

Usefulness of harvest index in plant breeding

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1. Introduction

Selection of superior plants is an age old practice exercised by man since prehistoric times. In the beginning of systematic plant improvement programmes, the selection was invariably based on yield of economic produce such as grain, tubers etc. Later on, improvement was sought through the management of different yield components and other plant characters like disease resistance, drought escape, earliness etc. Though breeding through yield components has often produced mixed results, as there has been cancelling effects and mutual adjustment and compensation of the yield components, yet manipulation of such plant traits and assessing the genotypes by economic yield alone has contributed considerably high to yield increases specially in cereals. Present day high yielding commercial cultivars have mostly been developed through this approach.

Donald and Hamblin [19] pointed out that selection on grain yield alone has two limitations. Firstly, it is unlikely to lead the breeder towards obtaining such a radical combination of plant characters which is likely to yield beyond our present imaginings. Secondly, it is an uncertain and sometimes misleading criterion in early generation selection, so that superior genotypes may go unrecognized. Consequently, progress through this procedure has depended on chance combinations of characters which may be better than the existing cultivars but do not necessarily represent the ideal combination. With the developing interest in the interdisciplinary approach towards crop improvement, a great emphasis was given to the physiological traits related to grain yield. However, recording observations for such traits which were mostly related to growth (leaf area index, relative growth rate, dry matter accumulation etc.), was difficult and time consuming. Also single plant selection based on them in segregating generations was, sometimes, not possible.

There has been renewed interest among breeders in selecting indirectly for grain yield. Under such situations, some single criterion representing overall efficiency of the plant coming from an ideal combination of morpho-physiological traits is likely to give fruitful results, if selection is based on such parameters. Harvest index (HI), defined by Donald [18] as the ratio of economic yield (grain or tuber) to the total biological yield and expressed as fraction of 1 or percent, is such a parameter which measures overall efficiency of the plant, is easily measurable, may serve as a potentially useful indicator of productivity and above all plant breeders have become deeply interested in it in the past. Present review elucidates an overview of various studies on harvest index specially from breeder's viewpoint.

2. The concept of harvest index

Expression of 'efficiency' of grain production through an index was proposed by Beaven, in the second decade of this century [19]. He used the term 'migration coefficient' for the proportion of dry matter of the entire ripe plant (excluding the root) which is accumulated in the grain. Beaven noted that the migration coefficient is much more constant for individual plants of a cultivar than other plant characters and that the different cultivars tend to maintain more or less the same rank for this ratio in different seasons while they vary for mean grain yield. In spite of its apparent usefulness, it was not widely adopted till Tsunoda [72] and Nichiporovich [49] emphasized that successful crop production depends on the effective exploration of photosynthesis to achieve maximum biological yield. But in most cases the economic product is not the whole crop but only its particular part like grain or tubers. For maximum economic yield, there must be a correct distribution of photosynthates at the right time. Nichiporovich's 'coefficient of effectiveness' and Tsunoda's 'migration coefficient' were described as 'Harvest Index' by Donald [18], a term proposed for the ratio of grain yield (or economic yield) to biological yield. Thus, harvest index, by definition, is a factor less than unity and can be expressed as a fraction of unity in decimal figures or in percent. Earlier, agronomists have been observing 'grain to straw' or 'straw to grain' ratio, but it was never given any physiological importance.

A general relationship between economic yield, biological yield and harvest index can be expressed in the following equation:

$$\text{Economical yield} = \text{Biological yield} \times \text{Harvest index.}$$

It becomes evident from this equation that:

- a) Increased economic yield can be obtained through an increase in biomass or in harvest index or in both.
- b) When biological yield is more or less constant (i.e. variation is less), economic yield is proportional to harvest index and there is perfect correlation in economic yield and biomass yield, while biomass yield and harvest index are uncorrelated.
- c) Improved harvest index represents increased physiological capacity to mobilize photosynthates and translate them into the organs of economic importance [24, 27].

With reference to the first point mentioned above, the relevant question is whether harvest index is genetically governed and whether it can be selected for improvement as other plant characters, finally aimed at improving economic

yield. It may also be necessary to mention here that, by and large, studies on harvest index have been conducted on cereals, but the concept has been extended on many other crops as well [4, 16, 25, 29, 39, 48, 52, 55, 56].

