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Genotypic Differences in Dry Weight Accumulation, N Assimilation and Redistribution, and the Effects on Seed Yield and Protein Content in Faba Beans

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ABSTRAK

Kajian ini dijalankan untuk mengkaji kesan-kesan perbezaan genotip dalam penumpukan berat kering, asimilasi dan pengagihan semula N, dan keberkesanan pengagihan semula N ke atas hasil dan kandungan protein di antara tiga kultivar kacang faba dengan menggunakan rekabentuk blok rawak lengkap. Jumlah penumpukan berat kering dalam berbagai peringkat pertumbuhan menunjukkan perbezaan yang bererti di antara kultivar semasa pertumbuhan vegetatif dan pembungaan awal, dan semasa pembungaan dan pengisian biji awal, tetapi tidak pada pengisian biji. Asimilasi N berlaku di sepanjang pertumbuhan tetapi sebahagian besar diasimilasikan semasa pengisian biji dengan julat 47.66 hingga 56.50% jumlah N dalam tumbuhan. Pengagihan semula N daripada daun, batang dan kulit lenggai kepada biji adalah masing-masing dengan julat 26.66 - 31.42%, 6.89 - 11.05% dan 12.24 - 20.51% kandungan N dalam biji. Kandungan N dalam biji yang selebihnya adalah diasimilasikan semasa pengisian biji yang terdiri daripada 40.04 - 52.15%. Kandungan protein yang tinggi dalam biji nampaknya disebabkan oleh asimilasi N yang banyak dalam masa pengisian biji dan bukan keberkesanan pengagihan semula N daripada bahagian-bahagian vegetatif tumbuhan.

ABSTRACT

This experiment was conducted to study the effects of genotypic differences in dry weight accumulation, N assimilation and redistribution, and N redistribution efficiency of different plant parts on seed yield and protein content among three faba bean cultivars, using a randomized complete block design. The total dry weight accumulated in different growth stages showed significant differences among cultivars during vegetative growth and early flowering, and during flowering and early seed filling, but not during seed filling. N was assimilated throughout growth but a large quantity was assimilated during seed filling ranging from 47.66 to 56.50% of the total plant N. The redistribution of N from leaves, stems and pod walls to the seeds ranged from 26.66 - 31.42%, 6.89 - 11.05% and 12.24 - 20.51% of the seed N content, respectively. The remaining seed N content was assimilated during seed filling which accounted for 40.04 - 52.15%. High protein content in seeds seemed to be due to greater N assimilation during seed filling rather than to the N redistribution efficiency from the vegetative plant parts.

INTRODUCTION

The important role of nitrogen (N) in plant productivity is obvious. Many studies in leguminous plants have shown that the loss of N in the vegetative tissues relates to the accumulation of N in the seed (Hanway and Weber 1971; Salado-Navaro *et al.* 1985; Westermann *et al.* 1985).

The proportion of seed N obtained from redistribution varies from 20% to essentially 100% in leguminous plants, depending on enviromental conditions (Egli *et al.* 1978; Minchin *et al.* 1980; Neves *et al.* 1981; Zeiher *et al.* 1982; Venekamp and Koot 1984). Although some studies have been carried out on the assimilation and redistribution of N in faba bean (e.g. Cooper *et al.* 1976; Dekhuijzen *et al.* 1981; Dekhuijzen and Verkerke 1984; Venekamp and Koot 1984), they are all based on single genotypes.

The present work was carried out to study the genotypic differences in dry weight accumulation, N assimilation and redistribution, and N redistribution efficiency of different plant parts, and the effects of these on seed yield and protein content among three faba bean (*Vicia faba* L.) cultivars.

MATERIALS AND METHODS

Three faba bean cultivars: Maris Bead, Maris Beagle and Aquadulce were chosen due to the difference in their protein content and seed size. They were sown in the Wye College Experimental Plot on 9 March 1984 in six-row plots at a density of 24 plants per m^2 using a randomized complete block design with three replicates. Each plot measured 3.6 x 1.8 m with 22 plants per row. No fertilizer or *Rhizobium* inoculation was given, since the plots were routinely fertilized with organic manure.

