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Protein content and dry weight of seeds from various pea genotypes

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Abstract – Pea seed protein content (SPC) and seed dry weight (SDW) are both influenced by genetic and environmental factors. To assess the variations of these within-plant traits between seeds, six genotypes were field tested. The sequential seed development at nodes along the main stem was determined. Nitrogen fixation was measured by the acetylene reduction assay (ARA). At maturity, protein content and dry weight were measured according to seed position on the plant. Individual protein content was determined by near-infrared transmission spectroscopy. The results show a significant difference in protein content between nodes of the genotypes Solara, L765 and L833. Protein content tended to decrease from the bottom to the top of the plant for these genotypes. The difference in protein content between the lowest and the uppermost node was about 26 g kg⁻¹ for Solara, 40 g kg⁻¹ for L765 and 49 g kg⁻¹ for L833. There were also significant differences in dry weight between plant nodes for all genotypes, except Finale. In addition, the range of difference in dry weight between plant nodes was higher than that for protein content. Further, to determine the influence of morphological position on individual protein content and dry weight, multiple linear regression was established on node position, pod position on the node, and seed position within pods. The results showed that protein content and dry weight were not influenced either by within-pod seed position or pod position on the raceme. Moreover, protein content and dry weight were mainly influenced by node position on the main stem. However, for protein content, the effect of node position varied with genotype, indicating a genetic variability for this character. This genetic variability could be attributed to the difference between genotypes in the ability to maintain nitrogen fixation during the onset of seed filling. For dry weight, the decrease in seed weight for upper nodes of the plant also varied with genotype in relation to the duration of seed filling and the seed growth rate.

pea *Pisum sativum* / seed protein content / seed dry weight / variation / node position / seed filling / physiological maturity

1. INTRODUCTION

One of the main problems of pea (*Pisum sativum* L.) is its genotypic and environmental variations in seed protein content [7]. Between and within genotypes, the seed N concentration at maturity varies between years and locations [16, 20]. Variations in seed N concentration are mainly due to environmental factors such as temperature and rainfall [14]. In addition, changes in seed N concentrations were mainly caused by variations in the seed N accumulation rates and dependant on N availability within the plant [21]. The level of plant N nutrition and the source-sink ratio at the beginning of seed filling influence final seed N concentration of grain legumes. For example, low levels of plant N nutrition at the beginning of seed filling in pea, resulting from soil compaction, led to a decrease in seed N concentration [9]. Depodding and defoliation performed before the beginning of seed filling increased and decreased seed N concentration, respectively [25, 31]. Therefore nitrogen stresses during seed filling caused a decrease in seed N concentration.

N for seeds can be obtained either by further N accumulation during seed filling or by N transfer from the vegetative com-

ponents of the plant [4]. During seed filling, the N being accumulated is destined predominantly for seeds, although there are temporary transfers to the vegetative organs [32, 34]. During this period, symbiotically-fixed N seems to be preferentially transferred to growing seeds while mineral N is equally distributed between seeds and mature vegetative organs [34, 37]. Furthermore, as the N concentration in the vegetative parts increases from the base to the top of the shoot [19], the amount of N available to the seeds may increase with their nodal position.

Within individual pea plants, variations in SPC were recorded among nodes [2, 6]. Similarly, early investigations [5] found a significant decrease in seed protein content from lower to upper nodes in "Primcovert" pea, but recorded no variation between seeds within pods. In other legume species, within-plant SPC variation has also been observed. For example, SPC decreased acropetally within individual *Vicia faba* plants [1]. Similarly, a decrease in protein content from the bottom to the top of *Phaseolus vulgaris* plants for varieties with indeterminate growth, but no variation for those with a determinate growth pattern were reported [36]. However, no significant difference within pods among seeds was recorded [18]. In another investigation [11], a linear increase in SPC from the base to the

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top of the plant within four soybean lines was also reported. Meanwhile, there was no variation in SPC according to pod level at a given node within two indeterminate genotypes of winter-type white lupin [8].

Pea is an indeterminate plant whose pods and seeds are set on successive reproductive nodes of the plant. The development of seeds at various positions is asynchronous [29, 30]. Thus the diversity of the response to environmental conditions of N and dry matter accumulation in seeds may depend on the plant development stage at the time of treatment application. Consequently, owing to the great range of seed development stages at a given time in a pea plant, analyzing mean seed N concentration at the plant level is unlikely to allow a precise understanding of the processes that cause the variations in seed N concentration. The objectives of the current investigations were to study, for six different pea genotypes: (1) the intra-plant variations in SPC and SDW in relation to the following sources of variation: node position, pod rank on the raceme, and seed position within pod, and (2) the interactions between seed development and nitrogen nutrition in these variations.

