Dry matter production and partitioning in potato plants subjected to combined deficiencies of nitrogen, phosphorus and potassium

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(Accepted 17 April 2003; Received 5 November 2002)

Summary

Three experiments examined effects on growth, dry matter partitioning and nutrient uptake in potato plants grown in large pots under different combinations of adequate and deficient levels of nitrogen, phosphorus and potassium. N supply affected the growth of all leaves, with low N reducing both the size of individual leaves and the extent of branch growth. P and K availability affected the growth of later formed leaves and only when both were deficient was branch growth substantially reduced. At later stages of growth, total green leaf area was significantly reduced by deficiency of each of the nutrients. Partitioning of dry matter to tubers was markedly reduced by K deficiency and increased in one experiment by P deficiency. When both P and K were deficient, partitioning approximated that under non-limiting conditions. Leaf weight ratio (LWR) was higher under K deficiency, but not when P was also deficient, and was consistently higher when the ratio of K : P in dry matter was less than approximately five. In these experiments, LWR was not consistently related to shoot N% and N supply had relatively little effect on partitioning. There were large treatment effects on tuber dry matter percentage, characterised by significant interactions especially between N and K. Deficiency of one nutrient increased the concentration of others but uptake was highly regulated as crop content of all three nutrients was reduced when the supply of any one was deficient. The results show that the response of potatoes to single deficiencies may be influenced greatly by the levels of other nutrients.

Key words: Solanum tuberosum, potato, nutrient deficiency, nitrogen, phosphorus, potassium, partitioning

Introduction

Crops grow by intercepting solar radiation and utilising part of the absorbed energy in the process of photosynthesis to create dry matter. Yield depends not only on the total amount of dry matter produced but also on how much is partitioned to the economically useful plant parts. In both of these yield-determining processes, mineral nutrients play a key rôle. Crop cultivars have been selected to optimise the distribution of dry matter in favour of yield formation, and whereas this character shows a high degree of genetic control, environmental factors, including the influence of available mineral nutrients, can perform a significant modulating function (Cakmak & Engels, 1999).

Early-maturing potato cultivars partition a significant amount of dry matter to tubers at relatively low total plant dry weight, thereby allowing crops to be harvested after comparatively short periods of growth. These cultivars are highly determinate in their growth characteristics with the production of new leaves ceasing at a relatively early stage (Allen & Scott, 1992). The ability of external factors to modify partitioning may be limited in such cultivars. For example, there is evidence that nitrogen (N) supply has little effect on the pattern of partitioning in determinate cultivars, in contrast to the situation in more indeterminate types where foliage growth is favoured at the expense of tubers when high levels of fertiliser N are supplied (Harris, 1992). Much less is known about the effects of phosphorus (P) and potassium (K) on partitioning in potatoes. Studies undertaken in other crop plants have shown the potential for marked effects, albeit at low levels of supply (Fredeen et al., 1989; Cakmak et al., 1994). The pattern of partitioning in potatoes is influenced greatly by the presence of the tubers which become very strong sinks for assimilates and any factor that influences the normal pattern of partitioning to tubers would be of considerable significance for yield formation.

Whilst it is recognised that different nutrients may interact in the way they influence crop growth and yield (Marschner, 1995), studies on potatoes have generally considered effects of single elements. Where the potential for interactions has been tested, the focus has been on yield responses in field trials with no detailed measurements of growth (e.g. Archer *et al.*, 1976; Farrar & Boyd, 1976). This study was undertaken to examine how factorial combinations of low and high levels of N, P and K influence dry matter production and partitioning in an early-maturing potato cultivar. The main objective was to examine the extent to which interactions between nutrients might influence these processes and, in order to regulate nutrient supply precisely, the experiments were conducted in sand culture in the glasshouse. An additional objective of the study was to determine whether imbalances in supply of these nutrients might lead to the accumulation of nitrate-N in tubers and other plant parts. These results will be reported in a subsequent paper.

Materials and Methods

Treatments

Three experiments conducted in consecutive years (1995-1997) examined effects on growth, dry matter distribution and nutrient uptake of factorial combinations of two levels each of N, P and K. The levels, generally designated high and low in the text, were chosen on the basis of unpublished work to allow unlimited growth at the high level and a significant limitation to growth at the low level. The potato plants used in the experiments were grown in a fine sand medium in the glasshouse in 20 litre plastic pots provided with deep saucers. A single pot represented one treatment plot. The temperatures were principally in the range 15-25°C and only natural light was provided. Expt 1 was conducted between May and September (107 days), Expt 2 between April and June (69 days), and Expt 3 between March and June (90 days).

Pre-sprouted seed tubers $(80 \pm 10g)$ of cv. Rocket, with longest sprouts of approximately 5 mm, were planted singly into each pot at a depth of 10 cm below the surface of the sand. At an early stage of growth, stems were thinned to leave only three mainstems per plant. P was provided in the form of superphosphate (2.00 g P and 0.20 g P pot⁻¹ at the high and low level respectively) and K in the form of muriate of potash (3.77 g K and 0.38 g K pot⁻¹ respectively), both of which were mixed uniformly into the sand below the level of the seed tuber immediately prior to planting. N was provided in 1 litre solutions of ammonium nitrate applied to the surface of the sand at concentrations of either 8.12 or 4.12 mM for the high and low levels respectively. In Expt 1, applications were made at 15 day intervals from 50% plant emergence for the first six wk and subsequently at weekly intervals. In Expts 2 and 3, applications were made from emergence at weekly intervals. In each experiment, nutrient supplementation ceased between 2 and 3 wk prior to the final harvest. The total amount of N applied at the two levels was, therefore, 1.82 g and 0.92 g pot⁻¹ in each experiment. Other nutrients were

supplied equally to all pots, as solution mixtures together with the N applications, at the following concentrations: $MgSO_4$ 4.99 mM, $CaCl_2$ 2.52 mM, H_3BO_3 0.50 mM, $MnSO_4$ 0.30 mM, MoO_3/H_2MoO_4 0.01 mM, $CoCl_2$ 0.01 mM, $ZnSO_4$ 0.20 mM, $CaCl_2$ 0.01 mM, $CuCl_2$ 0.20 mM, FeEDTA 0.20 mM. The pots were watered on a regular basis when required by application directly into the saucers.