3. Harvest index in old vis-a-vis modern cultivars

There have been several studies in which harvest index of several decades old cultivars has been compared with modern cultivars [11, 21, 36, 50, 63, 71, 73, 74, 75]. It was concluded from these studies that there are clear evidences of improved harvest index due to long term breeding in crops like wheat, rice, oats and field pea, resulting from a change in the source-sink relationship. Old cultivars were generally tall, more proportion of leaves and vegetative parts and, most often, are negatively responsive to nitrogen because of lodging and internal shading. However, in long term breeding for improved cultivars during past several decades, the efforts for improving the harvest index deliberately were never made. In fact, the emphasis in breeding new cultivars during this period has been on lodging resistance, reduced plant height and responsiveness to high fertility. Sinha *et al.* [67] reported that introduction of dwarfing genes and hence lodging resistance has shown a tendency of reduced biomass in most of the modern cultivars of cereals. This negative association between lodging resistance and biomass yield may explain why the variability in the latter was not exploited for increasing the grain yield and why genotypes with high harvest indices were selected unconsciously. Also, the genotypes characterized by high biomass most often mature late which is an undesirable feature of an agronomic cultivar. Nevertheless, a bird's eyeview of changing scenario of harvest index from the age old to modern cultivars shows its increasing trend and a further increase is likely to be accompanied by still higher yield levels.

4. Harvest index as selection criterion

As any other metric trait, harvest index also is a quantitatively varying character and can be equally accurately measured. Further, it is affected by the environmental factors as are other quantitatively inherited traits. Extent of genetic variation, heritability and genetic basis of a metric trait are important while making selection in the segregating generations.

Results of several different studies on heritability of harvest index have been reported in literature [1, 9, 20, 39, 40, 53, 60, 65, 68]. Moderate to high heritability for harvest index was observed in these studies. Fischer [22] reported a highly significant positive correlation of harvest index between genotypes from one generation to the next suggesting high heritability of this trait. Highly significant genetic differences among the genotypes for harvest index were reported in most of the above mentioned studies. Howell [26] reported consistent or nearly constant values of harvest index from a large range of treatments. More conservative or less variable nature of harvest index values observed by Howell suggests its high heritability. In aforesaid studies, the values of heritability for harvest index were moderate to high, often higher than those for grain yield.

The number of reports dealing with the genetics of harvest index which appeared in the literature is considerably high [1, 5, 8, 13, 30, 31, 37, 40, 47, 52, 54, 57, 60, 64, 68, 77, 78]. In these studies, genetics of harvest index was investigated by treating it as a quantitative trait under polygenic control and by following some kind of mating design. Though, these reports represent conflicting results to some extent, yet their

over-view clearly suggests that this trait is under the control of additive gene effects or additive and dominant genes are of equal importance. With this genetic background of harvest index, a breeder can safely base his selection on harvest index observations without any biasness or confusion, as the grain yield also has more or less similar genetic background, sometimes even more complex.

5. Relationship between harvest index and economic yield

Donald and Hamblin [19] described in detail various models and actual relationships between grain yield, biological yield and harvest index. It was found that almost always, there is a positive linear relationship between harvest index and grain yield. Only in exceptional circumstances such as moisture stress environments, harvest index is inversely related to grain yield. There are considerably high numbers of reports which support the observations of Donald and Hamblin [19] that there is a significant positive association between harvest index and economic yield (grain yield, tuber yield, yield of seed cotton etc.) not only in cereals [3, 9, 12, 23, 28, 54, 65] but also in legumes [6, 7, 38, 41, 66], tubers [29, 39, 48] and cotton [4].

Thus, having into consideration the gradual increase of harvest index from the old to the recently developed cultivars of field crops, fairly high heritability, its significant and positive association with other heritable and genetically governed traits like grain yield and its genetic architecture, as revealed from the above mentioned reports, it becomes substantially clear that harvest index can definitely be employed as a selection criterion in identifying high yielding genotypes in segregating generations.