Samples were taken at weekly intervals beginning at the ninth week after sowing until maturity. At each sampling period, four plants, one from each of the inner rows, were harvested except for the first two samplings for Maris Bead and Maris Beagle where eight plants were harvested to obtain sufficient materials for the near infrared (NIR) analyses.

The plants were separated into leaves (leaflets + stipules), stems (including petioles), flowers, pod walls and seeds where available. All the plant parts except the matured seeds was dried at 80°C, weighed and carefully mixed to give reasonable representative samples for grinding. The seeds were air dried. The N content in leaves, stems and matured seeds was analysed using the NIR analyser, after suitable calibration for each component was obtained. The N content in flowers, pod walls and developing seeds was analysed using the semi-micro Kjeldahl technique.

The amount of N redistributed was estimated from the change in total N in each plant part between the maximum N content and that at the final harvest at maturity (Cregan 1983). Thus the N redistributed from the leaves was represented by the total maximum N in the leaves minus the total N in leaves at maturity disregarding the fallen leaves. The calculation of N redistribution in leaves therefore overestimated the actual amount, since fallen leaves were not recovered at maturity. The extent of this bias due to fallen leaves was calculated by estimating the amount of fallen leaves. The difference between the maximum leaf dry weight and that at the final harvest was assumed to result from fallen leaves. It was also assumed that the fallen leaves were due to senescence and contained the minimum level of N which was considered equal to that at the final harvest. The amount of N redistributed from the stems and pod walls were also calculated, and the three values summed to give the total of redistributed N. The percentage of redistributed N from each plant part was designated as N redistribution efficiency. The loss of N from the vegetative plant parts and pod walls was assumed to be redistributed to seeds. If the total redistributed N from the vegetative plant parts and pod walls was less than the total seed N, then the difference was assumed to be derived from assimilation during seed filling (Pate and Minchin 1980).

From the above measurements, harvest index and N harvest index were calculated. Harvest index was calculated as the proportion of seed yield over the total above-ground yield, while the N harvest index was calculated as the proportion of seed N over the total above-ground N.

RESULTS

Dry Weight Accumulation

The total dry weight accumulation in the three faba bean cultivars, i.e. Aquadulce, Maris Bead and Maris Beagle showed a similar trend throughout growth but with higher dry weight accumulation for Aquadulce up to early seed filling stage (*Fig. 1*). The higher dry weight accumulation in Aquadulce compared to the other two cultivars was probably due to the influence of its large seed size (Table 1). However, at maturity, the total dry weight and seed yield were not significantly different among the three cultivars.

The total dry weight accumulated in different growth stages showed significant differences among cultivars during vegetative growth and early flowering, and during flowering and early seed filling but not during seed filling (Table 2). The proportion of dry weight accumulation ranged from 9.50 to 16.52%, 32.88 to 52.45% and 38.05 to 50.60% among the cultivars at three different growth stages respectively. *Fig. 2* shows

TABLE 1
Mean performance of three faba bean cultivars at maturity

Cultivar	Total dry wt (g/plant)	Seed yield (g/plant)	100-seed weight (g)	Seed protein (%)	Seed N yield (mg/plant)	Total N yield (mg/plant)	Harvest index (%)	N harvest index (%)
Aquadulce	62.81a (78.25a)[1]	31.84a	154.94c	30.00ab	1534.64a	1828.24a (1838.53a)	50.69a (42.78a)	83.94a (75.09a)
Maris Bead	68.76a (79.85a)	32.43a	43.90a	31.33b	1626.30a	1945.14a (1952.08a)	47.16a (42.06a)	83.61a (77.95a)
Maris Beagle	79.62a (88.73a)	34.71a	76.96a	29.34a	1629.64a	1957.08a (1964.76a)	43.60a (39.73a)	83.27a (76.94a)

[1]Values in parentheses indicate the inclusion of fallen leaves.
All means in a column followed by the same letter were not significantly different from another at 5% level of probability as determined by LSD test.