Expts 1 and 2 comprised eight treatments, representing all combinations of low and high levels of N, P and K, arranged in a randomised complete block design with six replications. A single destructive harvest was taken 92 days after 50% plant emergence in Expt 1 and 58 days after emergence in Expt 2. In Expt 3, there were four treatments comprising all combinations of low and high N and K, each provided with the high level of P. In each block of this experiment there were three pots per treatment combination, one of which was sampled at each of the three harvests, viz. 45, 57 and 79 days after 50% plant emergence. The design was a randomised complete block with five replications. In each experiment, the pots were arranged within blocks at 40 cm centres and rerandomised weekly. The treatments are indicated in the text by combinations of H and L (signifying high or low levels respectively of the particular nutrient) and presented in the order N-P-K; e.g. HLH signifies high N and K and low P.

Measurements

From soon after plant emergence, the total number of unfolded leaves and the length of selected leaves were assessed once or twice weekly. Leaves were numbered in ascending order from the base of the above-ground stem upwards so that, for example, leaf four on the main stem was the fourth visible leaf to appear. Similarly, on apical branches, the numbering proceeded in ascending order from the first leaf to appear. Leaf areas were derived from leaf lengths using relationships established at harvest in Expt 2 where 20 leaves from each treatment were sampled and their lengths regressed against their areas measured with a leaf area meter (Delta-T Ltd, Cambridge, UK) (Table 1). The chlorophyll content of the terminal leaflets of selected leaves was measured in Expts 1 and 2 using a calibrated SPAD meter (Minolta Ltd, Osaka, Japan). The calibration had been performed previously on potato leaves following extraction of chlorophyll in the dark in acetone with absorbance measured at 647 and 664 nm

At harvest, after removal from the pots, the roots were extracted from the sand by washing, and the plants were divided into green leaves, senesced leaves, above-ground stems plus branches, belowground stems plus stolons, roots and tubers. Total area of green leaves was assessed and all parts were dried at 80°C for 48 h. The numbers, fresh weight and dry matter percentage of tubers were also assessed. After weighing, the dried samples were analysed for N, P and K content using standard colorimetric procedures as described by Faithfull (1971).

Table 1. Relationships used to derive leaf area (y, cm²) from leaf length (x, cm) under different combinations of low (L) and high (H) levels of N, P and K

Treatment (N-P-K)	Equation	R ²
LLL	$y = 0.206x^{2.146}$	0.96
LLH	$y = 0.145x^{2.234}$	0.93
LHL	$y = 0.157 x^{2.213}$	0.95
LHH	$y = 0.169x^{2.156}$	0.98
HLL	$y = 0.348x^{1.969}$	0.96
HLH	$y = 0.082x^{2.429}$	0.97
ΗΗL	$y = 0.569 x^{1.807}$	0.88
HHH	$y = 0.239x^{2.063}$	0.93

Results

Leaf growth

The detailed leaf measurements made in Expt 1 are summarised in Tables 2 and 3 as mean values per stem. The mean number of above-ground leaves on the main stem axis, i.e. below the first flower, was $13.9 (\pm 0.12)$ and was not influenced significantly by treatments. However, other aspects of leaf production showed considerable sensitivity to nutrient supply. The growth of the earlier formed leaves (e.g. numbers 4 and 6) was influenced primarily by N supply, as indicated by the maximum area achieved, with overall means for high and low N of 144.3 and 107.3 for leaf 4 and the corresponding values for leaf 6 were 173.0 and 133.6. The growth of these leaves was not influenced significantly by P or K supply. The higher N level also resulted in consistently larger leaf areas of the later formed leaves but, in addition, effects of K supply were apparent on the growth of leaves 10 and 12. All comparisons of high K with the corresponding low K treatment indicated a restriction in the generation of leaf area as a consequence of inadequate K. P

Table 2. Effects of combinations of low (L) and high (H) levels of N, P and K on the maximum area (cm^2) of leaves on the main stem axis and on two leaves on the principal apical branch (Expt 1). Transformed data (ln (x+1)) in parentheses

Treatment		Ma	Apical branch leaf number				
combinations (N-P-K)	4	6	8	10	12	1	3
LLL	105.7	130.1	127.5	93.4	48.1	18.0 (1.4)	2.4 (0.7)
LLH	133.5	156.8	139.0	109.8	61.3	18.5 (2.2)	5.0 (1.4)
LHL	98.5	122.1	96.3	75.5	39.8	15.5 (1.6)	5.9 (1.2)
LHH	91.3	125.6	119.4	104.4	59.9	24.6 (2.7)	7.9 (1.7)
HLL	132.1	166.3	183.2	121.4	88.0	4.3 (0.7)	1.5 (0.5)
HLH	140.2	188.7	199.2	162.7	120.1	67.6 (4.2)	14.5 (2.3)
HHL	155.9	156.0	153.9	116.1	90.6	60.0 (4.1)	38.0 (3.6)
ННН	149.1	181.1	169.5	170.0	128.7	90.4 (4.4)	56.8 (3.9)
SE	13.05	13.28	15.78	12.26	11.01	(0.49)	(0.39)
(df = 35)							
Treatment main effects							
low N	107.3	133.6	120.5	95.8	52.3	19.2 (2.0)	5.3 (1.2)
high N	144.3	173.0	176.5	142.5	106.8	55.6 (3.3)	27.7 (2.6)
low P	127.9	160.5	162.2	121.8	79.4	27.1 (2.1)	5.9 (1.2)
high P	123.7	146.2	134.8	116.5	79.8	47.6 (3.2)	27.2 (2.6)
low K	123.0	143.6	140.2	101.6	66.6	24.4 (2.0)	12.0 (1.5)
high K	128.5	163.1	156.8	136.7	92.5	50.3 (3.4)	21.1 (2.3)
SE (df = 35)	6.53	6.64	7.89	6.13	5.51	(0.24)	(0.20)

supply did not affect the area of leaves on the main stem axis and neither were there any significant interactions between nutrients in relation to the area of these leaves.