2. MATERIALS AND METHODS

2.1. Plant material and growing conditions

A field experiment was sown in March 1994 at the INRA experimental station in Versailles (France). Six pea genotypes were grown along wires 2 m long and 1 m apart. Plants were sown at low density, about 15 seeds m^{-1} , in order to reduce competition. The plants therefore have a higher number of fruiting nodes, allowing the within-plant variations in SPC and SDW to be studied and the origins of these variations to be explored. The genotypes used in this experiment were INRA lines L765, L776, L833 and the commercial varieties Colmo, Finale and Solara, which are spring cultivars. The genotypes showed differences in maturity. Line L765 was the earliest genotype, flowering at node 14. Line L776 was the latest and flowered at node 19. The other genotypes were intermediate in flowering. All genotypes produce 2 pods per fruiting node, except L776 which is multipod, producing 3 to 5 pods per node. The genotypes also differed in other characters such as seed size, total number of fruiting nodes per plant at maturity, foliage (normal or afila) and the ability to maintain nitrogen fixation during the onset of seed filling [3]. The genotypes were also sown at normal density (100 plants m^{-2}), in order to measure nitrogen fixation during plant development.

2.2. Measurements

2.2.1. From three-leaf stage to maturity

At weekly intervals, one row of twenty plants per genotype was harvested and the symbiotic nitrogen fixation was assayed by acetylene reducing activity (ARA). Nodulated roots of each genotype were placed in a 1075 ml bottle and about 110 ml of the air volume was substituted by acetylene. Two samples of 3 ml were taken seven and fourteen minutes after acetylene injection. The ethylene concentration was subsequently measured with a Carlo Erba Strumentazione 4100 gas chromato-

graph equipped with a flame ionization detector (gas carrier: N_2 ; oven temperature: 45 °C). Then the acetylene reduction activity is expressed in micromoles of acetylene reduced per hour and per plant.

2.2.2. At the beginning of flowering

Ten plants of each genotype were tagged in order to measure the progression of flowering along the main stem, and intra-plant variations in SPC and SDW at maturity. Flowering nodes of the main stem of each plant were recorded at two-day intervals [24]. A node was considered as flowering when at least one flower was open.

2.2.3. From the beginning of seed filling to maturity

Rows of twenty plants per genotype were harvested at two-day intervals. Seeds at different nodal positions of the main stem were collected separately, grouped and counted. The position of the node on the main stem was scored acropetally from the first reproductive node. For each seed group, fresh weight and dry weight after oven-drying at 85 °C for 48 h, were measured in order to calculate the seed water concentration. At each of the nodal positions, the beginning of seed filling and physiological maturity were determined as times when the water concentrations were 850 and 550 $g\ kg^{-1}$, respectively, as determined by linear regression between the seed water concentration and the cumulative degree-days during the linear decline of seed water concentration [30]. The progression of these two stages along nodes was measured at two-day intervals. The rate of dry weight accumulation in the seed was also estimated (after non-linear points were excluded from the beginning and the end of the filling period) by fitting a linear regression line to the seed weights at different sampling times expressed in cumulative degree-days from sowing [10, 13]. The length of the effective seed filling of a given node was calculated as the period between the beginning and the end of seed filling of the node.

2.2.4. At maturity

At maturity, the ten tagged plants were harvested individually. The position of the node on the main stem was scored acropetally from the first reproductive node. In addition, the positions of pods at the node ("P" for proximal or "D" for distal) and of each individual seed within pods (counted from the peduncle) were recorded. The protein content of individual seeds of plants was then measured by near-infrared spectroscopy using the Near-Infrared Transmission spectrophotometer Infracore FFA 1255 manufactured by Tecator (Höganäs, Sweden). This instrument is equipped with a cupel containing 23 cells. Each cell received one seed placed with its cotyledon interface horizontal. The twenty-three seeds were analyzed for spectral characteristics. The average transmission spectrum was recorded over the region between 850 nm and 1050 nm. The spectrophotometer was previously calibrated using Kjeldahl measurements [22]. Measurements were repeated three times for each seed and the final individual SPC was the mean of these three replications adjusted to 0.0 $g\ kg^{-1}$ moisture. After this non-destructive measurement, the seeds were individually weighed. The branches of plants were discarded. In order to explain the intra-plant variation in SPC, individual seed protein

Table I. Flowering dates and rates of progression of flowering, initiation of seed filling and seed physiological maturity as influenced by genotypes.

