AUTO-PARASITIZATION OF LEAVES IN PULSES—N LIMITING OR C LIMITING?

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ABSTRACT

Self-distruction of leaves in pulses during seed filling period has been suggested to supplement seed N level. This has implied to mean that pulses are inefficient in taking up N. The object of this paper is to enquire whether this inefficiency is based on some inherent inability or only an apparent phenomenon consequent of some other limitations. Our analysis suggests that lack of carbohydrate during seed filling period is a major limitation in the ability of pulses to take up N when compared to cereals. This is further aggravated by the relatively poor N-translocation capacity of the pulses. An increase in the net photosynthesis during seed filling period as a means to alleviate the stress of C-availability and hence N-uptake is suggested.

THE phenomenon of auto-parasitization or self-destruction of leaves has been suggested as a way by which pulse crops accumulate high protein levels in seeds[1,2]. This self-destruction (senescence) of leaves is attributed to the inability of the species to respond to added N-fertilizers[3,4] implying their inefficiency in taking up N. The question of whether this inefficiency is due to an inherent inability of the species to take up N or is merely an apparent phenomenon consequent of other limitations, has not been made clear. Of late, C-limitation during peak nodulation (coinciding with flowering and seed set) has been suggested to cause N-limitation resulting in senescence and flower drop in pulses[5].

In this paper, we provide evidence to show that pulses are not inefficient to take up N due to any inherent inability when compared to cereals and oilseeds. Rather, their apparent inability is shown to be due to severe C-limitation in providing energy for N-uptake and its assimilation, caused largely through competing reproductive sinks. Using nitrogen harvest index values and yield harvest index values, we also attempt to compare the cereals and pulses for their efficiency in translocating N from leaves and stems to seeds.

MATERIALS AND METHODS

The basic data pertaining to the seed yield, biological yield and its glucose equivalents for a few cereal, pulse and oilseed crops was obtained from our earlier work[6]. A nitrogen uptake rate of 20 mg/g of glucose or photosynthate produced is considered to be in the range of maximal N-uptake rates[1,2]. Using this factor and the glucose equivalents of seed yields/ha, the maximum total N (N_{max}) that can possibly be taken during seed filling period was calculated for different crops. Further by knowing the seed protein contents[7] the total N-stored (N_s) in the seeds was calculated. By subtracting N_s from N_{max}, the excess or deficit of N-uptake in relation to seed N requirement during seed filling period was found.

The relative efficiencies of different species to take up N was estimated by two factors, namely (i) the amount of N taken up for every gram of glucose produced—calculated by dividing the total N-content by the glucose equivalent of the total biological yield, (ii) the amount of glucose produced and hence available for every 20 mg of N taken up, calculated as follows:

$$\frac{\text{glucose equivalent of total yield} \times 20}{\text{total N in biological yield}}$$

and expressed in g/mg N.

RESULTS AND DISCUSSION

Table I presents results on the excess or deficits of N-uptake in relation to seed N requirement during the seed filling period. It is seen that all cereals and oil seeds have a total N-uptake capacity (N_{max}) far in excess of what is stored in the seeds (N_s). Especially marked in this case were rice, maize and ragi. These are crops possessing a high biomass yield and a relatively low seed N. The excess in these crops ranged from 0·1843 to 0·6106 q N/ha.

On the other hand, were the pulse crops, whose N_{max} was far less than N_s. This deficit is seen in spite of the fact that the maximal N-uptake rate of 20 mg N/g glucose was considered in our calculations. This raises the question as to the source from which the deficits are made good. Sinclair and de Wit[1] proposed that such deficits might be filled up by the leaf N pool resulting from the proteolytic breakdown of leaf proteins. Such a theory also explains to a large extent the increased senescence of leaves in pulse crops. The latter process is frequently referred to as 'auto-parasitization'. This has been subsequently confirmed by other workers[8,9], who have demonstrated the break-

