Nitrogen Nutrition and Metabolism of Soybeans

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The soybean nutrition problem includes some puzzling aspects. A poor responsiveness of soybean yields to the directly applied N may be one such aspect. Under most conditions, the direct N application seldom increases soybean yields to an appreciable extent. This is strange even if the symbiotic relationship with N fixing bacteria is taken into consideration, since the amount of N from both the symbiotic and soil sources has been generally considered to be insufficient for maximum soybean yields. At present, no satisfactory explanation is available for the lack of profitable responses to N applications.

The first section of this paper deals with another curious phenomenon in soybean nutrition, a supra-normal growth of seeds under certain malnutritional conditions which was observed by the author[1]. In the subsequent sections the relationship between leaf protein turnover and plant growth is discussed, because it is thought that the protein breakdown products from the leaves might play an important role in the promotion of seed growth in the above mentioned phenomenon.

Temporary promotion of seed growth caused by mineral deficiencies

While studying the effects of mineral deficiencies on the growth of uninoculated soybeans, the author had noticed that the rate of seed growth of the plant that received −P or −K treatment for a short duration

Table 1. Effects of phosphorus and potassium deficiencies on the dry weight and N content of developing soybean seeds

Treatment	(a) Experiment 1 Seed group small	medium	large	Average	(b) Experiment 2 Seed group small	medium	large	Average
				Dry weight (g)/100 grains				
Control	5.46	9.68	12.60	8.26	2.35	3.20	4.50	3.41
—P	113	112	107	109	135	129	93	110
—K	102	111	100	102	124	119	100	106
				Total N content (mg)/100 grains				
Control	357	602	810	524	125	180	253	186
—P	111	110	111	109	132	126	98	113
—K	100	109	97	102	122	119	102	107
				Protein N content (mg)/100 grains				
Control	281	503	664	429	85	130	179	131
—P	113	111	93	107	132	127	101	113
—K	102	110	80	100	123	120	108	109

Note: Actual values are given for control plots only. Figures for —P and —K are shown in percentage of the control.

Table 2. Effects of phosphorus and potassium deficiencies on total and protein N contents of soybean leaves

Treatment		Total-N (%)	Total-N (mg)*	Protein-N (%)	Protein-N (mg)*
Control	Upper leaves	2.65	15.64	2.30	13.57
	Lower leaves	2.07	11.94	1.76	10.16
—P	Upper leaves	2.61	14.85	2.22	12.63
	Lower leaves	2.02	9.56	1.41	6.81
—K	Upper leaves	2.51	14.73	2.14	12.56
	Lower leaves	2.03	9.93	1.63	7.97

* mg in dm^2 leaf area.

during the pod filling stage might temporarily be increased as compared with that of the plant with a normal nutrition. This seemed to contradict with what one would expect to happen, so experiments were made repeatedly to confirm this phenomenon.

In one experiment, P or K was removed for 10 days from the nutrient solution during the mid pod-filling stage. At the end of the treatment, dry weights of the developing seeds were measured. As shown in Table 1(a), the dry weights of the treated plant's seeds were greater than the control's, on an average by 9% for –P and by 2% for –K treatment. When the seeds at the beginning of the treatments were classified according to their size into three groups, a tendency was found which showed that the growth of smaller seed groups is more favorably affected by these treatments. The total and protein N contents of the seeds were also affected in a manner similarly to that of the dry weights, except that the protein N content of the large seed group decreased rather than increased.

In another experiment, similar nutritional treatments were carried out during the early pod-filling stage. Again, the average seed dry weight was greater in the –P and –K treated plants than in the control plants (Table 1(b)). It may be interesting to note that this overall effect was entirely due to the promoted growth of small and medium sized seeds, no such effect being found on the large sized seeds. The total and protein N contents of the seeds changed almost exactly in parallel with their dry weights.

In contrast, the total and protein N contents of the leaves of treated plants were markedly reduced below that of the control (Table 2), indicating that the breakdown of leaf protein was accerelated under these malnutritional conditions. The protein breakdown products so formed must have been translocated to the developing seeds to be used as a source of N for protein synthesis.

It should be kept in mind, however, that nitrogen itself could hardly be a growth limiting factor in these experiments, since each plant had been supplied with ample N in the form of nitrates. Therefore, the possible cause of the growth promoting effect shown above could be attributable to the qualitative, but not quantitative, nature of the source of N sent to the growing seeds. In this respect, the protein breakdown products are considered to be superior to other N sources in supporting growth of especially very young tissues, and hence deserve a particular attention.

Protein turnover in mature leaves

Breakdown of leaf protein and subsequent translocation of the breakdown products are two of the main events typically observed in the senescent leaves. This is in a sharp contrast with the situation of mature leaves where protein levels are maintained at a steady state, and no net protein loss is occurring. However, this does not mean that protein degradation is not occurring in those

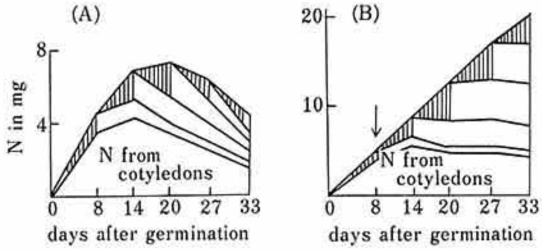

Fig. 1. Uptake and subsequent translocation of succesively applied ^{15}N by primary leaves of soybean plant. (A) Control plant, (B) plant with its apical growing region removed. The arrow indicates the time of removal. Shaded part represents the amount of ^{15}N taken up in each period. Similar pattern was obtained with protein N.

mature leaves.

