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Response of potatoes to N fertilizer: Quantitative relations for components of growth

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Summary Quantitative relationships for key processes influencing N response were derived from measurements of inorganic N in soil, the weights and N contents of foliage and tubers made at intervals during growth of maincrop potatoes in 11 N fertilizer experiments.

Apparent mineralization rates (calculated from measurements of N uptake and inorganic N in the top metre and averaged over the growth period) were remarkably similar from site to site despite wide differences in the textures, water contents and organic matter contents of the soils. They were mostly about 0.78 kg N ha^{-1} m^{-1} d^{-1}.

Inorganic N in the top 50 cm of soil was rapidly removed by the crop until it fell on all sites to a low value (about 4 μg N cm^{-3}) which was maintained for the remainder of the growth period. When N fertilizer was applied, growth rate until at least the end of July was always well defined by a single coefficient in a previously derived equation. Average values of this coefficient for each of the soil types and for each of the years in which the experiments were carried out were within 20% of each other.

The minimum %N in the dry matter needed to permit maximum growth rate declined with increase in plant weight in a similar manner to that previously found for other crops.

Equations were found for the partition of assimilate and of nitrogen between the foliage and tubers. The coefficients in them were little affected by whether or not N fertilizer was applied.

According to these relationships the maximum potential dry weight yield of tubers is 20 t ha^{-1} and requires the crop to contain at least 290 kg N ha^{-1}.

Introduction

Much uncertainty still exists about the causes of variation in N response and yield. To aid elucidation detailed measurements have been made during the growth of potatoes in 11 N fertilizer experiments on three widely different sites in the Netherlands[20]. Recently other workers have discovered that some of the key processes influencing crop growth can be defined by simple but widely applicable equations[12,16,21]. We have therefore attempted to find how far the data obtained in the Netherlands can be described in terms of such equations and to identify constancy in the parameter values. In this way it was hoped to throw new light on the causes of differences in N response and yield and to provide a better basis for developing computer models for predicting how to improve agronomic practice.

Experiments

Potatoes were grown on plots that received either no nitrogen fertilizer or a substantial quantity (see Table 1) shortly before planting. Thereafter the distribution of inorganic nitrogen down the soil profile and the dry weights and nitrogen contents of the foliage and tubers on all plots were determined at approximately 10 day intervals throughout growth.

Eleven such experiments were carried out in the Netherlands by the Institute for Soil Fertility as previously described[20]. One group of four was on a sandy soil (location Heino, Experiment PO 470; notation PO), another group of four was on a sandy loam (location Hornhuizen, Experiment Pr 1521; notation PZ) and a group of three was on a clay soil (location Nieuw-Beerta, Experiment IB 990/1800; notation IB).

All experiments in a group were carried out within the same farm but in different years. On the three soils the crop rotation was more or less the same: on the sandy soil potatoes–rye–oats–potatoes and on the sandy loam and the clay soil potatoes–spring wheat–oats–potatoes. The potato cultivar cropped on the sandy soil was Voran, the one on the sandy loam and the clay soil was Eigenheimer. Other essential features are summarised in Tables 1 and 2.

Quantities of inorganic N in the top metre of soil in spring varied from 37 to 141 kg of N ha^{-1}. The % soil organic matter was almost identical within a textural class but varied considerably from one class to another (Table 2). No irrigation was applied: rainfall varied greatly from experiment to experiment. On the other hand the monthly potential transpiration was almost constant and was on average about 110 mm $month^{-1}$ throughout the period of growth (June, July and August) and was largely unaffected by the site or the year.

Quantitative relationships

Dry-matter increase on N fertilized plots

Growth rate (dW/dt) of many West European crops when grown with ample water and nutrients during May to September has been found to follow Equation (1) until the onset of senescence[13]:

$$\frac{dW}{dt} = \frac{K_2 W}{K_1 + W} \qquad (1)$$

where W is total weight of plant dry matter and K_1 and K_2 are constants. K_1 is the dry weight when growth rate is half the maximum. K_2 is approximately equal to the relative growth rate when W is small and to the rate of dry-matter production (per unit area) when W is large. Theoretical work showed that for most crops K_1 should have a value of about 1 t ha^{-1} if W is expressed in t ha^{-1} and this has proved to be the case experimentally[13]. K_2 generally has a value of about[13] 0.2 t ha^{-1} d^{-1}.

Integration of Equation (1) gives

$$K_2(T-T_o) = K_1 \ln W + W - K_1 \ln W_o - W_o \qquad (2)$$

where W is plant weight at time T and W_o is the weight at the start time T_o.

Equation (2) with K_1 = 1 t ha^{-1} fitted the growth of dry matter for

Table 1. Experimental details

	Experiment										
	PO (sand)				PZ (sandy loam)				IB (clay)		
	69	70	71	72	69	70	71	72	70	71	72
Inorganic N near time of fertilizer application (kg N ha^{-1} m^{-1})	90	37	85	113	51	70	82	90	61	141	128
Level of N fertilizer* (kg N ha^{-1})	144	144	144	144	180	180	180	180	140	140	140
Time of fertilizer application (days from 1 January)	108	128	113	112	122	118	95	101	85	105	74
Weather conditions for May, June and July											
Total rain (mm)	193	190	179	286	157	167	176	289	184	222	236
Average temp. (°C)	15.4	15.4	14.9	14.1	14.7	14.7	14.5	14.0	14.7	14.5	14.0
Crop growth											
Maximum depth of rooting on plots receiving N fertilizer (cm)	85	90	90	80	50	40	52	50	n.r.	n.r.	n.r.
Maximum yield of DM (Tuber + foliage t ha^{-1})	13.0	12.6	12.4	10.9	18.5	18.0	17.1	15.1	14.6	12.2	18.4

