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Distribution of dry matter and nitrogen between the different plant parts in intact and depodded soya bean plants after flowering

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Summary

Soya bean plants were grown on nutrient solution in a growth room. One half developed normally (+pod plants), whereas the other half was depodded once a week (-pod plants). During nine weeks of seed development the growth of the roots, shoots, leaves and pods, as well as their total nitrogen percentage, was followed by weekly harvests.

In the +pod plants only the pods continued to increase in dry weight after the second harvest, the weight of the other plant parts remaining more or less constant. The amount of nitrogen in roots and stems of these plants decreased slightly during pod filling, that of the leaves considerably. The increase in the amount of nitrogen in the pods was relatively greater than the increase in the total dry weight. The amount of nitrogen taken up from the nutrient solution and that redistributed between plant parts was calculated (Table I).

In the —pod plants dry matter continued to accumulate in all plant parts throughout the experiment, including the detached pods. The amount of nitrogen also increased in all plant parts. The nitrogen uptake per unit of dry matter produced was about the same for both groups of plants (Table I).

The results are discussed in relation to the hypothesis that in leguminous plants the fixation or uptake of nitrogen by the roots cannot cope with the demand of the developing pods so that the necessary withdrawal from other plants parts, especially the leaves, causes the plants to die prematurely (theory of 'self-destruction').

Introduction

In recent years there has been a revived interest in pulse crops. The main reason for this is their ability to produce edible proteins without the use of nitrogenous fertilizers, which have become considerably more expensive since the energy crisis of 1973. Furthermore, the production of vegetative protein requires only one tenth of the acreage necessary for the production of an equal amount of animal protein. As the yield of the edible parts of these pulse crops is usually considerably lower than that of small grain crops, although there is no appreciable difference in canopy photosynthesis, some research has centered in recent years around the cause of this difference.

Penning de Vries et al. (1974, 1980) have calculated the energy costs of transforming the primary products, produced in photosynthesis, into different storage products on the basis of biochemical reactions. As substances like fats and proteins use more energy for their biosynthesis than carbohydrates like starch, hemicelluloses and fructosans, it is possible to explain differences in growth rate of storage organs in terms of their differing chemical composition, all other conditions being equal.

A second reason for the low yield of edible products in pulse crops may be a less favourable distribution of dry matter between vegetative and reproductive parts. The recent successes in increasing the yield of grain crops are not so much due to an increase in photosynthetic capacity of the green plant parts as to a better distribution of the photosynthates; e.g. in the short-stem varieties of maize and rice, and in the high harvest index of modern wheat varieties (Kramer, 1978; de Vos & Sinke, 1981). It can reasonably be expected that such a shift in dry matter distribution can also be achieved with pulse crops (Dantuma & Klein Hulze, 1979).

Another possible cause of yield differences between pulse crops, mainly producing proteins and fats, and small grains or other crops that mainly store carbohydrates was elaborated by Sinclair & de Wit (1975). They supposed that the demand for nitrogen during seed formation in pulse crops is so high that the capacity of the roots to supply this, either directly by uptake or via nitrogen fixation, is insufficient. This necessitates translocation of nitrogen from the leaves, leading to accelerated senescence and eventually their death, and this so called self destruction shortens the plant's life cycle and, hence, limits dry matter production. To obtain more information about this hypothesis, an experiment was carried out on soya bean plants with and without pods grown in nutrient solution in a growth room.

Materials and methods

Seeds of soya bean (*Glycine max.* L.) were germinated on moist filter paper in the dark. When the seedlings were of sufficient size they were taken one at a time, fixed by means of foam plastic strips in a central hole in a plastic lid and placed on 1-litre pots containing aerated nutrient solution (Hoagland, half strength). The pots were placed in a growth room at 20 °C and illuminated with 400 W high-pressure mercury vapour lamps, giving a light intensity of 80 W m^{-2} at plant height. The daylength was 17 hours. The nutrient solution was replaced twice a week. At the start of pod development the plants were shifted to 4-litre pots. The nitrate concentration in the solution was determined before and after each replenishment to ensure that sufficient nitrogen was available during the experiment. A sufficient number of plants of approximately equal size was selected on basis of their fresh weight and the experiment proper started a few days later with the first harvest and continued for nine weeks, plants being harvested weekly.

After the first week the plants were divided into two groups; in the first group the plants were allowed to develop normally (+pod plants), whereas in the other group all visible young pods were removed once every week (–pod plants).

At each harvest fresh and dry weights of roots, stems, leaves and pods were determined on 5 plants. As soon as this was possible, leaves were separated into live and dead leaves and pods into seeds and hulls. In all parts total nitrogen and nitrate nitrogen was determineed (Official methods of analysis of the AOAC, 13th ed., 1980, p. 129 (NO_3) 7.041 automated version; p. 15 (total N) 2.058, with $CuSO_4$-Se catalysator instead of Hg). The pods removed from the –pod plants were also weighed and analysed.