TABLE I

Extent of N excess or deficit in pulses during seed development period

Crop	Seed Yield (q/ha)	Glucose equivalent of seed yield (q/ha)	N_{max} (q/ha)	N_s (q/ha)	Excess or Deficit
Rice (*Oryza sativa*)	42·99	58·14	1·1600	0·5494	+0·6106
Ragi (*Eleusine coracana*)	32·72	41·54	0·8302	0·3436	+0·4866
Maize (*Zea mays*)	44·76	62·70	1·2540	0·6786	+0·5754
Sorghum (*Sorghum bicolor*)	43·20	49·52	0·9904	0·8061	+0·1843
Soybean (*Glycine max*)	11·64	23·14	0·4628	0·6587	−0·1959
Groundnut (*Arachis hypogaea*)	14·14	33·06	0·6612	0·5788	+0·0824
Cowpea (*Vigna unguiculata*)	12·70	19·88	0·3856	0·4880	−0·1024
Cajanus (*Cajanus cajana*)	11·04	16·74	0·3348	0·4242	−0·0894
Sunflower (*Helianthus annuus*)	16·27	31·72	0·6344	0·6150	+0·0194

TABLE II

Efficiency of pulses in taking up N, their glucose availability and nitrogen harvest index

Crop	Total Glucose Yield (q/ha)	Total N in Biological Yield (q/ha)	mg of N absorbed/gm of Glucose	gm Glucose produced/20 mg of N taken up	Nitrogen Harvest Index	Biological Harvest Index
Rice	122·60	0·82	6	3·33	0·66	0·40
Ragi	133·90	0·84	6·40	3·11	0·41	0·30
Maize	96·51	0·91	9	2·22	0·74	0·62
Sorghum	151·90	1·38	9	2·22	0·58	0·35
Soybean	53·02	1·18	22	0·91	0·56	0·33
Groundnut	50·81	1·01	19	1·05	0·57	0·51
Cowpea	38·06	0·83	22	0·91	0·59	0·45
Cajanus	74·95	0·92	12	1·66	0·46	0·17
Sunflower	50·08	1·10	9	2·22	0·58	0·49

down and re-distribution of leaf N to seeds during the seed development period.

The basic assumption made in the above theory has been that the 'self-destructive' species are not responsive to added N fertilizers and hence have to rely on an alternative source of N to meet their seed N requirement, that is, on the leaf proteins. But, does this mean that these species are less efficient in taking up available N?

As an attempt to answer this question, we found the relative efficiencies of different species to take up N as a function of mg N/taken up for every g of glucose produced. These values (Table II) show that pulses take up 2 to 3 times more N than cereals and oilseeds for every gram of glucose they produce. Thus, if cereals take up 6 to 9 mg N, pulses take up as much as 12 to 22 mg N/g of glucose produced, indicating that pulses are in fact more efficient than cereals and oilseeds in taking up N. However, this comparison does not indicate the efficiency in terms of energy spent on N-uptake.

A better picture emerged on calculating the glucose produced (made available) for every 20 mg N taken up. This reflects on two things, firstly the efficiency of crops in taking up N and secondly, the availability of C skeleton for N-uptake and utilization. Cereals and oilseeds have 2·22 to 3·33g of glucose available for every 20 mg N taken up, whereas pulses have only 0·91 to 1·66 g. Considering that 0·31 g of glucose is consumed in *utilising* 20 mg N *for protein synthesis*, it is seen that pulses are left with very little available C-skeleton for the synthesis of other metabolic products like carbohydrates and fats for the reproductive sinks and to provide as energy source for other metabolic processes. This sets in a competition for the use of every new molecule of glucose produced, bringing in a severe limitation of energy available for N-uptake. Thus, carbohydrate or glucose non-availability appears to be a major limiting factor contributing to the inability of pulses to take up N. This is confirmed by a number of workers who have shown either by CO_2 enrichment studies[10] or differential light intensity treatments[11], a marked increase in yield, presumably due to enhanced C-fixation, associated with higher N-content. The same point is also demonstrated by Garcia and Hanway[12], when they *observed significant* increases in soybean yield by foliar fertilization with N, P, K and S during pod filling period. This method circumvented the need for root activity in the uptake of N and hence its dependability on C-source during pod filling.

Finally, to compare the species in their efficiency to translocate N from leaves and stem to seeds, the nitrogen harvest index (NHI) was calculated as per the method of Desai and Bhatia[13]. It is found that pulses have a lower NHI than cereals (Table II), indicating that a substantial portion of leaf N remains untranslocated to the seeds. Thus, in spite of the severe senescence observed during the seed filling period, pulses appear to be less efficient than cereals in translocating N to seeds. When the NHI values were plotted against their corresponding biological harvest index (BHI) values (Fig. 1) a linear positive relationship was obtained, suggesting a close parallel between mobilization of N and dry matter to seeds. A similar conclusion was drawn by Bhatia *et al*[14], for a set of wheat genotypes. Such a relation is explained considering that increased dry matter in seed may facilitate storage of N either by way of providing C-skeleton (for converting N to protein in seeds) or providing physical space for N accumulation.