* Applied as ammonium nitrate limestone

Table 2. Soil characteristics

	Organic matter (%)		Fraction < 16 μm (%)	
Experiments	Depth 0–40 cm	40–100 cm	0–40 cm	40–100 cm
PO (sand)	4.9	4.7	0	0
PZ (sandy loam)	1.5	0.4	11.5	13.4
IB (clay)	3.3	2.7	54.0	53.7

a considerable period from emergence on the N fertilized plots of all 11 potato experiments (Fig. 1). This period however was followed in some experiments by a second phase during which growth rate became slower and Equation (2) no longer held.

For each experiment all values of lnW + W (W in t ha^{-1}) for T less than 210 days from January 1st were regressed against T. The regression was then repeated to include weights for the next harvest date and if this was not significantly ($p < 0.05$) below the line of best fit, the next one and so on. If the value of lnW + W was below the line of best fit a test was made to determine if the value at the next harvest was also below the line. If it was, no further regressions were calculated so that the final regression included neither value. If it was not, a regression was carried out with both points included and the procedure continued. For each experiment the gradient K_2 for the fitted points and duration for which the equation held (from when $W = 6.7 \times 10^{-3}$ t ha^{-1}) was calculated.

The values of K_2 were between 0.19 and 0.33 t ha^{-1} d^{-1} (Table 3) depending on the experiment and some were higher than those previously recorded for any C_3 crop[11,13]. Values of K_2 averaged over soils for each of the different years and values averaged over years for each soil type were within the range 0.23–0.28 t ha^{-1} d^{-1}. Soil type and inter-year variation in weather did not affect K_2 by more than 25%.

Maximum yields of total dry matter varied from 10.9 to 18.5 t ha^{-1} (Table 1). 84.1% of the variance in these yields was removed by joint regression against K_2 and the duration (T_D) for which Equation (2) held. Separate regression of yield against K_2 removed 24% of the variance and against T_D, 40%. Thus some of the inter-site yield variation could be attributed to differences in the periods during which growth was normal and followed Equation (2) before being restricted.

Growth in experiments 70 PO and 72 PZ followed equation (2) until final harvest (Fig. 1 and Table 3). Checks to growth occurred earlier in the other experiments. They tended to occur earlier and be more severe on the sand (PO experiments) than on the sandy loam and clay soils (Table 3 and Fig. 1). With two exceptions (72 IB and