Plants in all treatments produced a certain amount of branch growth, both apical and basal, after flower appearance on the main axis. The extent of branch growth varied considerably between treatments and was restricted by deficiency of all three nutrients. A deficiency of either P or K had a relatively small effect on the number of apical branches, but when both were deficient (i.e. HLL), apical branching was severely restricted not only in terms of the number of branches but also in terms of the number of leaves on these branches and their size. Thus, the lower level of either P or K limited the area of the apical branch leaves but when both were deficient very little expansion of these leaves occurred. There were also large effects of N supply on all aspects of branch growth with the higher level of supply increasing significantly the number of apical branches, the number of leaves on these branches and their

Table 3. Effects of combinations of low (L) and high (H) levels of N, P and K on the mean number of apical branches stem⁻¹, total number of leaves on apical branches, mean number of basal branches stem⁻¹, total number of leaves on basal branches (Expt 1). Transformed data (ln(x+1)) in parentheses

Treatment	Apica	l branches	Basal	branches
(N-P-K)	Number	Leaf number	Number	Leaf number
LLL	1.2 (0.7)	3.9 (1.4)	0.7 (0.5)	2.5 (1.0)
LLH	2.4 (1.2)	8.1 (2.2)	1.5 (0.9)	5.1 (1.7)
LHL	2.4 (1.2)	9.7 (2.3)	0.6 (0.4)	1.8 (0.8)
LHH	2.8 (1.3)	11.2 (2.5)	1.7 (0.9)	5.3 (1.8)
HLL	0.7 (0.4)	3.3 (0.8)	1.3 (0.8)	4.2 (1.6)
ΗLΗ	3.0 (1.4)	12.0 (2.5)	2.0 (1.1)	6.6 (2.0)
ΗΗL	3.3 (1.5)	18.4 (2.9)	2.6 (1.2)	8.9 (2.2)
ННН	3.7 (1.5)	16.4 (2.8)	3.7 (1.5)	14.6 (2.7)
SE	(0.12)	(0.23)	(0.12)	(0.21)
(df = 35)				
Treatment main effects				
low N	2.2 (1.1)	8.2 (2.1)	1.1 (0.7)	3.7 (1.3)
high N	2.7 (1.2)	12.5 (2.3)	2.4 (1.2)	8.6 (2.1)
low P	1.8 (0.9)	6.8 (1.7)	1.4 (0.8)	4.6 (1.6)
high P	3.0 (1.4)	13.9 (2.6)	2.1 (1.0)	7.6 (1.9)
low K	1.9 (0.9)	8.8 (1.8)	1.3 (0.7)	4.4 (1.4)
high K	3.0 (1.4)	11.9 (2.5)	2.2 (1.1)	7.9 (2.1)
SE	(0.06)	(0.12)	(0.06)	(0.10)

(df = 35)

individual size. Basal branches formed in the axils of the first four above-ground leaves (Table 3). Whilst very few appeared in LLL and LHL, it is clear that the potential number of basal branches was not achieved when any of the nutrients was present at the lower level of supply. The total number of leaves on basal branches varied considerably between treatments but correlated closely with the number of branches (r = 0.99, P < 0.001). Thus, in the control (HHH), a substantial amount of leaf was produced on the basal branches but this was limited to varying degrees in all other treatments.

At the time plants were sampled in Expt 2 there remained a substantial amount of green leaf and senescence was limited. This was also the case at the first two harvests in Expt 3, and therefore, in both experiments, total green leaf area per plant was determined. Single deficiencies of any one of the nutrients resulted in large reductions in leaf area (Table 4), the largest effect being shown by the low N levels. There were significant interactions between N and K in both experiments (P < 0.05) resulting from the relatively larger effect of low K in depressing leaf area under the conditions of higher N supply. In Expt 3, the suppressive effect of low K

Table 4. <i>Effects of combinations of low (L) and high</i>
(H) levels of N, P and K on the total green leaf area
$(cm^2 plant^1)$ in Expt 2 (58 days after emergence) and
in Expt 3 (45 days (S1) and 57 days (S2) after
emergence)

Treatment combinations	Expt 2	Ext	Expt 3			
(N-P-K)	F.	S 1	S 2			
LLL	2636	-	-			
LLH	3042	-	-			
LHL	3233	2653	1390			
LHH	3436	2728	1806			
HLL	3688	-	-			
HLH	4410	-	-			
HHL	4084	4350	2395			
ННН	5478	5232	3467			
SE (df = 35, Expt 2)	218.7	187.9	139.5			
(df = 12, Expt 3)						
Treatment main effects						
low N	3087	2691	1598			
high N	4415	4791	2931			
low P	3444					
high P	4058					
low K	3410	3502	1892			
high K	4091	3980	2636			
SE (df = 35, Expt 2) (df = 12, Expt 3)	109.3	132.8	98.6			

on leaf area appeared to become greater in the twelve days between harvests 1 and 2. For example, the single deficiency of K reduced leaf area by 17% at harvest 1 but by 31% at harvest 2 suggesting that the leaf senescence, apparent in all treatments at this time, occurred more rapidly under low K conditions compared with the control (HHH). By contrast, low N (LHH) reduced leaf area by 48% at both harvests.

Data were collected in Expts 1 and 2 on the chlorophyll concentration of individual leaves, and results for leaf 6 are presented to demonstrate the principal trends (Fig. 1). For much of the period of active growth of this leaf, the highest chlorophyll concentrations were found in the treatments deficient in K alone (HHL) or in both P and K (HLL). Maximum area of leaf 6 in all treatments occurred approximately 46 days after 50% plant emergence in Expt 1 and after approximately 42 days in Expt 2, and in most cases the chlorophyll content declined rapidly after this time. The rate of decline at these later stages of the leaf's growth was least rapid in HHH so that when the final measurements were made, 60 days after plant emergence in Expt 1 and after 54 days in Expt 2, HHH still retained a substantial amount of chlorophyll.



Fig. 1. Effect of combinations of low (L) and high (H) levels of N, P and K on the chlorophyll concentration (μ g cm⁻²) of leaf number 6 ((a) Expt 1, (b) Expt 2). Bar = SE (df = 35). LLL = O; LLH = \Box ; LHL = Δ ; LHH = \Diamond ; HLL

 $= \mathbf{O};$ HLH $= \mathbf{I};$ HHL $= \mathbf{A};$ HHH $= \mathbf{O}.$

Dry matter production

Different levels of dry matter were produced in the three experiments, at least partly as a consequence of different duration of growth from emergence to harvest, but these differences were apparent mainly in the treatment receiving adequate amounts of all three nutrients, i.e. HHH (Figs 2, 3 & 4). Where one or more of the nutrients were provided at a lower level, dry matter production was significantly reduced (P < 0.01), nevertheless, substantial growth was achieved in all treatments together with full development and tuber formation. Deficiency in P alone (HLH) reduced dry weight by 33% in Expt 1 and by 16% in Expt 2. For K, the single deficiency reduced dry weight by 45% and by 33% in Expts 1 and 2 respectively, while in Expt 3, the effect increased with delay in harvest from 21% at 45 days from emergence to 31% at 57 days and 58% at final harvest, 79 days after emergence. In HLL, the combined deficiencies of P and K were clearly not additive, and in both Expts 1 and 2, dry matter production in this treatment did not differ significantly from HHL.