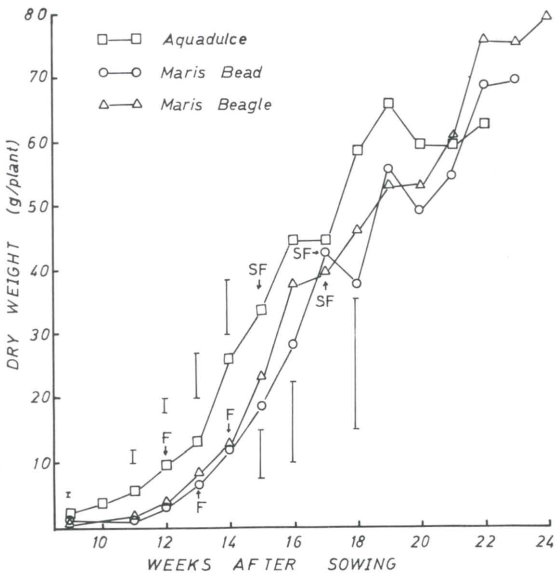

Fig. 1: Changes in total plant dry weight accumulation of three faba bean cultivars. F and SF indicate the beginning of flowering and seed filling respectively. The vertical bars represent the LSD at the 5% level of significance

the changes in total dry weight of different plant parts throughout growth and apparently indicated that most of the plant parts except seed attained maximum weight during early seed filling. Therefore, most of the dry weight accumulated during seed filling was devoted to seeds. Moreover, other plant parts showed decreasing dry weight during seed filling as is clearly shown

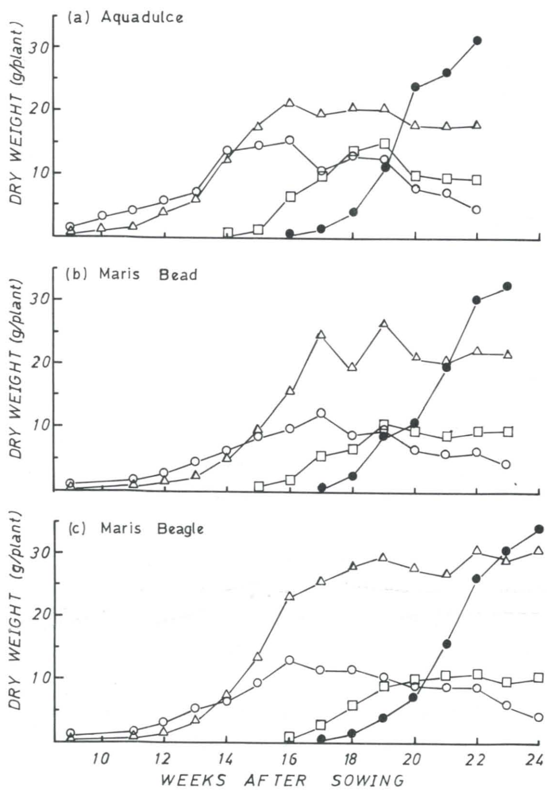

Fig. 2: Changes in dry weight of different plants parts of three faba bean cultivars. (○) leaves; (△) stems; (□) pod walls; (●) seeds

TABLE 2
Ontogenetics of dry weight (DW) and N accumulation in three faba bean cultivars

Cultivar	Character	Percentage of total DW and N accumulation during: vegetative growth and early flowering	flowering and early seed filling	seed filling
Aquadulce	DW	15.71b	38.03a	46.26a
	N	19.16b	24.35a	56.50a
Maris Bead	DW	9.50a	52.45b	38.05a
	N	13.92a	38.42a	47.66a
Maris Beagle	DW	16.52b	32.88a	50.60a
	N	23.36b	21.42a	55.22a

All means in a column followed by the same letter were not significantly different at 5% level of probability as determined by LSD test for DW and N respectively.

by leaves (most probably due to fallen leaves) and to some extent the stem and pod walls. Harvest indices ranged from 43.60% in Maris Beagle to 50.69% in Aquadulce (Table 1). The estimated fallen leaves comprised 8.19 to 15.44% of total dry weight and when these were included, the harvest indices ranged from 39.73 to 42.78%. No significant difference was observed among the cultivars.