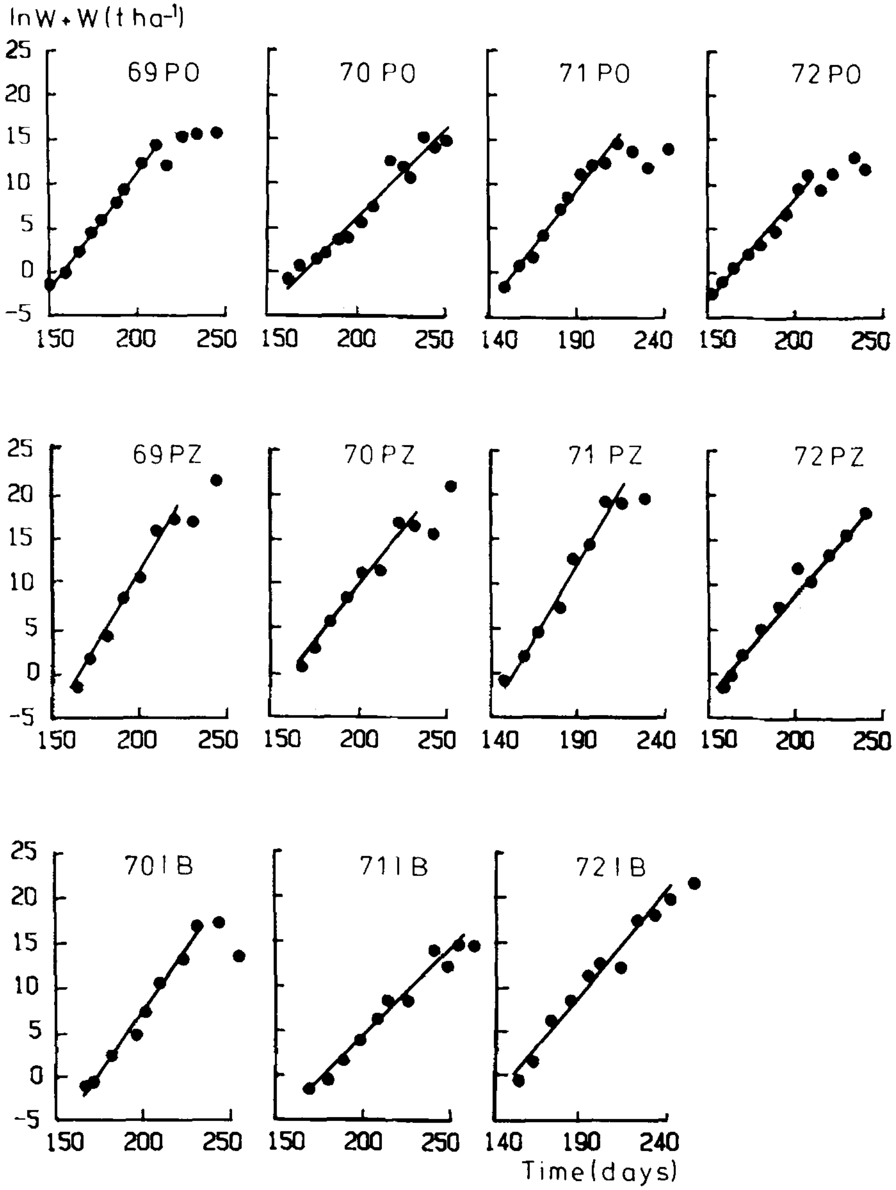

Fig. 1. Relationship between $W + K_1 \ln W$ and T where K_1 is 1 t ha^{-1}, W is in t ha^{-1} and T is in days from Jan. 1st. The lines were extended to include all measurements for which the line of best fit was calculated.

72 PO), whenever growth started to slow down, the SMD was more than half the value of the maximum available water capacity of the soil to the depth of rooting (Table 4 and Fig. 1). Lack of water therefore probably restricted growth in these experiments.

Table 3. Fitting of Equation (2)

Sand		Sandy loam		Clay		Average
Expt.	K_2	Expt.	K_2	Expt.	K_2	
Values of K_2 in Equation (2)						
69PO	0.26	69PZ	0.31	–	–	0.28
70PO	0.19	70PZ	0.25	70IB	0.28	0.24
71PO	0.26	71PZ	0.33	71IB	0.19	0.26
72PO	0.23	72PZ	0.23	72IB	0.22	0.23
Average	0.24		0.28		0.23	
				Overall average		0.25
No of days+ for which Equation (2) held (T_D)						
69PO	52	69PZ	59	–	–	56
70PO	85	70PZ	72	70IB	57	71
71PO	59	71PZ	64	71IB	76	66
72PO	44	72PZ	79	72IB	88	70
Average	60		69		74	
				Overall average		67

+ Calculated as the difference between the last day when Equation (2) held and the time when $K_1 \ln W + W = 0$ where K_1 is 1 t ha^{-1} and W is in t ha^{-1}.

Table 4. Estimated soil moisture deficit (SMD) at time when growth ceases to follow Equation (2)

Experiment	First day when eqtn. failed to hold	SMD* (cm) 10 days before-hand	Root** depth, cm	Estimated†† available water to root depth, cm
69PO	217	8.3	85	13.8
70PO	252†	8.5	90	14.3
71PO	221	10.0	90	14.3
72PO	216	5.5	80	13.2
69PZ	233	7.8	50	11.5
70PZ	243	5.8	40	9.2
71PZ	228	7.6	52	12.0
72PZ	243†	6.8	50	11.5
70IB	243	10.4	85	14.5
71IB	263	10.1	85	14.5
72IB	256	4.1	85	14.5

* Calculated as the difference between the volumetric soil moisture content at pF 2.0 and the measured soil moisture content at the indicated time.

** Root depth was measured in PO and PZ experiments and was estimated from depth of inorganic N uptake in IB experiments.

† The data fitted Equation (2) throughout the growing period.

†† Estimated as the difference between the volumetric water content at pF 2.0 and that at pF 4.2 to the depth of rooting.

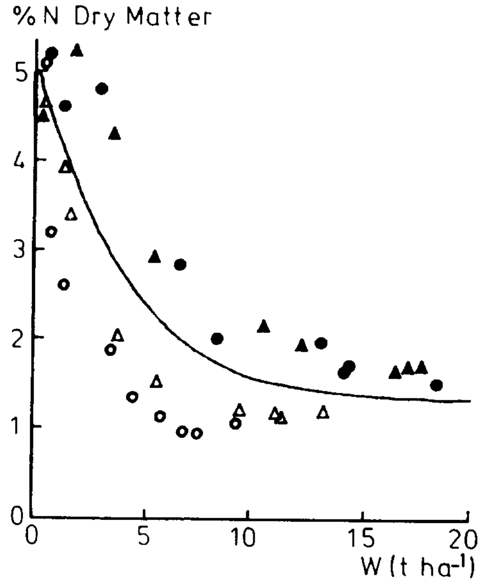

Fig. 2. Values of %N in the dry matter (of the entire plant) at different plant dry weights (W). Curve corresponds to $P_M = 1.35\ (1 + 3e^{-0.26W})$.

Legend

○	Expt. 69 PZ, – N fertilizer
●	Expt. 69 PZ, + N fertilizer
△	Expt. 71 PZ, – N fertilizer
▲	Expt. 71 PZ, + N fertilizer

Decline in percent N of dry matter with growth

The phenomenon was studied in two experiments (69PZ and 71PZ) where growth rates and yields on plots receiving N fertilizer were amongst the highest ever recorded[7,10] in the world.