6. Harvest index based selection

In the past, breeders have based their single plant selections in segregating generations on the grain yield alone or on the components of grain yield. This procedure has several drawbacks in identifying the high yielding genotypes specially in space planted early segregating generations. Donald and Hamblin [19] gave an account of such limitations where selection for grain yield, components of grain yield and for vegetative characters did not yield expected results. These authors advocated the use of harvest index (and biological yield) as simple criterion for the assessment of performance of different genotypes. This argument is supported by several published reports. Before making a mention of such reports, arguments in favour of employing harvest index as a selection criterion in comparison to grain yield may be pointed out. In view of positive correlation between grain yield and harvest index, one may suggest that harvest index measurements are unnecessary as grain yield alone may indicate higher yielding types and its measurements are simple and rapid. Arguments in favour of using harvest index as selection criterion are:

- a) Positive association between harvest index and grain yield may, sometimes, not be true [18, 32, 34].
- b) In comparison to harvest index, grain yield shows much higher degree of genotype x environment interaction and thus shows much non-genetic variation. Harvest index being a ratio is not affected that much [26, 62].
- c) Harvest index shows greater physiological efficiency of a genotype in terms of input-output ratio, i.e. high harvest index genotype will give more economic yield than the

low harvest index genotype when similar level of inputs is given to them.

Thus an F₂ or F₃ space planted individual plant may very well be selected due to its very high yield in comparison to other plants or due to very good expression of component traits. But later on, in subsequent generations, it may turn out a poor yielder due to high genotype x environment interaction. Due to additional advantage of space, such a plant will proportionately produce high biomass as well and hence its harvest index can be high (worth for selection) only when it really has a high physiological efficiency of converting the source into sink.

We now can mention the experimental evidences in support of this selection method. Syme [69] evaluated 16 wheat cultivars as single plants in pots for several characters and related them to the mean grain yield of the same cultivars grown at 63 sites throughout the world in the International Spring Wheat Yield Nursery (ISWYN). The analysis showed that harvest index accounted for 71,7 % of the variance of the mean plot yields in ISWYN. Direct correlation between ISWYN grain yields on one hand and single plant traits on the other gave correlation coefficients of 0,10 for grain yield, 0,85** for harvest index and -0,80** for straw yield. Thus, the harvest index of spaced plants had clear predictive value for crop yields in the field commercial plantings, while the grain yield of the same spaced plants had no such predictive value.

An extensive study of harvest index, grain yield and biological yield as selection criterion was made by Rosielle and Frey [53] using oat lines derived from a bulk population. They found that indirect selection for grain yield through harvest index would be 43 % as efficient as direct selection (i.e. using grain yield as selection criterion). Despite of such lower efficiency, they concluded that selection through harvest index would contribute to yield increase, height reduction and early maturity and that 'lines selected on the basis of harvest index may be agronomically superior to those selected for grain yield.' Extending their study, they further concluded that 'with heading date and height fixed much of the grain yield increase in oats may result from higher harvest index. Also, in a population with limited genetic variation for heading date and plant height, harvest index may be useful for indirect selection for grain yield.'

A study of prediction from performance of spaced plants in the field to the grain yields in large plots has been reported by Fischer [22]. The correlation coefficient between harvest index of spaced plants and those of field plots was 0,75. These results showed a clear cut superiority of the harvest index of the spaced plants over their grain yield for the prediction of crop performance with correlations of 0,54 and 0,31 respectively. When these comparisons were based with plot yields and harvest index of the central culm of the spaced plants, the correlation was strengthened to 0,65.

Fischer and Kertesz [23], in a similar study demonstrated the usefulness of harvest index of spaced plants as a criterion to predict yielding ability of the selected plants in subsequent generations. Ilucidating Knott's [33] view that grain yield per plant or its numerical components like number of tillers, grains per spike and thousand grain weight seem to be of dubious value, these authors emphasized the use of harvest index as selection criterion. Results of their study confirmed the results of earlier studies regarding the superiority of spaced plants' harvest index over spaced plants' yield as a predictor of yielding ability in large plots. The explanation may be that with spaced plantings, grain yield is related to the ability of the plants to occupy more space, thereby intercept-

ing more light. Yield potential is more a function of photosynthesis per unit of light captured, and apparently of greater importance is the distribution of the products of photosynthesis. Apparently, this distribution factor (harvest index) is little affected by population and hence can be assessed on spaced plants. Almost two-fold range in harvest index, found among the 40 genotypes studied here, appears to show sufficient variability specially when considered along with the weak influence of environment on this trait.