The +pod plants virtually stopped growth after the 7th week of the experiment; the experiment was continued for two weeks more.

In no case was there any appreciable formation of nodule on the roots.

Results

The changes in dry weight of the different plant parts with time are illustrated in Fig. 1. The upper half refers to the +pod plants; the lower half to the –pod plants. The weight of pods removed from these plants is indicated as accumulated pod weight.

During the first two weeks all parts of the +pod plants increased in weight; at the end of that period the first pods became visible. Thereafter the pods increased linearly in weight for a period of five weeks, but the other plant parts ceased to gain weight. Six weeks after the start the growth of the pods also more or less ceased.

For the –pod plants the situation was different. During the first 3 weeks there was not much difference in growth rate compared to the +pod plants; thereafter the –pod plants accumulated dry weight at a higher rate than the +pod plants and this increase continued in a linear way until the end of the experiment. This held not only for the accumulated pod weight, but also for the roots, stems and leaves.

As a result of these differences between the two groups the +pod plants had an ultimate total plant weight of 67.12 g and a pod weight of 40.45 g, whereas the –pod plants had produced a total of 103.61 g, including 29.65 g of pods. Thus the total amount of dry matter produced by the –pod plants was 50 % higher and the weight of the produced pods 25 % lower than that of the +pod plants.

Fig. 2 shows the nitrogen content of the plant parts of the two groups. For the sake of comparison the data of the two groups are presented in the same figure.

With the +pod plants the nitrogen content in the pods, roots and stems was approximately the same at the end of the experiment as at the start. Over the first 5-7 weeks there was a tendency towards an overall decrease in the nitrogen content; this was followed by an increase during the final weeks of the experiment. This phenomenon was very pronounced in the stem and to a lesser extent in pods and roots. In the leaves the nitrogen content declined steadily from about 5 % of the dry weight in week 1 to about 3 % in week 7; thereafter it remained more or less constant.

With the –pod plants the nitrogen content in the leaves followed approximately the same course as in the +pod leaves; that in other plant parts remained more or

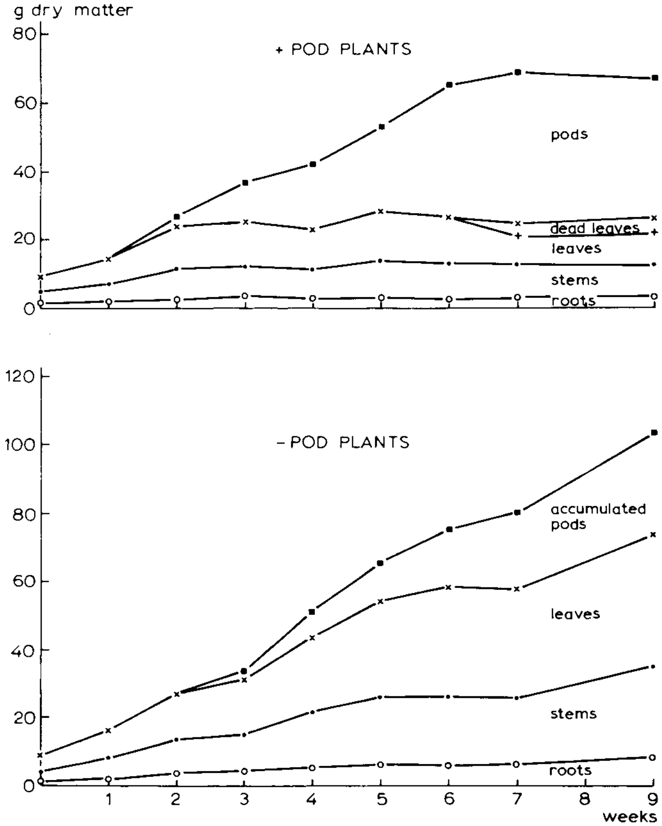

Fig. 1. Course of the increase in dry matter with time of the plant fractions indicated; upper half: intact plants; lower half: plants depodded every week.

less constant.

In the +pod plants the first dead leaves became visible at the seventh week and their weight increased slowly until the end of the experiment; in the -pod plants no leaves died during the experiment.

The course of the nitrate concentration was very irregular in all plant parts. For this reason no data are presented. A certain amount of nitrate in the tissue is an indication that nitrogen is not limiting growth. A concentration of 0.1 % of dry matter is often considered sufficient. The nitrate content in the roots was always higher than this value and in the pods it was always lower. In the leaves and stems the concentration was first above 0.1 % but dropped below it in the 6th experimental week in the +pods, and in the 3rd and 4th week in the leaves and stems of the -pods respectively.