Measurements of %N of the entire plant (except fibrous roots) grown on plots treated with N fertilizer fell on one curve when plotted against W and those made on plants from which N fertilizer had been withheld fell on another (Fig. 2). The differences between the two curves reflected the increase in %N in the dry matter brought about by applying N fertilizer. At every harvest the yields of dry matter on the N fertilized plots were greater than on those from which N fertilizer had been withheld. In these two high-yielding experiments the %N at each harvest of the N fertilizer plots was thus either equal to or greater than that needed for maximum growth whereas the %N on plots from which N fertilizer had been withheld was sub-optimum. We therefore estimated the relationship between the %N (P_M) needed for maximum growth rate and W on the basis that it was intermediate between the curve of %N *v* W for crops grown on plots receiving N

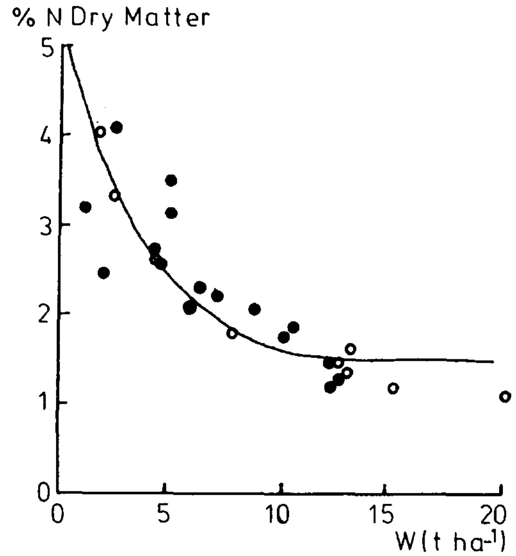

Fig. 3. Curve defines the relationship between the estimated optimum %N and W for potatoes calculated as $P_M = 1.35\ (1 + 3e^{-0.26W})$ obtained in Figure 2. Points are the average values of %N of entire plants (excluding fibrous roots) of different species.

Legend

- ○ Crops attained exceptionally high yields [grass (2), grass/clover, lucerne, potato, spring barley, sugar beet, winter wheat and winter barley; data were kindly provided by A.E. Johnston of Rothamsted Experimental Station (see also Ref.[11])].
- ● Crops were grown on plots that received the optimum levels of N fertilizer in N fertilizer experiments[11] (carrots, broad beans, French beans, leeks, lettuce, onions, peas, potatoes, radish, red beet, sugar beet, spinach, summer cabbage, winter cabbage, swede and turnip).

fertilizer and that for crops receiving none. The relationship between P_M and W estimated in this way was defined by the equation

$$P_M = 1.35\ (1 + 3e^{-0.26W}) \qquad (3)$$

It is illustrated graphically in Fig. 2 together with measurements of %N; a previously derived equation[11] was not used as it did not fit well when W was very high. Previous workers[11] measured the %N at harvest of many agricultural and vegetable crops after they had been grown with the optimum levels of N fertilizer. When plotted against W the points corresponding to all the different crops fitted closely about the curve relating P_M to W of potatoes expressed in Equation (2) (Fig. 3). The decrease in P_M of potatoes as crops get larger is thus similar to that for other crops. It appears that P_M is determined largely by W and hardly at all by the species.

Transformation of N in soil

Apparent mineralization. When there is no loss of nitrogen from the soil/plant system by leaching, or by other processes, the apparent amount of N mineralized ΔM_N over a given period is given by

$$\Delta M_N = \Delta N_S + \Delta U_P + \Delta U_R \qquad (4)$$

where ΔN_S is the change in the total amount of inorganic N in the top metre of soil, ΔU_P is the increment in the amount of N in the foliage plus tubers, and ΔU_R is the increment in the amount of Nin the fibrous roots (including soil organic N derived from their degradation). ΔU_R and ΔU_P must be related to one another. We estimated the relationship from the recoveries of N fertilizer by the foliage and tubers in all experiments except those where there was evidence that substantial leaching had taken place (72 PO and 72 PZ, see below). As the maximum recoveries of N fertilizer were close to 80% and as denitrification is usually small in arable soils[9] we considered that the 20% loss was due to fibrous roots *i.e.* $\Delta U_P/(\Delta U_P + \Delta U_R) = 0.8$. In consequence $\Delta U_R = 0.25\ \Delta U_P$ which on substitution in Equation (4) gives

$$\Delta M_N = \Delta N_S + 1.25\ \Delta U_P \qquad (5)$$

Calculations of M_N were made for numerous occasions during the growth period of each experiment. In every experiment M_N would be expected to increase with time but in two experiments, 72PO and 72PZ, no such increases occurred. The experiments were on the lightest soils and in the wettest year (Table 1) and were thus where leaching was likely to be most serious. If evaporation from the bare soil surface is assumed to be half the potential evapotranspiration then according to Burns's model[4,5], at least 30% of the inorganic N must have been leached out of the top metre of unfertilized soil in these two experiments but not in the others. In view of these losses subsequent analyses were therefore confined to the data from the remaining 9 experiments. For each of these experiments measurements of $N_S + 1.25\ U_P$ made on plots from which N fertilizer had been withheld fitted closely about a straight line when plotted against time (Fig. 4). The gradients are a measure of the apparent mineralization rate.