N Accumulation

The total N assimilation in the plant throughout the growth period among the cultivars showed a similar pattern to that of dry weight (*Fig. 3*). Although there were no significant differences in total N content of plants or seeds at maturity among the three cultivars (Table 1), significant differences were indicated for the percentage of total N assimilated during vegetative growth and early flowering (Table 2). About half of the N requirement seemed to be assimilated during seed filling, ranging from 47.66 to 56.50% of the total plant N, indicating the high requirement for N at this growth stage.

All the plant parts showed an overall decrease in N concentration between the initial sampling and maturity (*Fig. 4*), but this decrease was less in the seeds than in leaves, stems or pod walls. Except during early seed filling, seeds of Maris Bead exhibited consistently higher N concentrations throughout seed development compared to Aquadulce or Maris Beagle. At maturity, the seed protein content of Maris Bead was significantly higher than that of Maris Beagle but not with Aquadulce.

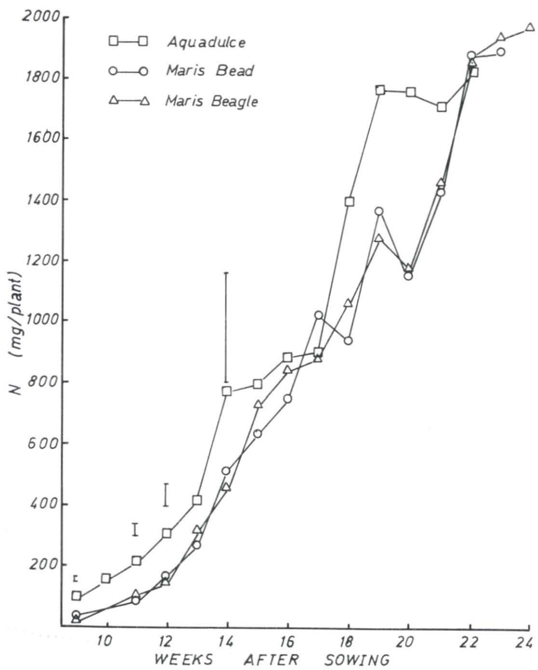

Fig. 3: Changes in total plant N accumulation of three faba bean cultivars. The verticals bars represent the LSD at 5% level of significance

The decrease of total N in the leaves, stems and pod walls was assumed to be caused by redistribution of N to the seeds during seed filling. The leaves seemed to be the major source of N to

TABLE 3
Sources of N to seeds in three faba bean cultivars. All values expressed as percentage of total N yield of seeds at final harvest

Source	Aquadulce	Maris Bead	Maris Beagle
Redistribution during seed filling from:			
leaves + stipules	30.86a(16.98a)[1]	26.66a(17.50a)	31.42a(20.42a)
stems + petioles	8.59a	6.89a	11.05a
pod walls	20.51a	14.30a	12.24a
Total redistribution	59.96a(46.08a)	47.85a(38.69a)	55.69a(43.71a)
Assimilation of N during seed filling	40.04a(53.92a)	52.15a(61.31a)	44.31a(56.29a)

[1]Values in parentheses indicate the percentage when fallen leaves were included.
All means in a row followed by the same letter were not significantly different at 5% level of probability as determined by LSD test.