Genotypes	Flowering date CDD	Rate of progression among main stem nodes		
		Flowering	Beginning of seed filling	End of seed filling
L765	717d [†]	0.0258b	0.0446a	0.0325d
L776	923a	0.0342a	0.0391ab	0.0476bc
L833	728cd	0.0311a	0.0428a	0.0436bc
Colmo	759b	0.0321a	0.0397a	0.0666a
Finale	735cd	0.0255b	0.0338ab	0.0554ab
Solara	745bc	0.0281b	0.0295bc	0.0397cd
Significance	**	**	**	**

CDD = cumulative degree-days from sowing.

** Indicates significant differences between genotypes at the $P = 0.01$ probability level.

[†] Values followed by the same letter in the same column are not significantly different at the $P = 0.01$ probability level.

content was regressed on the variable node number, pod position on the raceme, within-pod position of seed and seed dry weight.

3. RESULTS

3.1. Variation in flowering and seed development

The results indicated a genotypic variability for flowering, rates of progression of flowering and the beginning and end of seed filling along nodes of the main stem (Tab. I). Line L765 was the earliest flowering genotype, flowering at 717 cumulative degree-days from sowing, and L776, the latest one, flowered at 923 cumulative degree-days. The other genotypes were intermediates. There was also a significant difference in the rate of progression of flowering between genotypes. Plants of L776 and Colmo, which were the last to reach maturity (923 CDD and 759 CDD, respectively), had the highest flowering progression rates (Tab. I). Plants of Finale and L765 had the lowest rates. The plants of the other genotypes were intermediate.

There was also a significant difference between genotypes in the rates of progression of the beginning and the end of seed filling across nodes (Tab. I). Lines L765, L833 and Colmo had the highest rates of progression of the beginning of seed filling, 0.0446 nodes degree-day⁻¹, 0.0428 node degree-day⁻¹ and 0.0397 nodes degree-day⁻¹, respectively. Cultivar Solara had the lowest rate (0.0295 nodes degree-day⁻¹). Finale and L776 were intermediate. On the other hand, Colmo and Finale had the highest rates of progression of the end of seed filling along nodes of the main stem (0.0666 node degree-day⁻¹ and 0.0554 nodes degree-day⁻¹), while L765 had the lowest rate, about 0.0325 nodes degree-day⁻¹. In addition, the earliest flowering genotype, L765, which had the highest rate of progression of the beginning of seed filling had the lowest rate of progression of the end of seed filling. Consequently, this results in the increase in the duration of seed filling for the upper nodes of the plant of this genotype, whereas for Colmo and Solara this duration decreased. For most genotypes, the rate of progression

of the beginning of seed filling was higher than the rate of progression of flowering, indicating a decrease in the lag phase from the bottom to the top of the plant.

3.2. Variation in seed protein content and seed dry weight

3.2.1. Variation between genotypes

There were significant differences ($P = 0.01$) in SPC between genotypes (Tab. II). Line L833 had the lowest mean SPC, about 275 g kg⁻¹. For the other genotypes, the mean SPC was not significantly different, around 310 g kg⁻¹. The range of variation between genotypes was about 38 g kg⁻¹. The difference between genotypes was greater for SDW (Tab. III). Genotypes Finale, Solara, L833 and L765 had the highest SDW, 268 mg, 254 mg, 242 mg and 234 mg, respectively. Colmo had the lowest SDW, about 150 mg, while L776 was intermediate. The range of variation in SDW between genotypes (118 mg) was higher than that of SPC.

3.2.2. Variation between nodes

In order to determine the within-plant variation in SPC and SDW, seeds were collected according to their morphological position (on the node, on the raceme and within pods) on the plant. The differences in SPC and SDW varied depending on the genotype. The differences in SPC between nodes were significant for genotypes L833, L765, and Solara (Tab. II). The difference in SPC between the lowest and the uppermost node was about 49 g kg⁻¹ for L833, 40 g kg⁻¹ for L765 and 26 g kg⁻¹ for Solara. This indicated that for these genotypes, the protein content of the seed is related to its nodal position on the plant. Thus, seeds located at lower positions on the plant recorded higher protein content than those at upper positions. For genotypes L776, Colmo and Finale, the difference in SPC between nodes of the main stem of the plant was not significant.

There was also a large variation in SDW between nodes for all genotypes except Finale (Tab. III). Therefore, seeds located

Table II. Seed protein content as influenced by nodal position for six pea genotypes. Data are average of five plants.