Average values for the unfertilized plots in the nine experiments are given (Table 5). The rate was remarkably similar in 8 experiments (71PZ being excluded) and for these experiments it was on average $0.78\,\mathrm{kg}$ of $\mathrm{N\,ha^{-1}\ m^{-1}\ d^{-1}}$. The experiments covered soils with textures ranging from sands to clays and having organic N contents that differed by more than 300% (Table 2). The implication is therefore

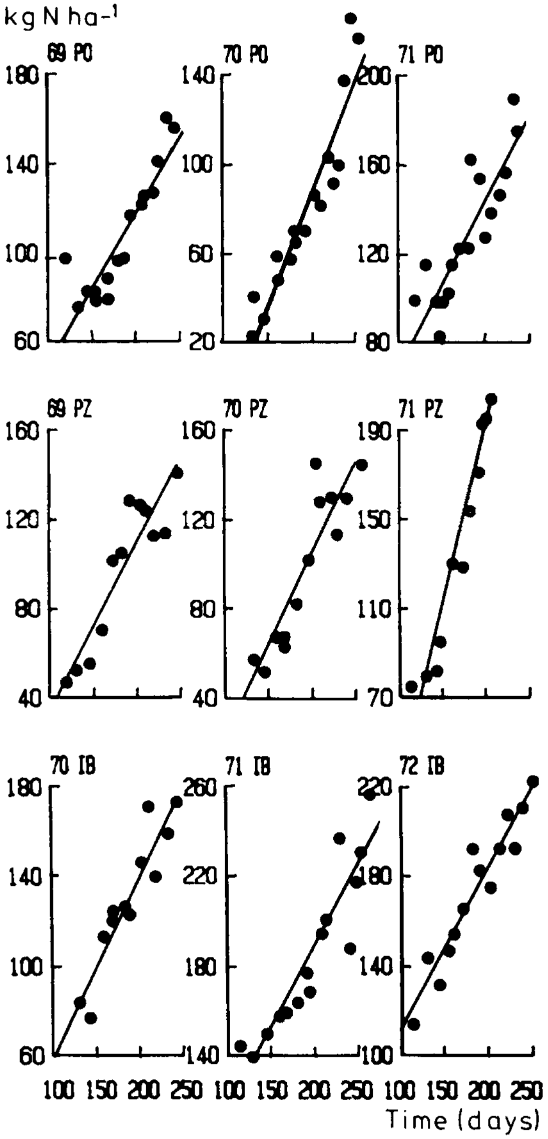

Fig. 4. Relationship between apparent mineralization of N, kg ha^{-1}, measured as $N_S + 1.25\ U_P$ on plots receiving no fertilizer and number of days from Jan. 1st.

that effects of soil texture and soil organic content *per se* on mineralization rate may be small.

When N fertilizer was applied, correlations between $N_S + 1.25\ U_P$ and time were less accurate, and the mineralization rates varied more than those obtained on plots from which N fertilizer had been withheld (Table 5).

Thirty days after applying fertilizer the difference between the

Table 5. Average apparent mineralization rates after time when fertilizer applied (kg N ha^{-1} m^{-1} d^{-1} ± S.E.)

Experiment	Fertilizer N withheld	Fertilizer N applied
69PO	0.69 ± 0.09	0.55 ± 0.12
70PO	1.03 ± 0.11	1.53 ± 0.28
71PO	0.71 ± 0.11	0.74 ± 0.28
69PZ	0.75 ± 0.11	1.88 ± 0.28
70PZ	0.84 ± 0.13	0.36 ± 0.24
71PZ	1.59 ± 0.13	1.82 ± 0.32
70IB	0.80 ± 0.11	0.58 ± 0.24
71IB	0.71 ± 0.09	0.47 ± 0.17
72IB	0.72 ± 0.07	0.86 ± 0.14

Calculated from data in Fig. 4.

Table 6. Comparison of various models for the distribution of nitrogen between foliage and tubers

Model	Residual sum of squares after fitting model	Residual d.f.	Mean square due to extra terms	D.f. due to extra model terms
(1) $R_u = a$	19.16	243	–	–
(2) $R_u = A \quad -B \quad (T-T_p)$	1.47	242	17.700	1
(3) $R_u = A_N \ -B \quad (T-T_p)$	1.45	241	0.017	1
(4) $R_u = A_{NE}-B \quad (T-T_p)$	1.17	221	0.014	20
(5) $R_u = A_{NE}-B_N \ (T-T_p)$	1.17	220	0.000	1
(6) $R_u = A_{NE}-B_{NE}(T-T_p)$	0.74	200	0.022	20
Residual mean square = 0.0037	d.f. 200			

Description of the models:

(1) : Null model.

(2) : Two coefficients: A and B.

(3) : Single value for B; A_N depends on level of N fertilizer.

(4) : Single value for B; A_{NE} depends on level of N fertilizer and on experiment.

(5) : B_N depends on level of N fertilizer; A_{NE} depends on level of N fertilizer and on experiment.

(6) : Both A_{NE} and B_{NE} depend on level of N fertilizer and on experiment.

total inorganic N to a depth of a metre on plots receiving fertilizer N and that on plots receiving none was often less than the total amount of N fertilizer applied. There was therefore, on occasion, an apparent 'disappearance' of inorganic N from the profile. This apparent disappearance was correlated ($r^2 = 0.52$) with the increase in the gradient of $N_S + 1.25\ U_P$ ν time on the fertilized compared with that on the unfertilized plots (Fig. 5). The greater the disappearance of inorganic N the greater the increase. Fertilizer N was thus apparently immobilized, in clays or organic matter, and was subsequently released during the growing season. The importance of these processes however varied from experiment to experiment.