the seeds, contributing from 26.66 to 31.42% of the seeds' requirement (Table 3). However, when the fallen leaves, which accounted for 6.94 to 10.29% of the total plant N, were taken into account, the total leaves contributed only from 16.98 to 20.42%. This was followed by the pod walls which contributed from 12.24 to 20.51% of the seed N requirement. The stems, although having the highest dry weight (*Fig. 2*), contributed only 6.89 to 11.05% of the seed N requirement. The total amount of N redistributed from the vegetative plant parts and pod walls ranged from 47.85

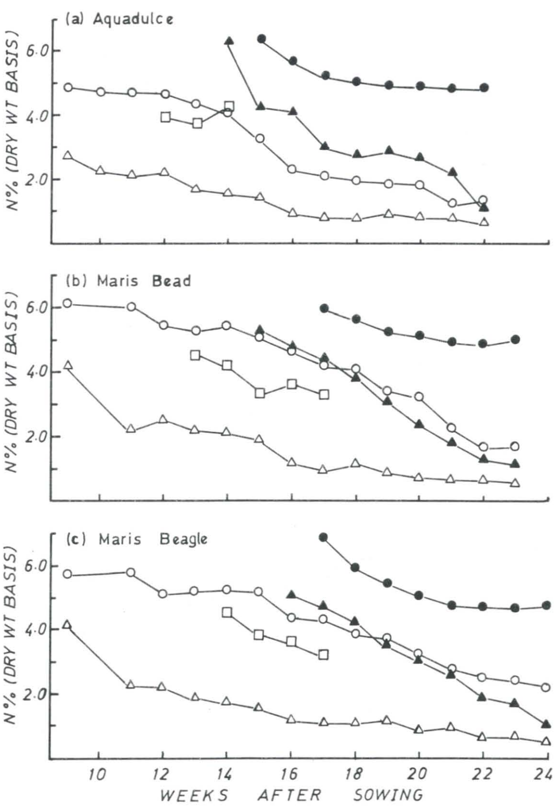

Fig. 4: *Changes in N content of different plant parts of three faba bean cultivars.* (○) leaves; (△) stems; (□) flowers; (●) seeds; (▲) pod walls

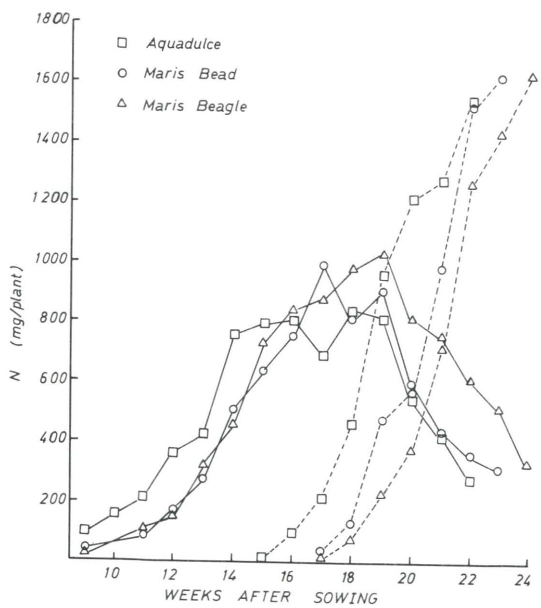

Fig. 5: *The relationship of total N in vegetative parts + pod walls and seeds throughout growth of three faba bean cultivars.* ___ *vegetative parts + pod walls;*.........*seeds*

TABLE 4
N redistribution efficiency (%) of different plant parts in three faba bean cultivars

Plant part	Aquadulce	Maris Bead	Maris Beagle
Leaves + stipules	85.95a(47.76a)[1]	84.70a(57.56a)	86.24a(56.49a)
Stems + petioles	49.03a	46.23a	53.28a
Pod walls	76.30a	65.07a	65.75a
Total N redistribution efficiency	75.79a(58.51a)	70.94a(57.88a)	72.57a(58.48a)

[1]Values in parentheses indicate the percentage when fallen leaves were included.
All means in a row followed by the same letter were not significantly different at 5% level of probability as determined by LSD test.

to 59.96% but only 38.69 to 46.08% when fallen leaves were included. The remainder of the N in the seeds was therefore assumed to be assimilated during seed filling, and accounted for 40.04 to 52.15% among the three cultivars and with even higher proportions (53.92 to 61.31%) when the fallen leaves were taken into account.