Nodal position of seed	L765	L776	L833	Colmo	Finale	Solara
	g·kg ⁻¹					
1	329a†	319	298a	300	312	316ab
2	317b	312	293ab	297	312	323a
3	313bc	319	286abc	292	310	315ab
4	307bcd	312	277cd	296	307	306abc
5	299ed	307	279bcd	293	311	304bc
6	299ed	307	271cd	293	301	301bc
7	302cde	313	265de	291		299bc
8	289ef	310	252ef	302		297c
9	301cde	312	255ef	300		299c
10	289f	318	249f	299		
11				309		
Significance	**	NS	**	NS	NS	**
Difference‡	40	12	49	18	11	26
Means¶	307a	313a	275b	296a	310a	308a

** Indicates significant differences between nodes at the 0.01 probability level.

NS = non significant.

† Values in the same column with the same letter (s) are not significantly different.

‡ Range of difference in seed protein between nodes of the same genotype.

¶ Mean of the genotype; means followed by the same letter (s) are not significantly different at the 0.01 probably level.

Table III. Seed dry weight as influenced by nodal position for six pea genotypes. Data are average of five plants.

Reproductive node number	L765	L776	L833	Colmo	Finale	Solara
	mg/seed					
1	256a†	195a	275abc	175ab	275	278a
2	254a	196a	281a	177a	269	289a
3	261a	191a	278ab	155abc	269	264ab
4	259a	189a	259abc	147bc	278	258abc
5	266a	187ab	243cd	154abc	272	276ab
6	259a	181abc	247bcd	141c	246	271ab
7	233ab	166bcd	247bcd	135cd		216cd
8	199bc	163cd	224de	135cd		207d
9	169c	147d	198e	140c		228bcd
10	187c	116e	168f	142c		
11				108d		
Significance	**	**	**	**	NS	**
Difference‡	97	80	113	69	32	82
Means¶	234a	173b	242a	150c	268a	254a

** Indicates significant differences between nodes at the 0.01 probability level.

NS = non-significant.

† Values in the same column with the same letter (s) are not significantly different.

‡ Range of difference in seed dry weight between nodes of the same genotype.

¶ Mean of the genotype; means followed by the same letter (s) are not significantly different at the 0.01 probably level.

at lower positions on the main stem tended to have higher dry weight. The variation in SDW between nodes was higher than that of SPC. The magnitude of the difference in SDW between the lowest and the uppermost node of the plant was about 113 mg for L833, 97 mg for L765, 82 mg for Solara, 80 mg for L776 and 69 mg for Colmo. Indeed, Finale recorded the lowest number of fruiting nodes, about 6 nodes.

3.2.3. Relationships within individual plants

Within individual plants, there was a large variation in SPC and SDW which resulted from the variations between nodes, between pods at different positions on the raceme, and between individual seeds within pods. For example, a representation of individual SPC and SDW which includes the morphological