The lower level of N also resulted in dramatic decreases in dry weight. For example, in LHH, dry matter production was 49% less than in HHH in Expt 1 and a similar reduction occurred at final harvest in Expt 3. The corresponding figure for Expt 2 was 29%. The treatments receiving the lower level of N showed a much smaller range of total dry weights than the corresponding high N treatments.

Although terminated after different periods of



Fig. 2. Effect of combinations of low (L) and high (H) levels of N, P and K on the dry weights (g plant⁻¹) of tubers, senesced leaves, green leaves, below-ground stems, above-ground stems plus branches, and roots (Expt 1). SE for total dry weight plant⁻¹ = 2.904 (df = 35).

Black = tubers; stripes = dead leaves; dark grey = green leaves; mid-grey = below-ground stem; light grey = above-ground stem; unshaded = roots. growth, tubers constituted at least 68% of total dry weight by the time of final harvest in each experiment. In Expt 1, leaf senescence was well advanced by this time, especially in LLL, LHL and HLL where very little green leaf was present. By contrast in Expt 2, a substantial amount of green leaf was still present at harvest, with HHL and HHH giving very similar amounts. Although there was little leaf senescence in Expt 3 at the first two harvests, by the final harvest very little green leaf remained in LHL, LHH and HHL.

Dry matter distribution Harvest index (HI)

This is defined here as the tuber dry weight expressed as a proportion of total plant dry weight. The general trend was for deficiency of N and P to increase HI while it was reduced by low K levels (Table 5). However, the largest effect, seen in each experiment, was produced by the single deficiency of K which gave a markedly lower HI in comparison with all other nutrient combinations, indicating a substantial reduction in the amount of dry matter partitioned to tubers in this treatment. This was apparent at both low and high levels of N supply but the effect was relatively greater in the latter. In Expt 2, the single deficiency of P resulted in a significant increase in HI compared with HHH (P <0.01) but when both P and K were deficient (i.e. in treatment HLL), the pattern of partitioning to tubers reverted to that demonstrated by HHH. Similarly, in Expt 1, HLL did not differ significantly from HHH. When all three nutrients were supplied at the lower



Fig. 3. Effect of combinations of low (L) and high (H) levels of N, P and K on the dry weights (g plant⁻¹) of tubers, leaves, below-ground stems, above-ground stems plus branches, and roots (Expt 2). SE for total dry weight plant⁻¹ = 4.369 (df = 35).

Black = tubers; dark grey = green leaves; midgrey = below-ground stem; light grey = aboveground stem; unshaded = roots. level the resulting HI was also very similar to that of the control.

Leaf weight ratio (LWR)

This is defined here as leaf weight expressed as a proportion of total plant dry weight. The most pronounced effect in each experiment was again the different pattern of partitioning shown by HHL in which significantly more dry matter was retained in leaves compared with all other treatments (P < 0.01; Table 5). In Expt 3, this effect was apparent by the time of the first harvest (data not presented). A similar trend was seen in LHL but the effect was much smaller. In Expt 2, the combined deficiency of P and K in HLL produced a pattern of partitioning to leaves identical to that of the control and therefore markedly different from where only K was deficient. This was not apparent to the same extent in Expt 1 although, even in this experiment, LWR in HLL was



Fig. 4. Effect of combinations of low (L) and high (H) levels of N, P and K on the dry weights (g plant⁻¹) of tubers, senesced leaves, green leaves, stems (above and below-ground), and roots sampled 45 (a), 57 (b) and 79 (c) days after 50% emergence (Expt 3). SEs for total dry weight plant⁻¹ = (a) 3.055, (b) 5.507, (c) 3.772 (df = 12). Black = tubers; stripes = dead leaves; dark grey = green leaves; light grey = stem; unshaded = roots.

markedly lower than that of HHL. N supplied at the higher level also increased LWR significantly in each experiment (P < 0.001) although the degree of response depended on the level of the other nutrients. The positive response to N was greater at the high level of P and at the low level of K. Most of the interactions involving K were influenced greatly, however, by the very marked response in HHL noted above.

Root dry weight fraction (RDWF)

By final harvest, root weight accounted for less than approx. 3% of total plant dry weight (Table 5). Despite the relatively high SEs significant treatment differences occurred, although the effects were not consistent across all experiments. In Expt 1, the general trend was towards lower RDWF where K was deficient but, in Expt 2, this was only apparent in HHL. In contrast, the main effect in Expt 3 was a higher RDWF in the low N treatments and K supply showed no significant effect.

Specific leaf area (SLA)

Data were available from Expts 2 and 3 (harvest 2) to calculate SLA, i.e. leaf area per unit leaf dry

weight (Table 5). The measurements are assumed to indicate the relative thickness of leaves, i.e. higher values suggesting thinner leaves, but differences in tissue density could also be involved. Only green leaves were used in calculations. Low levels of K reduced SLA significantly in both experiments (P <0.001) while the overall effect of low P in Expt 2 was to increase SLA significantly (P < 0.01). In Expt 2, the combined deficiency of P and K (HLL) resulted in a SLA intermediate in value between that of the single deficiencies and not significantly different from that of the control. N level had no significant effect on SLA in these experiments.

Tuber production

Total tuber numbers

The number of tubers produced varied considerably between experiments (Table 6). The relatively low numbers in Expt 1 were associated with an absence of any significant treatment effects but such effects were apparent in Expt 2 where almost double the number of tubers were recorded and both N and K increased numbers when applied at the higher level. In this experiment, the lowest numbers were produced when K alone was deficient.

Table 5. Effects of combinations of low (L) and high (H) levels of N, P and K on harvest index (HI), leaf weight ratio (LWR), root dry weight fraction (root dry weight/total dry weight) and specific leaf area $(cm^2 g^{-1})$ assessed 92 (Expt 1), 58 (Expt 2) and 79 (Expt 3) days after emergence

Treatment		HI			LWR			Root dry wt fraction			Specific leaf area	
(N-P-K)	Expt 1	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3	Expt 2	Expt 3^{\dagger}	
LLL	0.78	0.80	-	0.16	0.14	-	0.016	0.029	-	236.8	-	
LLH	0.79	0.83	-	0.14	0.12	-	0.021	0.026	-	282.8	-	
LHL	0.76	0.77	0.75	0.18	0.17	0.18	0.021	0.026	0.022	220.2	124.9	
LHH	0.78	0.83	0.83	0.14	0.12	0.11	0.020	0.031	0.020	296.8	159.8	
HLL	0.78	0.80	-	0.17	0.15	-	0.015	0.030	-	251.9	-	
HLH	0.78	0.83	-	0.15	0.12	-	0.021	0.024	-	299.4	-	
HHL	0.69	0.72	0.68	0.24	0.23	0.24	0.016	0.022	0.016	190.1	129.3	
ННН	0.80	0.80	0.83	0.13	0.15	0.12	0.020	0.029	0.014	267.4	159.1	
SE	0.010	0.007	0.011	0.006	0.006	0.008	0.0019	0.0025	0.0020	13.04	5.81	
(df = 35, Expts 1)	,2; df = 12, 12	Expt 3)										