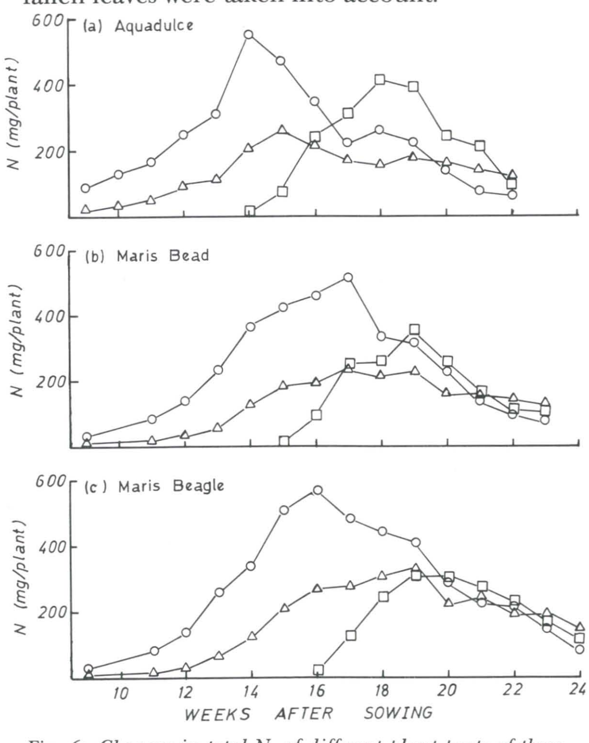

Fig. 6: Changes in total N of different plant parts of three faba bean cultivars. (○) leaves; (△) stems; (□) pod walls;

The relationship of the total N in the vegetative plant parts and pod walls and the assimilation of N in the seeds is shown in *Fig. 5.* The total N in the vegetative plant parts and pod walls reached maximum values during early seed filling and then showed a rapid decline which coincided with the linear phase of N assimilation in the seeds. When the total N in each plant part, i.e. leaves, stems and pod walls was examined separately, it was found that the redistribution commenced at different periods (*Fig. 6*). The leaves were found to redistribute N at the commencement of seed filling followed by the stems, and finally, by the middle of seed filling, the pod walls. The N redistribution efficiencies of different plant parts were not significantly different among the cultivars and similarly when the fallen leaves were included (Table 4).

DISCUSSION

The plant parts of faba bean have been reported to provide from 21 to 50% of redistributed N to the seeds (Pate and Minchin 1980; Dekhuijzen and Verkerke 1983; Venekamp and Koot 1984), indicating their importance for N storage. In this study, the plant parts continued to develop until their maximum dry weights during seed filling were attained. Thereafter, dry weight increases were mainly restricted to seeds which accounted for 43.60 to 50.69% of the total dry weight at maturity. The harvest indices were similar to those reported by Redshaw and Gaudiel (1982), Thompson and Taylor (1982) and Ebmeyer (1984). Total dry weight accumulation showed a close correspondence with the total N assimilation throughout the development.

There were significant differences of percentage N assimilated among the three cultivars only up to early flowering. By early seed filling about half of the total N had been assimilated and the remainder during seed filling which ranged from 47.66% in Maris Bead to 56.50% in Aquadulce, indicating some differences in the efficiency of assimilating N at different growing periods.