Although not much value can be attached to these numbers, they show that in the intact plants the nitrate content of leaves and stems remained at a fairly high level

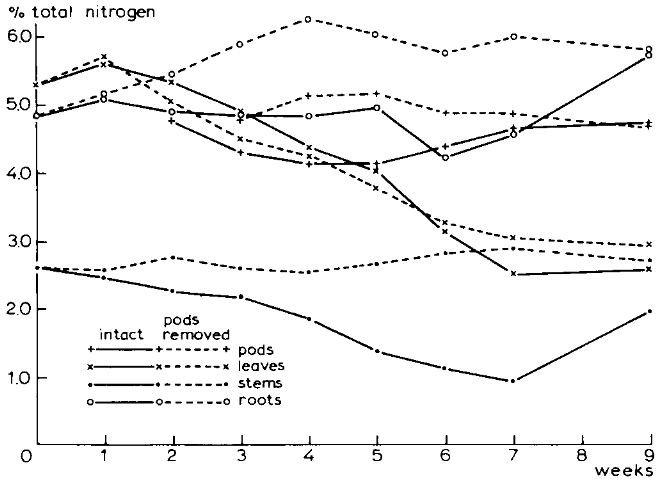

Fig. 2. Course of the nitrogen content with time of the fractions indicated, expressed as the percentage total nitrogen of the dry weight.

during the greater part of the experiment. At the last harvest date nitrate was still present in low concentrations in all plant parts, and in higher concentration in dead leaves (± 0.08 %) than in living leaves (± 0.03 %).

Discussion

Annual plants are bound to die after having completed their reproductive cycle. By changing the external conditions it is often possible to change the life span, but never drastically relative to the normal length of the cycle. The life span may also be influenced by applying growth regulators to the plant or by taking away some plant parts, but these manipulations too can only evoke relatively small changes in the length of the growing period. The present knowledge of senescence in annual plants has recently been extensively reviewed by Noodén (1980).

In the present experiment the normal growth pattern was altered as a result of depodding. Dry matter accumulation was not confined to the developing fruit, as in the intact (+pod) plants, and all vegetative plant parts continued to grow until the end of the experiment. There was also no sign of leaf death in the depodded (–pod) plants, whereas with the +pod plants dead leaves were observed 5 weeks after the first pods became visible.

As the growth of the +pod plants came to a standstill at week 7, when the first dead leaves appeared, one can best compare both groups of plants over a period in which the growth rates were approximately constant and the plants were fully green, that is from week 2 to week 6. Over this period the mean growth rate of the individual +pod plants was 1.37 g plant^{-1} day^{-1}, while that of the –pod plants with accumulated pod weight was 1.70 g plant^{-1} day^{-1}.

The higher growth rate of the –pod plants during pod setting cannot be explained by the possible reduction in the respiration load occasioned by repeated removal of the young pods as this could not account for the observed difference in growth rate. It seems more likely that the difference in growth rate is related to the difference in chemical composition. In the –pod plants the chemical compositon of pod tissue and vegetative plant parts did not differ greatly whereas the composition of the seeds in the +pod plants was presumably more like that of soya bean seeds (Sinclair & de Wit 1975). The formation of the latter demands a larger amount of primary photosynthetic product than would be required for an equal weight of vegetative tissue. Calculations with data of Penning de Vries et al. (1980) for 'tomato' as representative of the more or less vegetative tissue of the –pod plants and for 'soya bean, pod with seed' as representative of the combined tissues of the +pod plants, show that the amounts of dry matter that can be formed from 1 kg glucose are 0.65 kg and 0.49 kg respectively. The ratio of these two values is 1.32, which is about the same as the ratio of 1.24 calculated for the –pod and +pod plants in Table 1. This calculation cannot, of course, prove the point, but it does show that the differences in growth rate found do not necessarily indicate a difference in photosynthetic rate caused by a nitrogen deficiency of the leaves of the +pod plants.

As can be seen from Fig. 2, the total nitrogen content of the leaves decreased in both groups of plants in the same way. Values were also very similar. With the +pod plants this decrease was caused by transport out of the leaves, as the leaf weight did not change during the experiment (Fig. 1). With the –pod plants the weight increase of the leaves resulted in a net uptake of nitrogen. In the other plant parts the changes in weight and nitrogen content were less conspicuous; they are included together as 'remainder' in Table 1, which shows the changes in total plant weight and in the amount of nitrogen in the different plant parts.

The data show that the total amount of nitrogen taken up from the nutrient solution is far greater in the –pod plants than in the +pod plants. However, the uptake is almost identical when calculated per gram of dry matter produced. The amount of nitrogen taken up by the pods of intact plants was about equal to that taken up by the whole depodded plants, only with the +pod plants 22 % of the amount taken up by the pods was translocated from other plant parts.

