson, 1990).

The question is, therefore, whether harvest index, as a concept in crop physiology and improvement, has done its work and will now slip out of fashion. This may prove to be the case for crop cultivars bred for intensive production, but, as cropping is forced into marginal, low-yielding areas by population pressures, there will be an increasing need to understand the physiology of cultivars adapted to less favourable environments. The work of Kawano (1990) on rice (Table 3) and Silim & Saxena (1993*a,b*) on chickpea confirms that there is a great deal to be learnt about crops grown on infertile and dry soils. Furthermore, there is growing evidence that, in spite of its high heritability, harvest index may prove to be a useful first index of the response of crops to climatic change (e.g. Ludlow & Muchow, 1993). It seems unlikely, therefore, that harvest index will disappear from the world literature in the near future.

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