According to the well recognized concept of protein turnover, the leaf proteins are undergoing constant breakdown and resynthesis[9]. When the rate of synthesis is equal to the rate of breakdown, the protein level remains unchanged as often observed in the mature leaves. The presence of protein turnover in soybean leaves[1,5] as well as in leaves of other species[6,7] has been demonstrated.

Although little is known about the fate of protein breakdown products formed in attached mature leaves, there is a circumstantial evidence to suggest that at least a part of the breakdown products is routinely translocated to the growing region of the plant. For example, the pulse-chase experiment[4] using ^{15}N as a tracer showed that (a) the release of the label from leaf protein is generally accompanied by the loss of label from the leaf, (b) the release from the leaf protein was remarkably reduced when the apical growing region of the plant was removed, whereas it did occur in the normal control plant with the released label exported out of the leaf (Fig. 1). In addition, it has been found that the apical growing region ordinarily derives necessary N much more from the older parts of the plant than directly from the root[2].

These findings suggest not only a translocation of protein breakdown products and their possible involvement in apical growth, but also that the activities of a growing region may even regulate protein turnover in the mature leaves.

Relationship between growth and protein turnover

The close relation between growth and protein turnover was found in the tissues of cultured carrot explants[8]. In soybeans, as described above, the removal of the apical growing region brought about a serious reduction in the breakdown of protein in the leaves. Accordingly it is of interest to determine whether this relationship could also be extended to the reverse direction; namely whether the turnover rate could be increased by increasing the growth activity of the plant.

To test this hypothesis the soybean plants at their seed developing stage were subjected to ^{15}N pulse-feeding experiment[1]. Actually the growing region, developing seeds in this case, was left intact owing to the technical difficulties to enlarge it freely, but instead the number of leaves was reduced to ½. This treatment was conducted with the hope of establishing within the plants to be examined a physiological status which would simulate the one that normally exists in those plants bearing twice as many pods as usual.

Immediately after the 24-hour feeding, the concentration of ^{15}N in the leaves of ½ defoliated plants was 3 times as high as that in the control (Fig. 2). The amount of total ^{15}N taken up by the former was therefore 1.5 times more than that of the latter, in spite of the ½ defoliation. Furthermore, both the incorporation of ^{15}N into and its subsequent release from the leaf protein were correspondingly greater in the treated leaves (Fig. 2). Thus, it is evident that the soybean leaves at the seed-developing stages still maintain a high potential for protein synthesis and turnover.

The results of this experiment may be

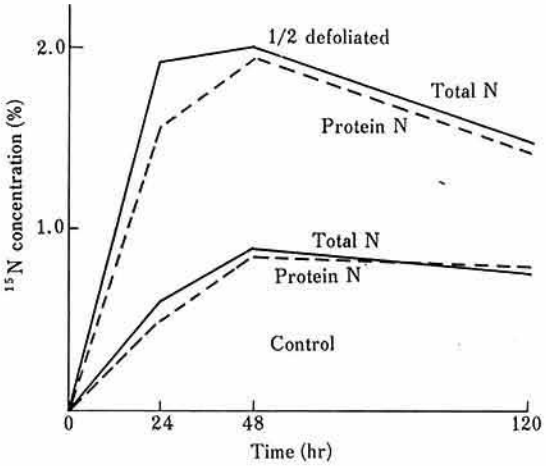

Fig. 2. Effect of partial defoliation on the turnover rate of total and protein N of the soybean leaves. ^{15}N was pulse-fed for the first 24 hours.

interpreted as indicating that the rate of protein turnover in the leaf could be increased to a large extent as the 'nutritional' demands or 'sink power(s)' from a site of growth increase. If this situation has been attained, both breakdown of leaf protein and translocation of the breakdown products could occur rapidly without lowering the protein level of the leaf seriously, provided that the plant is supplied with an adequate amount of N. Under such conditions, the applied N will find its way more easily into the leave and be metabolized there than otherwise reach directly the growing parts. It may be possible, therefore, for a mature leaf of a soybean plant to take up the new nitrogen continuously for building up its own proteins on the one hand and constantly eliminate the breakdown products, an assumed suitable source of N for the growth of the seeds, on the other. This is thought —at least by this author—to be an ideal condition especially for the growth and development of soybean seeds. And perhaps, it is when this condition is created that the soybeans are able to respond to fertilizer N.

From the view point of nitrogen metabolism described above, a mechanism appears to exists, at least in uninoculated soybeans, which makes a more efficient use of applied N possible when the number of pods per plant is reasonably high relative to the amount of leaves. In this connection, increasing the number of pods per plant should be of primary significance. Since the soybeans are generally known to suffer considerable abortion of the flowers and young fruits, the full operation of this mechanism would not be expected at the present levels of average fruit set.

As the explanations presented here are only tentative, much more work is needed before better understanding of the nitrogen nutrition problem of soybeans is obtained.

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