Bhatt [9] reported that harvest index was a useful selection criterion for improving grain yield of wheat. Harvest index was found to have a definite merit as a selection criterion for grain yield in wheat and was considered more reliable at high population densities than at low densities [45].

Sharma and Smith [58] conducted a study on selection for high and low harvest index in three winter wheat populations. They concluded that harvest index in F₃ generations was a good indicator of harvest index in F₄ but not for grain yield. Thus, harvest index by itself may have limited use in selecting for high grain yield. Nevertheless, it is an important means of identifying physiologically valuable genotypes in terms of their assimilates partitioning ability.

Sharma *et al.* [62], on the basis of a broad based study, demonstrated that selecting for high harvest index was a more effective method of obtaining high yielding genotypes than direct selection for grain yield in wheat. Selection for harvest index and grain yield was exercised in F₂ and F₃ generations of 36 crosses resulting from 9 x 9 diallel cross. It was observed that position of different genotypes with respect to harvest index remain more or less constant in different environments [61]. Correlation coefficients between F₂ and F₃ and between F₃ and F₄ were high and significant for harvest index but not for grain yield suggesting that former is a better selection criterion. It was, finally, supported by high yields of the selected plants (based on high harvest index) in F₄ generation.

In these studies, single plants in pots or spaced plants in the field represent an isolation environment where free tillering genotypes are able to achieve high biological and grain yields - relatively higher to other genotypes than they would under commercial plantings. Consequently, the relationship of grain yield of spaced plants to their grain yield under commercial plantings is distorted and correlation is low. On the other hand, harvest index, which depends much more on the performance of the individual culms, tends to remain constant. The harvest index of spaced plants, therefore, tends to show a lesser genotype x density interaction than does single plant grain yield and hence it shows a better relationship to plot grain yield.

7. Limitations

Austin *et al.* [2] pointed out that one sided improvement of the harvest index may be restricted because considerable amounts of non-soluble carbohydrates are required to build up an efficient plant canopy and a stable culm. Secondly, disproportionately heavy ears of high harvest index types may lead to lodging. They speculated that the cultivars with harvest index of 60 % could possibly be produced which are likely to yield by nearly 20 % higher than the recent best ones with 50 % harvest index, if biomass remains unaltered.

Comeau and Barnett [14] reported that harvest index generally had a lower coefficient of variation than grain yield or biological yield. This was supported by Cooper and Sorrells [15] who observed lower coefficient of variation for harvest index for two seasons as compared to other traits inclu-

ding economic index (ratio of grain to straw). Pokhrel et al. [51] used the term attraction index for the ratio of grain to straw and emphasized that it gives much better explanation of source-sink relationship. Biological yield or biomass yield used in the estimation of harvest index includes weight of grain which can never act as source for the development of sink. They also observed more variation for attraction index than for harvest index.

Donald and Hamblin [19] summarized that although harvest index may be a valuable criterion for early generation selection among spaced plants where performance per culm is carried forward to the commercial crop situation, it may not hold true for the prediction of crop grain yield from a segregating population to the commercial crop at the same (high) density. Also, competitive ability and harvest index are negatively associated, as tallness and large leaves add to the competitive ability.

Results of some studies have raised doubts concerning the use of harvest index as a selection criterion for grain yield. Whan et al. [76] reported that selection for improvement of grain yield using harvest index was no more effective than selection for grain yield directly. Nass [46] found no additional advantage of harvest index over visual selection for grain yield. McVetty and Evans [43] suggested a limited effectiveness of harvest index in selecting for grain yield so that a combined selection procedure utilizing productivity in a high framework had merit. Supporting this study, Nass and Jui [47] suggested that the use of harvest index as a selection criterion for grain yield appears beneficial primarily when utilized in conjunction with other traits like biomass yield, plant height and actual grain yield. Khurana and Yadava [32] reported that high harvest index of a soybean cultivar was not related to its high yielding ability. Bebyakin and Starichkova [5] observed predominance of dominant genes and overdominance in the genetic control of harvest index and suggested that early selection of progeny with high harvest index value may not give required results.