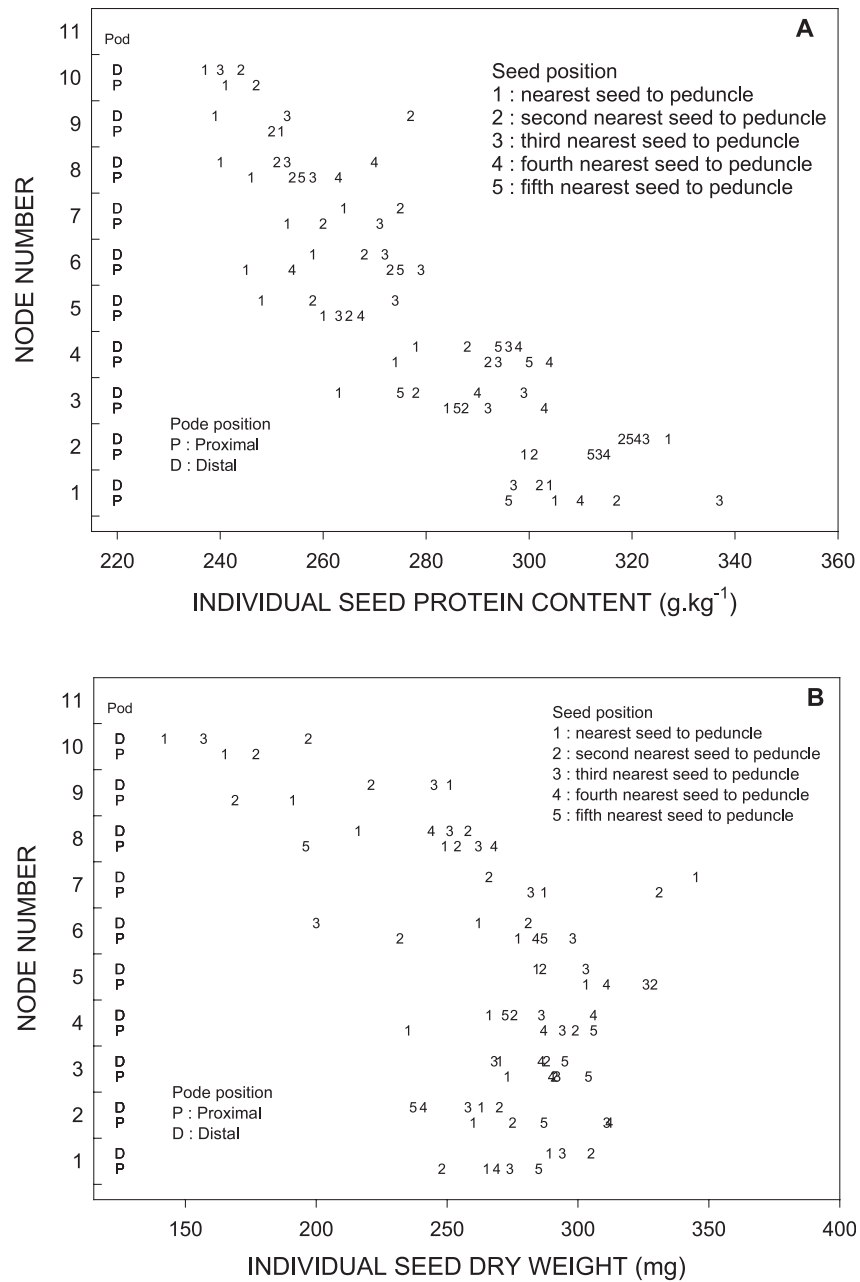


Figure 1. Individual seed protein content (A) and seed dry weight (B) according to seed position on the main stem of a single plant of L833. The column at the left represents pod position on the raceme. P and D represent proximal and distal positions of the pods at a given node, respectively. Positions of seeds within pods were counted from the peduncle.

position is given in Figure 1 for one plant of L833 and Figure 2 for one plant of Colmo. The general trends observed in these plants were typical of the pattern in most of the other plants of these genotypes. This representation revealed some of the relationships between biological organization of a typical plant and both SPC and SDW.

For the L833 plant, with respect to nodes, SPC (Fig. 1A) and SDW (Fig. 1B) decreased for the most part progressively with increasing node number. In comparisons between positions of

pods on the raceme (proximal or distal), there is no general trend either for mean SPC or mean SDW. The representation shows a large variation in SPC (Fig. 1A) between individual seeds of the same plant for L833, from 337 g kg⁻¹ (seed 3, pod P, node 1) to 237 g kg⁻¹ (seed 1, pod D, node 10). The corresponding variation in SDW (Fig. 1B) is, respectively, about 345 mg (seed 1, pod D, node 7) and 142 mg (seed 1, pod D, node 10). Within pods, the largest difference recorded in SPC between individual seeds in the same pod of this plant was about 41 g kg⁻¹