Treatment HI				LWR			Root dry wt fraction			Specific leaf area	
main effects	Expt 1	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3	Expt 1	Expt 2	Expt 3	Êxpt 2	Expt 3 ⁺
low N	0.78	0.81	0.79	0.15	0.14	0.14	0.020	0.028	0.021	259.2	142.4
high N	0.76	0.79	0.75	0.17	0.16	0.18	0.018	0.026	0.015	252.2	144. 2
low P	0.78	0.81		0.16	0.13		0.018	0.027		267.7	
high P	0.76	0.78		0.17	0.17		0.019	0.027		243.6	
low K	0.75	0.77	0.71	0.19	0.17	0.21	0.017	0.027	0.019	224.8	127.1
high K	0.79	0.82	0.83	0.14	0.13	0.11	0.021	0.027	0.017	286.6	159.5
SE	0.005	0.004	0.008	0.003	0.003	0.006	0.0009	0.0013	0.0014	6.52	4.11
(df = 35, Expts 1,2	; $df = 12$,	Expt 3)									

[†] Assessed 57 days after emergence

However, when both K and P were deficient (HLL), significantly more tubers were produced (P < 0.01), resulting in total number not significantly different from the control. In this experiment, the beneficial effect of the higher level of either N or K on numbers was greater when the other nutrient was also applied at the higher level, resulting in a significant $N \times K$ interaction (P < 0.05). A similar interaction was also apparent in Expt 3 at the final harvest (Table 7). The level of P had no overall effect. The successive harvests in Expt 3 enabled treatment effects to be monitored over time. In the control (HHH), numbers remained relatively constant in the period of 34 days between the three harvests, whereas in other treatments, numbers declined markedly. Although treatment differences were not apparent at the first two harvests, large effects were seen at the final harvest with the deficiencies of N and K, both singly and in combination, producing similar numbers of tubers and substantially fewer than the control. From the first two harvests, it appears that initiation of tubers was not greatly influenced by nutrient level, but reabsorption of some tubers was a significant feature under conditions of inadequate nutrient

sampled 92 days (Expt 1), 58 days (Expt 2) and 45, 57, and 79 days (S 1-3 respectively; Expt 3), after emergence Treatment Expt 1 Expt 2 Expt 3 combinations (N-P-K) S2 **S**1 **S**3 LLL 8.8 21.3 _ 9.5 LLH 21.0 LHL 9.7 20.2 15.8 15.4 8.6 LHH 11.5 21.3 16.2 16.0 10.2 HLL 9.5 25.2 HLH 27.3 11.0 8.2 HHL 10.8 17.8 16.8 16.6 ННН 11.2 27.5 18.4 18.0 20.6 1.59 1.00 1.12 1.32 2.18 SE (df = 35, Expts 1,2; df = 12, Expt 3) Treatment main effects low N 9.9 16.0 9.4 21.0 15.7 high N 10.6 24.5 17.6 17.3 14.4 low P 9.7 237 high P 10.8 21.7 low K 9.7 211 16.3 16.0 8.4 high K 10.8 24.3 17.3 17.0 15.4 0.56 0.79 0.93 1.54 0.71 SE (df = 35, Expts 1, 2; df = 12, Expt 3)

Table 6. Effects of combinations of low (L) and high (H) levels of N, P and K on total tuber numbers plant⁻¹

Table 7. Significance of main effects and interactions for total tuber number and tuber dry matter percentage

	Total tuber number						Tuber dry matter %				
	Expt 1	Expt 2 Expt 3			Expt 1	Expt 2		Expt 3			
			S 1	S2	S3			S1	S2	S3	
N	ns	<i>P</i> < 0.01	ns	ns	<i>P</i> < 0.001	ns	<i>P</i> < 0.001	ns	<i>P</i> < 0.05	ns	
Р	ns	ns	-	-	-	P < 0.01	ns	-	-	-	
Κ	ns	P < 0.01	ns	ns	P < 0.001	P < 0.001	ns	P < 0.01	ns	ns	
N×P	ns	ns	-	-	-	ns	P < 0.05	-	-	-	
N×K	ns	P < 0.05	ns	ns	P < 0.001	P < 0.05	P < 0.001	ns	ns	P < 0.05	
P×K	ns	ns	-	-	-	ns	P < 0.001	-	-	-	
N×P×K	ns	ns	-	-	-	ns	ns	-	-	-	

ns = not significant

supply.

Tuber fresh weight

Tuber yield was generally much greater when all three nutrients were supplied at the higher level (Table 8). A single deficiency of K (HHL) reduced yield by 52% and 34% in Expts 1 and 2 respectively and by 63% at final harvest in Expt 3. These reductions were thus slightly greater than for total dry weight. The corresponding figures for a single N deficiency (LHH) showed reductions of 47%, 26% and 44% for Expts 1 to 3 respectively, slightly smaller than those for total dry weight. Effects of P deficiency were smaller but still substantial in Expt 1 (30% yield reduction in HLH) but were nonsignificant in Expt 2. When seen in combination, the effects of nutrient deficiency were clearly nonadditive, nevertheless, the smallest yields were obtained when both N and K were deficient. In Expt 3, substantial yield increases occurred in the control between successive harvests, whereas the other treatments showed much slower rates of tuber growth and in HHL no yield increase occurred after 57 days post-emergence.