Though, these appear only a few sporadic and isolated studies, the breeder should keep in mind these limitations while breeding for high grain yields through the use of harvest index as a selection criterion.

8. Summary and conclusions

Harvest index, also called as 'migration coefficient' or 'coefficient of effectiveness', is the proportion of the economic yield (e.g. grain or tuber) to the total biological dry matter yield and most often is expressed in percent. Like any other metric trait, it shows quantitative variation and is under genetic control. It is, therefore, apparent that it can be improved genetically through selection. Though, the concept of harvest index is known since the second decade of present century, more extensive studies have been conducted in the recent past. There are ample evidences of improved harvest index due to long term breeding in the crops like wheat, rice, oats and field pea primarily because of changed source-sink relationship. A significant linear relationship has been observed between harvest index and economic yield in a large number of studies. It is a moderate to highly heritable character. Though, the studies on its genetics, sometimes, represent conflicting results, an overview suggests the involvement of mostly additive genes in its expression.

Results of several studies in which harvest index has been used as selection criterion have been reported in the literature. Harvest index has been found to have definite merit as a

selection criterion for grain yield, specially in cereals, and was found more reliable at high population densities. Being a ratio, it is less influenced by the environment as compared to other traits like grain yield and its component characters. However, one sided improvement of harvest index may cause problems of lodging. There are speculations that cultivars with 60 % harvest index could possibly be produced which are likely to yield about 20 % higher than existing cultivars with 50 % harvest index. Further improvement in grain yield is suggested through increased biomass but not the harvest index. Finally, the breeder should view harvest index not in isolation but along with biomass yield.

Brauchbarkeit des harvest index in der Pflanzenzüchtung

Der harvest index, auch als 'migration coefficient' oder 'coefficient of effectiveness' bezeichnet, ist der Anteil des ökonomischen Ertrages (z.B. Körner oder Knollen) am gesamten biologischen Trockenmasseertrag und wird meist in Prozent ausgedrückt. Wie jedes andere metrische Merkmal zeigt der harvest index eine genetisch kontrollierte quantitative Variation. Demzufolge ist eine züchterische Verbesserung durch Selektion möglich. Obgleich das Konzept des harvest index seit dem zweiten Jahrzehnt dieses Jahrhunderts bekannt ist, wurden umfangreichere Untersuchungen erst in jüngerer Zeit durchgeführt. Es gibt eine Reihe von Hinweisen dafür, daß der harvest index durch die langjährige züchterische Bearbeitung bei Pflanzenarten wie beispielsweise Weizen, Reis, Hafer und Erbsen insbesondere durch die Veränderung der source-sink Beziehung verbessert wurde. In zahlreichen Untersuchungen wurde eine signifikant lineare Beziehung zwischen dem harvest index und dem ökonomischen Ertrag festgestellt. Der harvest index ist ein Merkmal mit mittlerer bis hoher Erbllichkeit. Obgleich genetische Experimente manchmal widersprüchliche Ergebnisse lieferten, dominieren die Hinweise für das Vorliegen überwiegend additiv wirkender Gene.

In der Literatur finden sich zahlreiche Experimente, bei denen der harvest index als Selektionskriterium verwendet wurde. Dabei wurde festgestellt, daß der harvest index speziell bei Getreide einen deutlichen Vorzug bei der Selektion auf Kornertrag hat und besonders unter hohen Bestandesdichten zuverlässiger ist. Da er ein Verhältnis ausdrückt, wird er weniger durch die Umwelt beeinflusst als andere Merkmale wie beispielsweise der Kornertrag oder dessen Komponentenmerkmale. Bei der einseitigen Verbesserung des harvest index besteht die Gefahr, daß sich die Lageranfälligkeit erhöht. Es gibt Mutmaßungen, wonach Sorten mit einem harvest index von 60 % erstellt werden können, mit einem Mehrertrag von 20 % gegenüber den derzeit existierenden Sorten mit einem harvest index von 50 %. Die weitere Steigerung des Kornertrages sollte durch Erhöhung der Biomasse und nicht des harvest index erfolgen. Der Züchter sollte den harvest index nicht isoliert, sondern im Zusammenhang mit dem Biomasseertrag betrachten.

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