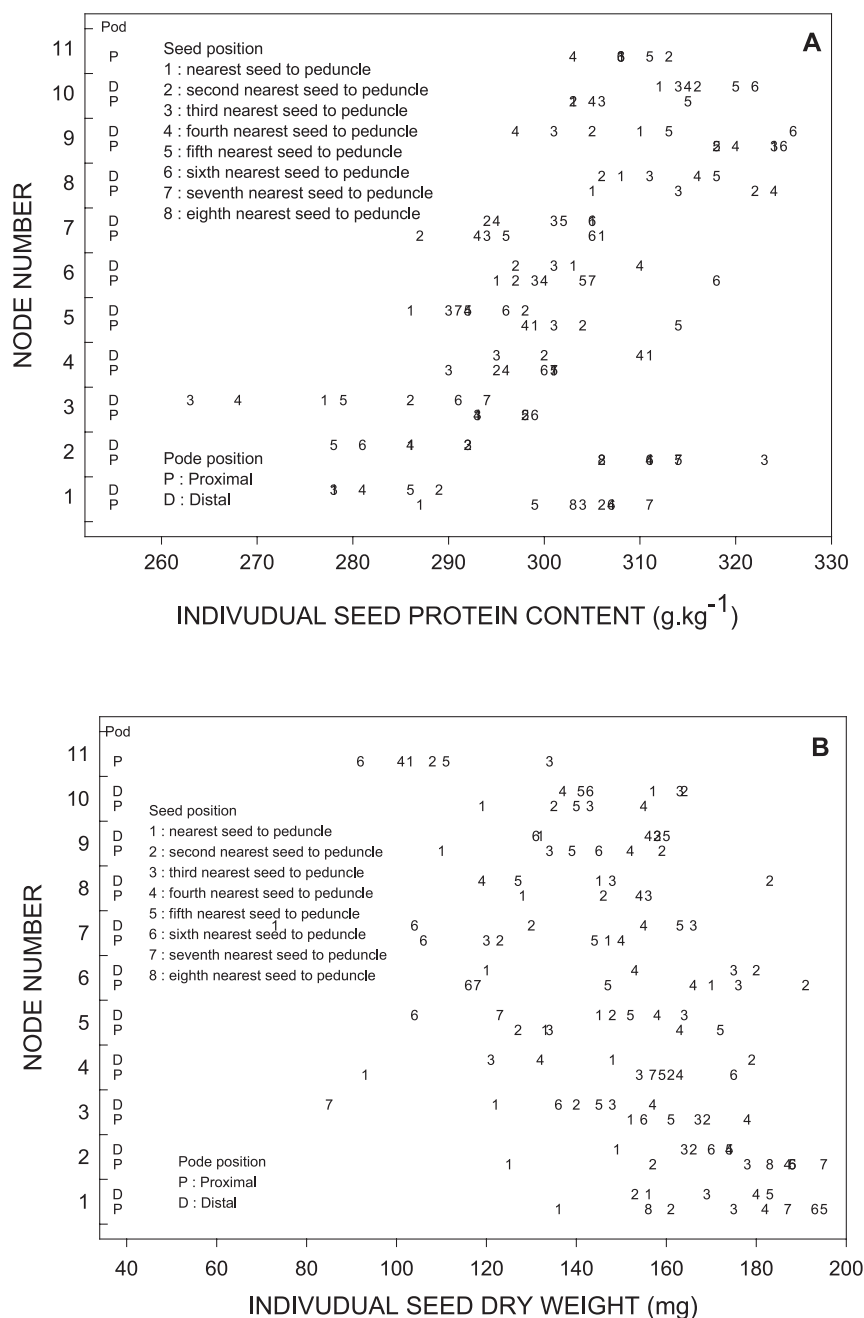


Figure 2. Individual seed protein content (A) and seed dry weight (B) according to seed position on the main stem of a single plant of cv. Colmo. The column at the left represents pod position on the raceme. P and D represent proximal and distal positions of the pods at a given node, respectively. Positions of seeds within pods were counted from the peduncle.

in pod P of node 1, while that in SDW, which was about 81 g kg⁻¹, was recorded in pod D of node 6. However, the relative SPC and SDW at different positions within pods had no clear trend. Within a given pod, SPC and SDW was not linked to seed position. In addition, the difference in mean SPC and SDW between pods of the same node was slight.

For the Colmo plant, with respect to nodes, SPC tended to increase for the most part progressively with increasing node

number (Fig. 2A). However, this trend was not recorded for SDW (Fig. 2B). The largest variation observed in SPC between individual seeds of this plant was from 326 g kg⁻¹ (seed 6, pod D, node 9) to 263 g kg⁻¹ (seed 3, pod D, node 3). The corresponding variation in SDW was from 195 g kg⁻¹ (seed 7, pod P, node 2) to 73 g kg⁻¹ (seed 1, pod D, node 7). Within pods, the largest variation recorded between seeds was about 31 g kg⁻¹ for SPC (pod D, node 3), and 93 g kg⁻¹ for SDW (pod D, node 7).

Table IV. Table of F Snedecor for intra- plant variation in seed protein content (SPC) and seed dry weight (SDW). Data are individual SPC and SDW from five plants of each genotype.

Genotypes	SPC				SDW			
	Plants	Position of			Plants	Position of		
		Node	Pod on the raceme	Seed within pod		Node	Pod on the raceme	Seed within pod
L765	61.3***	34.3***	1.4 NS	0.1 NS	20.0***	8.2**	1.3 NS	3.0 NS
L776	46.1***	1.8NS	0.0 NS	0.2 NS	–	–	–	–
L833	35.4***	124.6***	0.6 NS	2.7 NS	17.9***	96.0***	1.6 NS	3.6 NS
Colmo	13.0***	12.1***	0.1 NS	1.4 NS	68.5***	46.1***	2.3 NS	7.8**
Finale	36.7***	10.1**	5.4 NS	0.6 NS	34.6***	7.7**	2.4 NS	10.3**
Solara	18.7***	18.5***	4.4 NS	3.5 NS	1.3 NS	31.9***	8.7**	0.0 NS

, *: Indicate significant differences at the 0.01 and 0.001 probability levels, respectively.

NS = non-significant.

–: not performed.