All the plant parts showed decreasing N concentrations throughout growth, most notably during seed filling. Maris Bead which had a significantly higher protein content in mature seeds than Maris Beagle generally had a higher seed N concentration throughout development. Barrat (1982) reported that a line with higher protein concentration in the mature seed maintains a higher percentage of total N in the seed throughout development than a low protein line of the same cultivar. The higher seed N concentration in a high protein plant when compared with a low protein plant is presumably caused by a higher N supply. Barrat and Pullen (1984) studied the changes in the total amino acid and 3,4-dehydroxyphenylalanine (DOPA) content of faba bean pod phloem sap during development and found that the high protein line had a greater amino acid concentration with lower proportion of DOPA than the low protein line.

The supply of N to the seeds can be accomplished by continuous assimilation of N during seed filling and its redistribution from other plant parts. The values of redistributed N from leaves reported here are double those reported by Pate and Minchin (1980) who found that pod walls sent the highest proportion of N to seeds in faba bean. This may partly be due to the overestimation caused by neglecting the fallen leaves. Other species, such as cowpea, soybean and chickpea, all showed high proportions of seed N derived from leaves (Pate and Minchin 1980). The total contribution of redistributed N from the vegetative plant parts and pod walls in all the three cultivars were generally in agreement with values obtained by Pate and Minchin (1980) but were higher than those reported by Cooper *et al.* (1976), Dekhuijzen and Verkerke (1984), Venekamp and Koot (1984) who concluded that redistributed N made only a small contribution to total seed N.

Maris Bead which had the highest protein content in the mature seeds obtained most of its seed N from assimilation during seed filling rather than redistribution from the vegetative plant parts and pod walls; the estimate was even higher when fallen leaves were taken into account. However, the effects of N assimilation during seed filling and N redistribution efficiency on seed protein content could not be ascertained as both were not significantly different among the cultivars. But a low N redistribution efficiency might have the possibility of delaying the decline in N assimilatory processes, nitrate reduction and N_2 fixation and therefore enabling the extra assimilation of N during seed filling, since faba bean has the capability of fixing N_2 throughout seed filling (Schilling 1983). The result is in accordance with that of Westermann *et al.* (1985) who found that the photosynthetic and N_2 fixation activities during seed filling can have a significant influence on total seed N concentration and yield in *Phaseolus vulgaris*. A similar assumption was made by Dekhuijzen and Verkerke (1984), who found that more ^{15}N was recovered in the seed at maturity when it was applied to the soil at early pod filling than when applied during early flowering. This indicated that assimilated N during seed filling was preferentially distributed to the developing seeds and the more N was assimilated during this period the less was redistributed from the vegetative plant parts and pod walls.

The present results are in contrast to those of Dickson and Hackler (1975) who found that high protein content in seeds of *Phaseolus vulgaris* was due to greater transfer efficiency from other plant parts. It is assumed that a high N redistribution efficiency would be more important in cereals than in legumes, since most of the plant's N requirement in cereals accumulated by anthesis (Polmer *et al.* 1979; Cregan 1983). Moreover, the amount of N accumulated in the grain of wheat or oat plants was positively related to the amount of N in the vegetative tissues at anthesis (Peterson *et al.* 1975; Cross and Haslemore 1979).

All the three cultivars used here possessed high and apparently similar N harvest indices. The values are, however, lower than those reported by Dantuma and Klein-Hulze (1979) who obtained an N harvest index of 90% with variety Minica. When the fallen leaves were included, the N harvest indices ranged from 75.09 to 77.95%, decreasing between 5.66 to 8.85%. Similarly, Dekhuijzen and Verkerke (1984) also reported a high N harvest index which decreased from 86 to 70% when the fallen leaves and roots were taken into account. Richards and Soper (1979) found a relatively lower N harvest index of 60%. These various reports suggest that there is some variation within faba beans for N harvest indices, although some differences may be due to changing environmental conditions.

The results of this study indicate the presence of genotypic differences for N assimilation and redistribution within faba beans. The leaves were the main contributor of N to the seeds followed by pod walls and stem. However, high protein content in seeds seemed to be due to greater N assimilation during seed filling rather than N redistribution efficiency from the vegetative plant parts. The effects on yield could not be generalised due to the small variation of yield between the cultivars.

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