Tuber dry matter percentage (TDM%)

This measure of dry matter concentration is an

important determinant of tuber quality and, therefore, of considerable practical significance. The effects of the different nutrient regimes were to produce considerable variability in TDM% suggesting complex interactions between individual nutrients and levels of supply (Tables 7 and 9). In Expt 1, the low level of P produced a lower TDM% overall but interactions involving P were not significant. In Expt 2, there was a general trend for the low level of N to produce a higher TDM% but only at the high level of P and at the low level of K, the latter effect also being found in Expt 3. Effects of K were quite variable across experiments. In Expt 1, the higher level of K decreased TDM% overall but not when both N and P were provided at the higher level. In Expt 2, although there was no significant effect of K overall, a significant interaction occurred with P (P < 0.001) whereby the higher K level reduced TDM% at low P level but not at high P (Table 7). It is clear from Expt 3, however, that the relative differences between treatments changed at successive harvests. Thus, at the first harvest, HHL and LHL showed significantly greater values than HHH and LHH respectively (P < 0.05), whereas at the second the corresponding differences were not significant. At the final harvest, the limited supply of K in HHL gave the lowest TDM% but, when both

Table 8. Effects of combinations of low (L) and high	n (H) levels of N, P and I	K on total tuber fresh weight (g plant ¹)
sampled 92 days (Expt 1), 58 days (Expt 2) and 45,	, 57, and 79 days (S 1-3	respectively; Expt 3), after emergence

Treatment combinations	Expt 1	Expt 2		Expt 3	
(N-P-K)			S 1	S2	S3
LLL	282.2	349.0	-	-	-
LLH	351.6	448.4	-	-	-
LHL	275.8	350.7	158.8	222.0	270.4
LHH	370.2	465.0	185.4	331.2	477.9
HLL	348.5	448.8	-	-	-
HLH	489.9	586.9	-	-	-
HHL	338.1	417.8	187.4	318.0	317.2
ННН	701.2	629.0	282.8	501.7	859.4
SE	14.48	17.76	14.06	21.79	19.45
(df = 35, Expts 1,2; df =1 2, E	(xpt 3)				
Treatment main effects					
low N	320.0	403.3	172.1	276.6	374.2
high N	469.4	520.6	235.1	409.8	588.3
low P	368.1	458.3			
high P	421.3	465.6			
low K	311.1	391.6	173.1	270.0	293.8
high K	478.2	532.3	234.1	416.5	668.7
SE	7.24	8.88	9.94	15.40	13.76
(df = 35, Expts 1,2; df = 12, E	(xpt 3)				

N and K were deficient (i.e. LHL), the TDM% was significantly higher (P < 0.05).

Plant nutrient content

As expected, there was a general trend for the higher supply level of a nutrient to result in a higher tissue concentration for that nutrient and a higher uptake level (Table 10). The only exceptions were seen in Expts 1 and 3 in the comparison between HHH and LHH in which N% was very similar. There was also a general trend for deficiency in one nutrient to lead to a higher concentration of the other two nutrients. However, effects on nutrient uptake were more complicated (Table 11). For example, a deficiency of P or K reduced N uptake but only when N was supplied at the higher level. Similarly, at high N and P levels, P uptake was markedly reduced when K was deficient but at low levels of N and/or P, K deficiency had little effect on P uptake, at least in Expts 1 and 2. The general response, therefore, was for uptake of nutrient *x* to be reduced by deficiency of nutrient y but only when x was provided at the higher level. A growth restriction imposed by the deficiency of any one nutrient limited the uptake of not only that nutrient but also both other nutrients if they were being provided at the higher supply level. The results demonstrate a highly regulated system

controlling uptake of nutrients.

The treatment combinations produced wide variations in the ratios of N:P:K in total dry matter. In view of the interactive effects of P and K supply found on dry matter partitioning in these experiments, relationships were examined between K:P ratios (derived from K and P percentages in total dry matter) and measurements of partitioning. Fig. 5 illustrates the relationship between LWR and K:P ratio. The highest values for LWR were associated with K:P ratios of < 5, whereas at higher values there was no consistent relationship between the two variables. Correlation analysis was also employed to test the association between LWR and N% in above-ground (i.e. haulm) dry matter. There was a significant positive correlation in Expt 1 (r = 0.89, P < 0.01) but the relationship was influenced greatly by the values for HHL so that when this treatment was removed from the analysis the correlation was no longer significant. A significant correlation was found between these two variables at the final harvest of Expt 3 (r = 0.99, P < 0.01) but not at the first two harvests or in Expt 2.

Discussion

Growth of crop plants can be analysed in terms of

Treatment combinations	Expt 1	Expt 2		Expt 3	
(N-P-K)		•	S1	\$2	S3
LLL	18.0	18.2	-	-	-
LLH	16.3	16.6	-	-	-
LHL	19.0	18.6	16.4	17.9	18.6
LHH	17.4	17.8	15.3	17.1	17.7
HLL	18.1	17.4	-	-	-
HLH	17.0	16.8	-	-	-
HHL	17.8	16.1	16.0	16.8	17.2
ННН	18.2	17.9	14.8	16.3	18.4
SE	0.39	0.28	0.29	0.34	0.38
(df = 35, Expts 1,2; df = 12, E	Expt 3)				
Treatment main effects					
low N	17.7	17.8	15.8	17.5	18.1
high N	17.8	17.1	15.4	16.6	17.8
low P	17.4	17.2			
high P	18.1	17.6			
low K	18.2	17.6	16.2	17.3	17.9
high K	17.2	17.3	15.1	16.7	18.1
SE	0.19	0.14	0.20	0.24	0.27
(df = 35, Expts 1,2; df = 12, E	Expt 3)				

Table 9. Effects of combinations of low (L) and high (H) levels of N, P and K on tuber dry matter percentage 92 days (Expt 1), 58 days (Expt 2) and 45, 57, and 79 days (S 1-3 respectively; Expt 3), after emergence

their capacity to intercept solar radiation, their efficiency in converting intercepted radiation into dry matter and the distribution of the latter between the range of competing plant sinks. In potatoes, additional factors such as the number of tubers produced and tuber dry matter percentage need also to be considered. The way these factors respond to nutrient supply, especially N, has been the subject of numerous investigations but the effect of interactions between nutrients, the subject of this article, has not been reported extensively. Effects on light use efficiency were not included in this study and deserve investigation.

In the work reported here, the capacity of plants to intercept solar radiation would have been limited to varying degrees in all treatments where at least one of the nutrients was present at the lower level. Expt 1 showed that the area of all leaves was reduced by low N supply, as noted by Vos & Biemond (1992), but only the later formed leaves, including those on branches, were affected by K and P supply. However, the data on total green leaf area recorded in Expts 2 and 3 indicated the potential of all nutrients to reduce substantially the photosynthetic leaf area when provided at sub-optimal levels. Higher concentrations of chlorophyll were found under conditions of low P and K supply. Rao & Terry (1989) noted that under P deficiency sugar beet leaves were markedly greener, the explanation being that chloroplast and chlorophyll production are influenced less than leaf expansion under these conditions. The limited data on chlorophyll concentration also point to a more rapid loss of chlorophyll under conditions of P and K deficiency, which would result in more rapid senescence of green leaves and lower total green leaf area at later stages of growth. The recycling of P and K from older leaves to sustain the growth of younger leaves would have lead to a premature loss of physiological functioning and early senescence (Marschner, 1995). Very few studies on potatoes have examined in detail the effect of P or K supply on leaf growth although those of Watson & Wilson (1956) and Dyson & Watson (1971) suggest a marked sensitivity of leaf growth to supply of these nutrients. Jenkins & Ali (1999) demonstrated the potential for large reductions in total leaf area at low P levels in field grown plants but the response was affected substantially by the cultivar type with earliermaturing and more determinate types showing the