The degree to which morphological position accounted for the intra-plant variability in SPC and SDW was quantified by using multiple linear regression of degree 1, 2 and 3. Only the linear regressions which had higher effects compared with other regressions were recorded. The F values of Snedecor and the significance of the different variables are shown in Table IV.

The results indicated a very highly significant effect ($P = 0.01$) of the plant both for SPC or for SDW and for all genotypes. In contrast, the effect of pod position on the raceme was not significant for these parameters, not even for the multipod genotype L776. The effect of seed position within the pod was also not significant for SPC. For SDW, this effect was significant for only two genotypes, Colmo and Finale. The effect of node position on the plant was significant for SDW of both genotypes. SDW tended to decrease acropetally on the plant. For SPC, the effect of node position varied according to the genotype (Tab. IV). This effect was highly significant for L765, L833 and Solara, slightly significant for Colmo and Finale, and not significant for L776. These results indicated a genetic variability in SPC dependant on node position.

3.3. Nitrogen fixation

For all genotypes, the duration of nitrogen fixation was the same, about 900 degree-days, and maximum nitrogen fixation occurred between 690 and 900 degree-days from sowing (Fig. 3). Between genotypes, there was a huge variation in maximum nitrogen fixation. Genotype L833 (Fig. 3A) recorded the highest rate of nitrogen fixation (about 49 $\mu\text{moles C}_2\text{H}_2$ reduced/h/plant) while L776 (Fig. 3B) had the lowest one (about 25 $\mu\text{moles C}_2\text{H}_2$ reduced/h/plant). The other genotypes were intermediate. For genotype L776 (Fig. 3B), nitrogenase activity declined rapidly during the flowering of the different nodes and ceased at the beginning of seed filling. However, for L833, nitrogenase activity tended to increase during flowering (Fig. 3A) then decrease during seed filling.

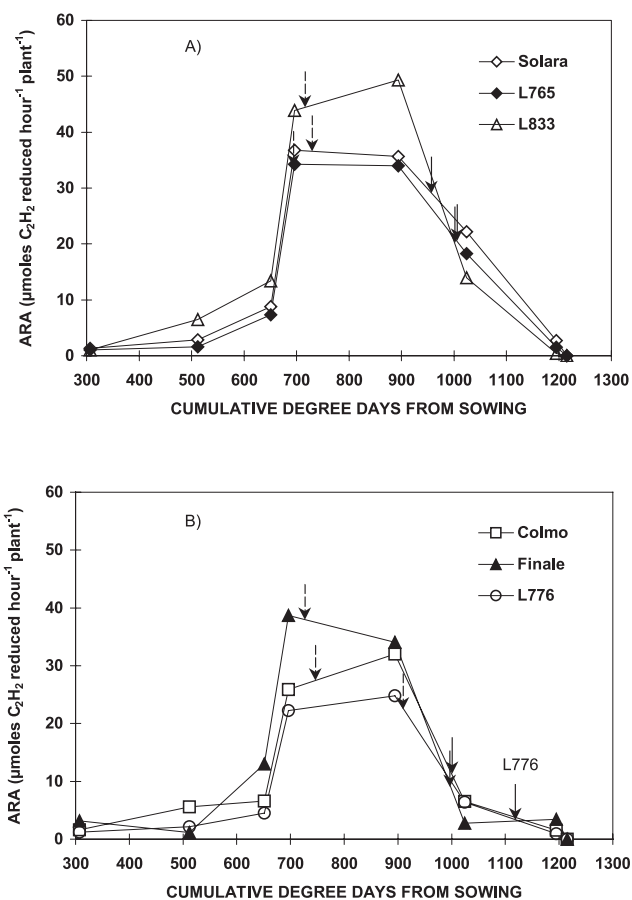


Figure 3. Evolution of nitrogen fixation (Acetylene Reduction Assay) during plant cycle for six pea genotypes. Broken and solid arrows indicate, respectively, flowering and initiation of seed filling of the first reproductive node of the genotype.

Table V. Duration of seed filling for six pea genotypes according to nodal position of the seed on the main stem.

Reproductive node number	L765	L776	L833	Colmo	Finale	Solara
	CDD†					
1	349	334	314	316	300	364
2	370	329	314	306	277	340
3	392	382	333	295	299	351
4	367	369	303	285	239	307
5	404	306	332	275	246	306
6	398	325	263	265	254	291
7	388	344	244	255		337
8	432	351	270	245		323
9			307			319
10			349			
Mean	388	343	303	280	269	326

† CDD = cumulative degree-days.