Sinclair & de Wit (1975) supposed that this translocation of nitrogen was caused

Table 1. Increase in total plant weight and in the amount of total nitrogen in different plant parts during a period of 4 weeks, from 28 August to 25 September.

Group	Weight increase of total plant (g)	Uptake (mg) of nitrogen by				Net redistribution of N between plant parts (mg)	Nitrogen content in biomass (mg g^{-1})
		total plant	pods	leaves	remainder		
+pod	38.34	1211	1551	–227	–113	340	31.59
–pod	47.70	1628	822	377	429	0	34.13

by the inability of the roots to meet the nitrogen demands of the seeds resulting in a reduced photosynthetic capacity of the leaves, ultimately leading to plant death, a process they called 'self-destruction'. Although this kind of self destruction could occur as a response to nitrogen shortage in other crops with less proteinaceous storage organs (like small grain crops) they thought it must occur in pulse crops, as the uptake capacity of the roots of these crops would not be able to cope with the high demand for nitrogen of the developing fruit.

The decrease in total nitrogen content in the leaves (Fig. 2) was exactly the same in both groups of plants and it is unlikely that this content causes a slowing down of the growth rate and death of leaves in the +pod plants, and is sufficient to maintain full functioning in the -pod plants at the same time. Moreover, as the nitrate content in the leaves of the +pod plants was always higher than or equal to that of the -pod plants, it cannot be argued that leaves in intact plants die as a result of nitrogen shortage. The -pod plants had the same total nitrogen content and (usually) a lower nitrate content, but no dead leaves were observed during the whole experiment.

Sinclair & de Wit (1975) supposed that growing closed crops are not able to take up more nitrogen than 5 kg $ha^{-1}day^{-1}$. It can be demonstrated, however, that actively growing closed crops are able to take up considerably more. Calculations based on data from Italian ryegrass and turnips (Darwinkel, 1975), broad beans (Dantuma & Klein Hulze, 1979) and lucerne (Versteeg et al., 1981) indicate rates of uptake between 6 and 9 kg $ha^{-1}day^{-1}$. These figures clearly demonstrate that crops, including leguminous crops, can take up nitrogen far beyond the limit of 5 kg N $ha^{-1}day^{-1}$ proposed by Sinclair & de Wit (1975). Calculations by the same authors (Sinclair & de Wit, 1976) show that with N-uptake rates of 6 kg $ha^{-1}day^{-1}$ or higher the N needs of the developing seed could be met without the leaves becoming depleted.

The +pod plants in our experiment had a nitrogen uptake of over 30 mg N per gram of dry matter produced. For a daily growth rate of 200 kg ha^{-1} this would mean a nitrogen uptake rate of around 6 kg N $ha^{-1}day^{-1}$, well above the maximum rate of uptake which Sinclair and de Wit suggest is the upper limit in practice. It could be argued, however, that a growth room experiment is so different from a field experiment that such a calculation has no value. Comparison of our soya bean plants with the field bean data obtained by Dantuma & Klein Hulze (Table 2) indicates, however, that similar values for harvest index and relative uptake of nitrogen may be

Table 2. The harvest index for dry weight and nitrogen at the end of our experiment and in field beans at a comparable stage of leaf deterioration (Dantuma, pers. comm.).

	Leaf weight as % of max. leaf weight	Seed weight as % of total weight	Seed N as % of total N
Dantuma	76.6	49.4	73.8
Our experiment	84.0	44.7	75.3

expected in the field. Thus, although the absolute values of growth and nitrogen uptake may be much lower in growth rooms than in the field, there is not much difference in relative values.

Although small grain crops (unlike pulse crops) do not need more nitrogen in the seed than in the vegetative parts (Penning de Vries et al., 1980) nitrogen is notwithstanding translocated from the leaves to the developing ear (Spiertz, 1977; Vos, 1981).

Dilz (1964) in fact demonstrated a severe drop in the nitrogen content of oat leaves prior to flowering which was not accompanied by observable senescence.

The success of Abu-Shakra et al. (1978) in selecting soya bean plants with leaves which remained fully green during pod ripening, further demonstrates that soya bean plants have the capacity to produce ripe seeds without destruction of the leaves.

The process of senescence in annual plants has recently been reviewed by Noodén (1980). Such a review again illustrates the complexity of the whole process and reveals how little yet is known about causal relations between the different biochemical reactions and transfer processes that lead to the ultimate death of the plant, nor of internal of external factors that trigger and mediate these processes. Self-destruction is inherent in all annual plants and includes redistribution of nitrogen from the leaves to the developing fruits. Death of these leaves is also often the first visible sign of the onset of total plant senescence, but this is true for all annuals and not specifically for legumious annuals.

Both the result of our experiments and published data thus show that pod development in leguminous plants does not necessarily lead to leaf death, and also that the nitrogen content of leaves can drop to an appreciable extent without leading to their self destruction.

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