 Table 10. Effects of combinations of low (L) and high (H) levels of N, P and K on the concentration of nutrients in total dry matter

Treatment	N%				Р%			К%		
Combinations (N-P-K)	Expt 1	Expt 2	Expt 3^{\dagger}	Expt 1	Expt 2	Expt 3^{\dagger}	Expt 1	Expt 2	Expt 3 [†]	
LLL	1.45	1.29	-	0.15	0.17	-	1.59	1.44	-	
LLH	1.34	1.17	-	0.13	0.14	-	2.94	3.32	-	
LHL	1.48	1.39	1.47	0.33	0.37	0.40	1.52	1.45	1.50	
LHH	1.32	1.16	1.06	0.28	0.30	0.34	2.88	2.94	2.96	
HLL	1.74	1.71	-	0.13	0.15	-	1.48	1.33	-	
HLH	1.50	1.39	-	0.10	0.11	-	2.91	3.15	-	
HHL	1.93	1.85	1.94	0.34	0.36	0.42	1.27	1.24	1.21	
ННН	1.34	1.37	1.06	0.26	0.29	0.32	2.18	2.70	2.18	
SE (df = 35, Expts 1,2	0.045 2; df = 12, E	0.039 xpt 3)	0.028	0.006	0.006	0.016	0.098	0.093	0.100	
Treatment main effects										
low N	1.40	1.25	1.26	0.22	0.25	0.37	2.23	2.29	2.23	
high N	1.63	1.58	1.50	0.21	0.23	0.37	1.96	2.11	1.69	
low P	1.51	1.39		0.13	0.14		2.23	2.31		
high P	1.52	1.44		0.30	0.33		1.96	2.08		
low K	1.65	1.56	1.71	0.24	0.26	0.41	1.46	1.37	1.36	
high K	1.38	1.27	1.06	0.19	0.21	0.33	2.73	3.03	2.57	
SE	0.023	0.019	0.020	0.003	0.003	0.011	0.049	0.047	0.071	
(df = 35, Expts 1, 2)	$2; df = 12, E_2$	xpt 3)								

[†] At final harvest

largest reductions in leaf canopy size. Work on other crops has also concluded that leaf growth is very sensitive to P supply (e.g. Mollier & Pellerin, 1999).



Fig. 5. Relationship between leaf weight ratio (LWR) and K:P ratio in Expts 1, 2 and 3 (final harvest). Expt $1 = \blacklozenge$; Expt $2 = \blacksquare$; Expt $3 = \blacktriangle$.

Some of the largest interactions between treatments were for branch growth. Branch growth was markedly affected by N supply, as seen in many other studies (Millard & MacKerron, 1986; Vos & Biemond, 1992), but the single deficiency of P or K had only a small effect on the number of apical branches. However, when both P and K were deficient, growth of apical branches was largely inhibited. This was not simply related to N uptake as the treatments receiving low N took up less N than HLL but still produced more branches. The inherent capacity to continue leaf growth on branches is limited in an early-maturing cultivar such as that used in this study. Later-maturing types with greater potential for the continuation of leaf production on branches may respond differently.

In potatoes, most studies on the effect of nutrients on dry-matter partitioning have focused on nitrogen, the increased supply of which may, depending on maturity type, produce preferential enhancement of foliage growth at the temporary expense of tubers (Harris, 1992). This emphasis on nitrogen is understandable as this is the nutrient that has the largest effect on growth and is the one most likely to be deficient. In the work reported here, however,

Table 11. Effects of combinations of low (L) and high (H) levels of N, P and K on total nutrient uptake (g plant¹)

Treatment	Ν			Р			К		
(N-P-K)	Expt 1	Expt 2	Expt 3^{\dagger}	Expt 1	Expt 2	Expt 3^{\dagger}	Expt 1	Expt 2	Expt 3^{\dagger}
LLL	0.94	1.02	-	0.10	0.14	-	1.03	1.14	-
LLH	0.96	1.04	-	0.09	0.13	-	2.13	2.96	-
LHL	1.01	1.17	0.99	0.22	0.31	0.26	1.04	1.23	0.99
LHH	1.08	1.16	1.08	0.23	0.30	0.36	2.35	2.92	3.12
HLL	1.42	1.68	-	0.10	0.15	-	1.21	1.31	-
ΗLΗ	1.61	1.64	-	0.11	0.13	-	3.12	3.73	-
ΗΗL	1.69	1.73	1.57	0.30	0.34	0.34	1.11	1.17	0.98
ННН	2.14	1.92	2.05	0.42	0.41	0.61	3.49	3.78	4.15
SE	0.066	0.043	0.036	0.008	0.009	0.023	0.115	0.093	0.116
(df = 35, Expts 1,	2; $df = 12$, E	xpt 3)							
Treatment main effects									
low N	1.00	1.10	1.04	0.16	0.22	0.31	1.64	2.06	2.06
high N	1.72	1.74	1.81	0.23	0.26	0.48	2.23	2.50	2.56
low P	1.23	1.35		0.10	0.14		1.87	2.29	
high P	1.48	1.49		0.29	0.34		2.00	2.27	
low K	1.27	1.40	1.28	0.18	0.23	0.30	1.10	1.21	0.98
high K	1.45	1.44	1.57	0.21	0.24	0.48	2.77	3.35	3.63
SE	0.033	0.022	0.026	0.004	0.005	0.016	0.057	0.046	0.082
(df = 35, Expts 1,2; df = 12, Expt 3)									

[†] At final harvest

the pattern of distribution of dry-matter was affected to only a small degree by N supply. This may be because the higher N rate was too low to produce significant responses but also may be a consequence of the early-maturing characteristics of the cultivar which, as a determinate type, may have been less liable to perturbations in dry-matter partitioning than more indeterminate cultivars (Harris, 1992). The principal effect on partitioning was seen at low K levels and resulted in a substantial reduction in allocation of dry-matter to tubers (i.e. lower harvest index) with relatively more retained within the foliage. This was seen consistently in each experiment. Pronounced effects of K deficiency on dry matter partitioning have been reported for other species, primarily in studies employing nutrient solutions. The ratio of shoot to root dry matter (S:R) was generally increased under K deficiency, the suggested mechanism being the failure of effective phloem loading of sucrose leading to the retention of carbohydrate in leaves (Cakmak et al., 1994; McDonald et al., 1996). However, Andrews et al. (1999) found no effect on S:R in K-deficient beans (Phaseolus vulgaris), while in wheat, S:R was significantly lower under these conditions.