4. DISCUSSION

The multiple linear regression analysis (Tab. IV) indicated that the node position on the main stem was the main factor which influenced the seed protein content (SPC) and seed dry weight (SDW). Indeed, for genotypes L833, L765 and Solara, protein content of the seed is related to its nodal position on the plant. Therefore, seeds located at the lower positions on the plant recorded higher protein content than those at upper positions (Tab. II). This result agrees with previous work [5, 6, 26] which showed an acropetal decrease in SPC in pea. However, for the other genotypes, the difference in SPC between nodes was not significant, as previously observed in some lines from the John Innes Institute [23]. Thus these results indicated a genetic variability for this character. In addition, there was a large variation in SDW between nodes for all genotypes except Finale (Tab. III) which had a lower number of fertile nodes (about 6). Therefore, seeds located at lower positions on the main stem also tended to have higher dry weights. Variation was similar for all varieties and the genetic variability for the SDW was lower than that for SPC.

Pea is an indeterminate plant whose pods and seeds are set on successive reproductive nodes at different heights on the plant. The development of pods at various positions is asynchronous and the seeds in higher pods begin to fill later than seeds in lower pods [30]. This characteristic may lead to variations in the seed N accumulation rate between nodes. Therefore nitrogen accumulation by seeds during the seed-filling period depends upon the external N supply, N retrieval from the soil and symbiotic fixation of atmospheric N₂, which generally cannot sustain the high demand of developing seeds [12, 15, 33, 34]. Therefore the difference in SPC and SDW between nodes of certain genotypes, such as L833, could be attributed to differences in seed nutrition. For this genotype, nitrogenase activity was maintained after flowering (Fig. 3A) then decreased during seed filling of upper nodes. Thus only early-formed seeds of this genotype would benefit from being filled by both nitrogen fixation and nitrogen remobilization, inducing higher SPC. However, filling of seeds of upper nodes of the

main stem, formed when nitrogen fixation has ceased, can be achieved only by remobilization of nitrogen previously accumulated in vegetative organs, as supported by the “self destruction” hypothesis [35], resulting in lower SPC. Indeed, the difference in nutrition between early and later-formed seeds could explain the difference in seed protein content recorded between nodes of the plant. In addition, for genotypes such as L776, nitrogenase activity declined before flowering (Fig. 3B). Thus filling of seeds at different positions on the plant will be achieved only by remobilization. Other studies [17] have suggested three distinct patterns of N accumulation by plants and partitioning to the seeds during seed fill: (1) no accumulation during seed fill, (2) accumulation only in early seed fill, and (3) constant accumulation throughout seed fill. Our results confirm the first two suggested patterns.

In most seed crops, individual seed weight is commonly analyzed as the product of the individual seed growth rate and the duration of seed filling [27]. Our results indicated a genetic variability for both characteristics. The duration of seed filling decreased from the bottom to the top of the plant for genotypes Colmo, Finale and Solara, increased slightly for L776 and L833, and more significantly for L765 (Tab. V). The seed growth rate (Tab. VI) tended to decrease acropetally for all genotypes although mainly for L765, L833 and Solara, which also exhibited a significant decrease in SPC from the bottom to the top of the plant. Our results confirm previous observations [28] which indicated that genotypic variation in individual seed weight is mainly due to differences in individual seed growth rates. Therefore genotypes such as Finale, L833 and Solara, which had a high seed growth rate (Tab. VI), also had a high seed dry weight at maturity (Tab. III). Equally, the genotypes with lower seed growth rates, such as Colmo and L776, had low seed dry weight. The highest difference in SPC and SDW between the uppermost and the lowest nodes of the main stem were recorded for L833. This difference could be attributed to the combination of three factors during seed filling: the decrease in nitrogen fixation and the seed growth rate, and the slight increase in the duration of seed filling.

Table VI. Seed growth rate of dry matter for six pea genotypes according to nodal position of the seed on the main stem.

Reproductive node number	L765	L776	L833	Colmo	Finale	Solara
	mg seed ⁻¹ degree-day ⁻¹					
1	0.660	0.351	0.734	0.408	0.695	0.678
2	0.579	0.341	0.734	0.416	0.759	0.616
3	0.579	0.347	0.698	0.439	0.731	0.611
4	0.508	0.346	0.720	0.405	0.693	0.552
5	0.557	0.412	0.761	0.435	0.671	0.517
6	0.587	0.374	0.680	0.415	0.690	0.594
7	0.596	0.379	0.610	0.402		0.550
8	0.552	0.370	0.514	0.325		0.512
9	0.516	0.320		0.291		
10				0.239		
Mean	0.570	0.360	0.681	0.378	0.707	0.579

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