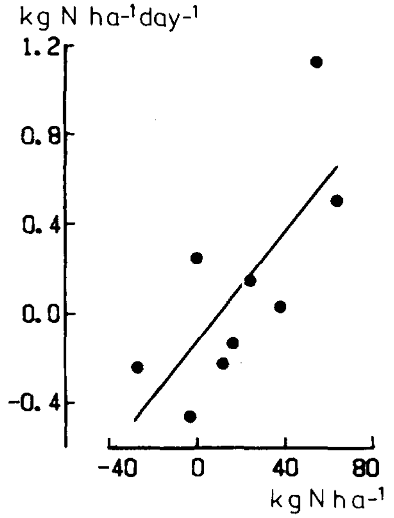

Fig. 5. Relation between the apparent disappearance of inorganic N within the first 30 days after applying fertilizer (x axis) and the apparent increase in mineralization rate.

Decline in inorganic N in the upper 50 cm of soil. Examples of the time-course of decline are given in Fig. 6. Once the crop had been established the total inorganic N in the uppermost 50 cm of soil of plots that received N fertilizer first fell sharply to a low value and then remained at this value for the rest of the growth period. During the initial phase the amount of inorganic N in soil declined at between 3.8 and 9.3 kg ha^{-1} d^{-1}, the lower figures being generally associated with the clay rather than with the sands and sandy loam soils. The constant low value was approximately the same in all experiments, on average 27.6 kg N ha^{-1} (SEM = 3.25) of inorganic N in the top 50 cm. When no fertilizer was applied the inorganic N in the top 50 cm also fell and then remained approximately constant. On average the constant value was 22.6 kg N ha^{-1} (SEM = 3.67) which corresponds to a concentration of about 4 μg N cm^{-3}. It is within the range of values predicted in past theoretical studies[6,11].

Partition of nitrogen between foliage and tubers

The ratio R_U of the amount of nitrogen in the foliage to the total amount in the foliage plus tubers declined linearly with time in every experiment (Fig. 7). The gradient was largely unaffected by whether the plants were grown with or without fertilizer N. It was also largely

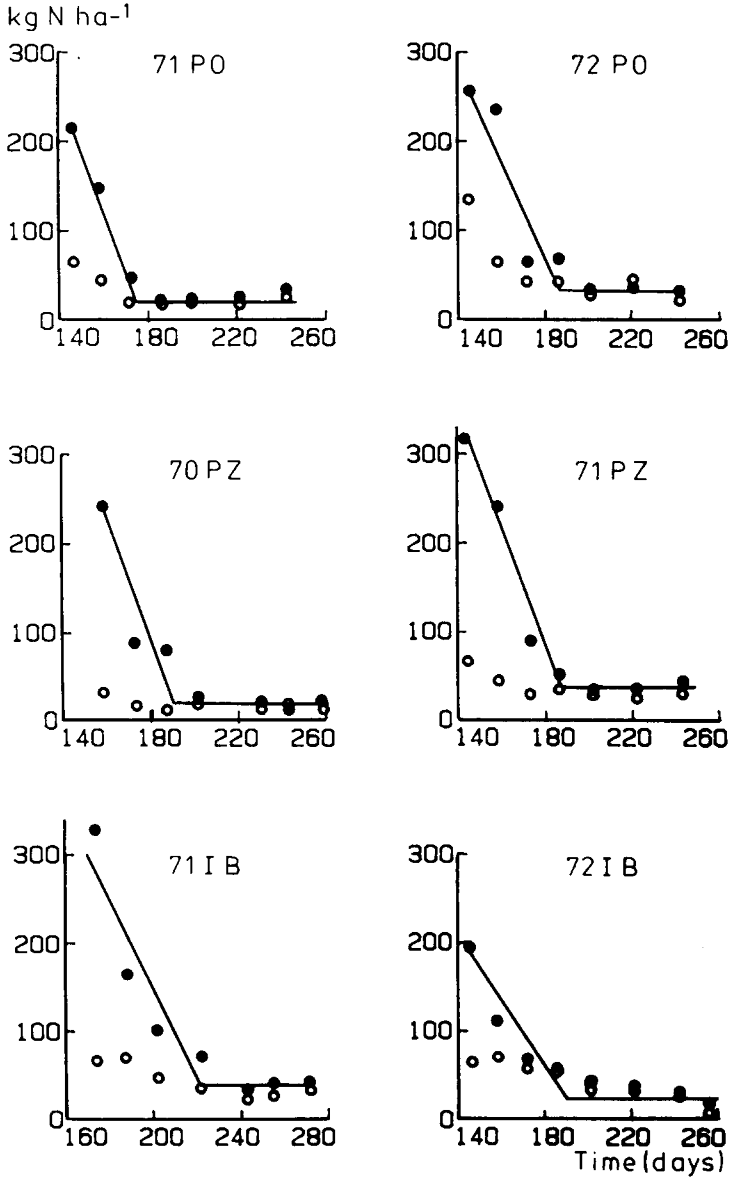

Fig. 6. Inorganic soil N (kg ha^{-1}) in the top 50 cm at different times during growth of potatoes. Times are expressed as days from Jan. 1.