In the experiments reported here, reduced P supply had smaller effects on partitioning, although in Expt 2, low P resulted in a significantly higher harvest index than the control, indicative of relatively more dry-matter being allocated to tubers. Studies on other species have shown that under low P supply proportionally more dry-matter was allocated to below-ground plant parts (Fredeen et al., 1989; Rufty et al., 1993; Cakmak et al. 1994; Andrews et al. 1999). The likely mechanism in this case is the greater sink strength of below-ground parts under conditions of low P supply which has a very negative effect on leaf growth (Mollier & Pellerin, 1999). Surprisingly, the marked effects of low K on partitioning seen in these potato experiments were not observed when P was also deficient, so that in treatment HLL the harvest index, leaf weight ratio, root dry weight fraction and specific leaf area were generally very similar to the control treatment where each nutrient was supplied at an adequate level. Clearly, the deficiency of either P or K alone produced the opposite response to each other and in combination their individual effects may be cancelled out. However, the ratio of the two may also be important as more normal patterns of partitioning were obtained whenever the ratio of K:P exceeded approximately five. This occurred whenever K was supplied at the higher level or at the lower when P was also deficient. The balance between anions and cations may, therefore, be important in controlling the pattern of allocation. Whatever the mechanism, it is clear that the responses to nutrient deficiency are affected by the levels of other nutrients which may explain some of the apparent inconsistencies in the literature over effects of K deficiency on partitioning.

Studies on N supply have consistently shown positive correlations between S:R and shoot N % which were independent of nutrient effects on overall growth (e.g. Caloin et al., 1980; Andrews, 1993; Paponov et al., 1999). Andrews et al. (1999, 2001) proposed that shoot protein concentration may have a key role in determining S:R under a wide range of environmental conditions and could provide the basis of a mechanism for the effect of a range of different nutrient deficiencies. Shoot protein concentrations were not measured in these experiments but evidence for shoot N concentration influencing the pattern of partitioning between above and below-ground parts is equivocal. The positive correlation in Expt 1 between LWR and shoot N% was largely due to the contribution of HHL which consistently showed an elevated LWR and N% in comparison with other treatments. Although K deficiency consistently increased N%, P% was also increased under these conditions, as the general trend was for deficiency of one nutrient to increase the concentrations of others. No correlation was found in Expt 2 and, in Expt 3, the positive correlation between LWR and shoot N% occurred only at the final harvest whereas a significantly higher LWR was detected under K deficiency even at earlier harvests when shoot N% and LWR were not significantly correlated. As also shown by Andrews et al. (1999, 2001), it seems unlikely that shoot N% had a controlling influence on dry matter distribution. However, if the single deficiencies of K and P had increased and decreased shoot protein concentration, respectively, the possibility of which can be inferred from the studies of Andrews et al. (1999, 2001), then a possible explanation emerges for the patterns of dry matter partitioning observed in these experiments.

Treatment interactions were also found for tuber dry matter percentage, although the effects were not always consistent between experiments. The higher N level produced a significantly lower TDM% in Expt 2 but interacted with K supply in all three experiments. Numerous studies have demonstrated a significant effect of N and K on dry matter concentration. In most cases, increasing N levels decreased the concentration (Yungen et al., 1958; Painter & Augustin, 1976; MacKerron & Davies, 1986), although some investigations failed to demonstrate a response (Millard & Marshall, 1986) or indeed reported an increase following N application (Birch et al., 1967; Gray, 1974). Similarly, increasing K supply is often associated with a depression in TDM% (Kunkel & Holstad, 1972) although the form in which it is applied may influence the response (Dickens et al., 1962; Birch et al., 1967). In most cases, P supply has not been

shown to have a significant effect. Nutrient supply may influence TDM% in two different ways, through effects on tuber growth and the degree of tuber hydration. Jenkins & Nelson (1992) showed that over successive harvests TDM% increased linearly in relation to mean tuber size but the regression coefficient was decreased with increasing N supply. If growth continued significantly longer as a consequence of the extra available N, the final dry matter concentration at harvest could be greater than in those treatments receiving a lower level of N. Therefore, if tuber growth is significantly reduced by an inadequate supply of a particular nutrient the effect at harvest will be reduced dry matter concentration. However, both N and K also influence the water content of cells (Marschner, 1995) so that lower tissue concentrations of these nutrients may be expected to result in lower water content, i.e. higher dry matter percentage, the final outcome thus depending on the interaction of these two opposite effects. The potential exists, therefore, for quite complex interactions where different nutrients are supplied at a range of different levels. For example, in Expt 1, the low K level produced a higher TDM% but not when N and P where applied at the higher level. In Expt 2 and Expt 3, low N gave a higher TDM% at low K but not at high K. Schippers (1968) also provided some evidence for an interaction between N and K supply although less marked than that reported here.

Tuber numbers varied considerably between the three experiments reflecting a sensitivity to a wide range of environmental variables (Wurr et al., 1997). Given that studies on field-grown crops have shown marked responses to P application (Jenkins & Ali, 2000), it was surprising that P showed no effect on numbers in these experiments. It is possible that more tubers were reabsorbed in the high P treatments, as shown by Jenkins & Ali (2000), so that at harvest differences had diminished. Reabsorption of tubers was apparent in Expt 3 indicating an inability to maintain the potential number when either N or K was available at the lower level. Most studies have failed to show a significant effect of N or K level on tuber numbers but both produced large effects in these investigations, at least in Expts 2 and 3

There is a clear need for a better understanding of how nutrients interact to influence growth and partitioning in crop plants. Considerable differences in the patterns of partitioning of dry matter were found in these experiments and further studies are necessary to examine the mechanisms controlling these effects. It is also known that considerable differences exist between potato cultivars in the period over which the initiation, unfolding and expansion of new leaves occur. The type of cultivar used here represents one extreme in which this period is relatively limited. The extent to which the responses found would be replicated by latermaturing cultivars with a more extended period of leaf growth and greater propensity for shifts in partitioning needs to be investigated. These studies need to be extended to the field and should test for interactions at the higher levels of overall nutrient supply that are more usual under normal cultivation practice.

Acknowledgement

The authors acknowledge with gratitude the award of a post-graduate studentship from the Government of Pakistan to Sajjad Mahmood during the tenure of which this work was carried out.

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