In conclusion, it is reiterated that C-limitations appear to be a major limiting factor in N-uptake and utilization in pulse crops and that there might not be any inherent inability in them to take up added N. This limitation may be alleviated by increasing the rates of photosynthesis during seed fill period, thereby enhancing N-uptake and utilization for seed development.

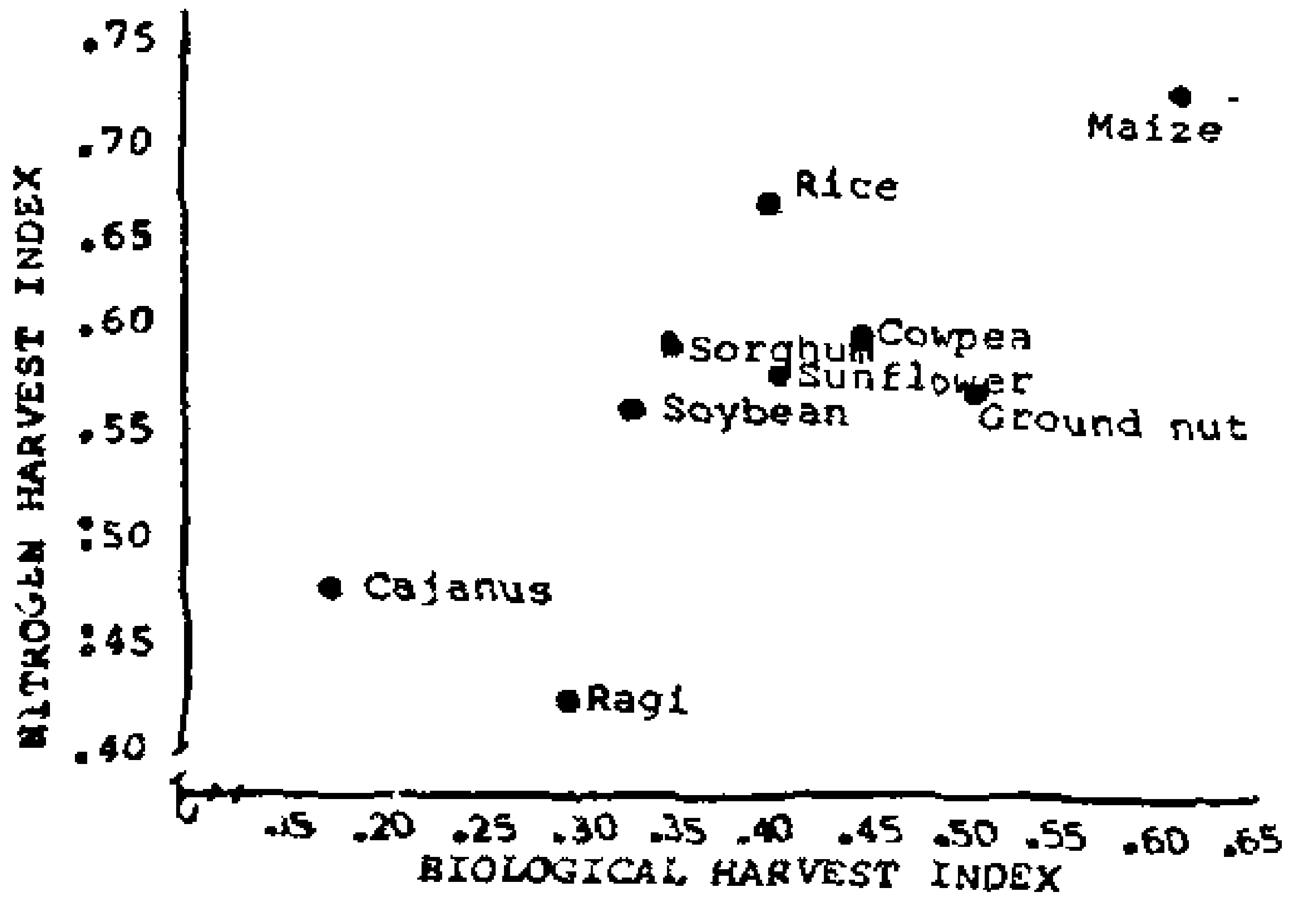

Fig.1. Relation between biological harvest index and Nitrogen harvest index for a few pulses, cereals and oilseeds.

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