Legend

o plots without N fertilizer

● plots with N fertilizer

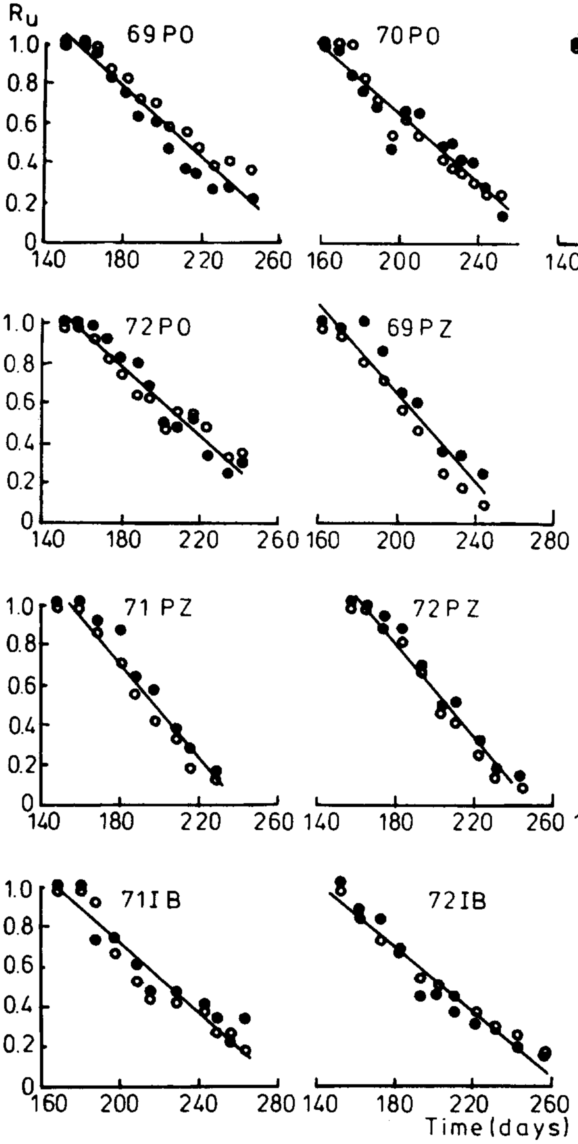

Fig. 7. Relationship between R_U, the ratio of the total amount of nitrogen in the top to that in the whole plant (top plus tuber) and time.

Legend

o crops grown without N fertilizer

• crops grown with N fertilizer

independent of the experiment. An effective time of planting (T_P) for each experiment was calculated. It was taken to be the time when $\ln W + W = -5$ and was estimated from the time when $\ln W + W = 0$ and the average gradient of the graphs in Fig. 1. Using this value of

Table 7. Comparison of various models for the distribution of dry matter between foliage and tubers

Model*	Residual sum of squares after fitting model	Residual d.f.	Mean square due to extra terms	D.f. due to extra model terms
(1) $\ln R = a$	22.50	243	–	–
(2) $\ln(R-R') = D\,(T-T_p) + C$	2.34	241	10.080	2
(3) $\ln(R-R'_N) = D\,(T-T_p) + C_N$	2.21	239	0.063	2
(4) $\ln(R-R'_{NE}) = D\,(T-T_p) + C_{NE}$	1.27	199	0.024	40
(5) $\ln(R-R'_{NE}) = D_N\,(T-T_p) + C_{NE}$	1.25	198	0.021	1
(6) $\ln(R-R'_{NE}) = D_{NE}(T-T_p) + C_{NE}$	0.94	178	0.016	20

Residual mean square = 0.0053 d.f. = 178

* Differences between the sums of squares of the untransformed values of R and those estimated from the model were minimized during model fitting.

Description of the models:

(1) : Null model value.

(2) : Three coefficients : R', D and C.

(3) : Single value for D; R'_N and C_N depend on level of N fertilizer.

(4) : Single value for D; R'_{NE} and C_{NE} depend on level of N fertilizer and on experiment.

(5) : D_N depends on level of N fertilizer; R'_{NE} and C_{NE} depend on level of N fertilizer and on experiment.

(6) : R'_{NE}, D_{NE} and C_{NE} depend on level of N fertilizer and on experiment.

T_p regression analyses were carried out with the following equation and variants of it

$$R_U = A - B\,(T-T_p) \qquad (6)$$

where T is actual time and A and B are coefficients.

The equation with just the two coefficients A and B reduced the residual sums of squares of all values of R_U from 19.16 for the sum of squares of deviations about the mean (null model) to 1.47. The value of A and B was 1.1409 and 0.009364 d^{-1} respectively. Table 6 shows the effects on the residual sum of square of allowing A and B to vary either separately or together with the level of fertilizer and with the experiment. The effects were small though generally significant (at the 5% level). Increasing the number of coefficients from 2 to 44 resulted in the removal of the sum of squares being increased from 92.3 to 96.1% (Table 6). For practical purposes it is therefore reasonable to use Equation (6) with $A = 1.1409$ and $B = 0.009364\ d^{-1}$.

Partition of assimilate between foliage and tubers

Linear regression of R (the ratio of the dry weight of foliage to that of tuber plus foliage) against time was not satisfactory because of curvature in the measured relationships. Nor did the model[3,16]

$$\ln \text{shoot} = \alpha - \eta \text{ Time} + \gamma \ln \text{storage root} \tag{7}$$

(where α, η and γ are coefficients) which had described the partition of assimilate between roots and shoots of carrots, fit our data on potatoes.

Good fits to all the data on potatoes were however obtained with the equation

$$\ln (R-R') = D(T-T_p) + C \tag{8}$$

where T and T_p have the meanings assigned in Equation (6) and R′, D and C are coefficients. Table 7 shows the effects on the residual sums of squares of allowing R′, D and C to vary in different ways with the experiment and the N level. Equation (8) with just one value for R′, D and C reduced the residual sum of squares from 22.5 with the null model to 2.3365 (almost 90%). Introducing more coefficients always brought about significant (at the 5% level) but small improvements in the degree of fit (Table 7). Thus increasing the number of coefficients in the model from 3 to 66 resulted in the percentage removal of the sum of squares being increased from 89.6 to 95.8. For practical purposes it is therefore reasonable to use Equation (8) with the best estimates of the coefficients which were $R' = -0.0759$, $D = -0.0193\ d^{-1}$ and $C = 0.3543$.

Discussion

Important quantitative relationships for various features of the potato crop have been reported by previous workers[1,19]. For example the final yield of potatoes grown with adequate water and nutrients has been found to be almost proportional to the interception of radiaton by the crop canopy[1]. Also the amount of N in the leaves and stems as a fraction of the total amount in the plant has been found to decline linearly with time[15]. Other evidence, however, emphasises the extraordinary complexity of the growth and development of potatoes[19]. The partition of assimilate within the crop canopy can be critically dependent on the spectral distribution of incoming radiation and the rate of photosynthesis can at least in the short term be determined largely by the weight of tubers which presumably determines their strength as sinks for carbohydrate. Net assimilation rate generally falls from its value at the time of tuber initiation to a minimum when the leaf area is maximum and then rises as the leaves senesce[19]. In view of these interacting processes it is perhaps rather surprising that whenever a high yield was obtained in our work the rate of dry-matter increase throughout growth was determined by a simple equation (Equation 2). Furthermore the ratio of nitrogen and dry matter in the foliage to that in the whole plant was determined almost entirely by plant age and was hardly affected by other factors such as nitrogen level (Tables 6 and 7). The total amount of N in the leaf canopy at any time is the product of R_u (Equation 6) and the total amount of N in the crop. Thus the duration of the period before the amount of N in the leaf canopy falls below a critical level is affected by uptake of N. These relationships are thus consistent with the widely accepted conclusion that N affects leaf-area duration, albeit to a small extent over the range of normal agronomic practices[1,19].

Equations (1, 3, 6 and 8) can be combined to calculate the minimum amounts of nitrogen that must be absorbed at each stage of growth if maximum yields are to be achieved. According to Equation (6) the amount of N in the foliage would fall to zero when $T-T_p = 122$ days. The data (Fig. 1) however, from those experiments, 70PO and 72PZ, where there appeared to be no restriction of growth from lack of water or nitrogen, suggest that growth continued at near-maximum rate until $T-T_p = 113$ days. No great error will therefore result by assuming that under these conditions growth rate is the maximum possible until $T-T_p = 113$ days and thereafter declines linearly with time until $T-T_p = 121$ days. From these premises and by setting $K_2 = 0.25\ \mathrm{t\ ha^{-1}}$ (see Table 3) we have predicted the time course of dry matter accumulation and N uptake for potatoes growing with just sufficient N to permit maximum growth rate. The outcome is summarized in Table 8.

According to this analysis it should be possible to obtain a yield of 20 t ha^{-1} tuber dry matter in the Netherlands. This figure compares with a tuber dry-matter yield of 19 t ha^{-1} which has been obtained in the UK[10] and 22 t ha^{-1} in the Netherlands[23,25]. The %N in the potato-tuber dry matter is at its highest when plants are small, falls to a minimum when the tuber dry weight is about 10 t ha^{-1} and then rises steadily as the plants increase in size. The total uptake of N by the plant is about 200 kg N ha^{-1} when tuber dry matter yield is 10 t ha^{-1} but about 290 kg when it is 20 t ha^{-1}. Much more nitrogen must be absorbed by the plants to grow a tonne of tuber in the early stages than in the later stages of growth.

The analysis also indicates that the maximum rate of N uptake by the crop oscillates with time (Table 8). The most rapid uptake is needed shortly after emergence when the plants and root systems are small and least able to extract nitrogen from the soil. The rate of uptake then falls and is beween 2 and 3 kg N ha^{-1} d^{-1} for most of the

Table 8. Predicted development of potatoes grown with minimum amount of N to permit maximum growth rate

	Time from effective planting data (days)					
	26	50	80	100	110	122
Rate of dry weight increases of the total plant (t ha^{-1} d^{-1})	0.13	0.21	0.23	0.24	0.24	0.03
Rate of N uptake (kg ha^{-1} d^{-1})	4.6	2.0	2.3	2.8	3.0	0.36
Tuber dry weight (t ha^{-1})	0.2	2.9	9.4	14.6	17.4	20.2
Top dry weight (t ha^{-1})	0.9	2.6	2.8	2.2	1.8	1.3
%N in tuber DM	2.1	1.4	1.2	1.3	1.4	1.4
%N in top DM	5.0	3.4	2.6	2.2	1.6	0.17
Total N uptake (kg N ha^{-1})	48	128	185	236	266	294

remainder of the growing period (Table 8). It must be emphasised, however, that these calculations assume that on each day throughout the growth the plant just takes up sufficient N for growth to be unrestricted through lack of N. Our results suggest that in practice, if there is plenty of inorganic N in soil, plants can take up N far faster than is needed, and so build up reserves within the plant. Such reserves permit maximum growth rate to be maintained for subsequent long periods when N supply is restricted. The point is well illustrated by the results of experiment 71PO. When the crop was grown on N fertilized plots it absorbed N at an average rate of 6.4 kg N ha^{-1} d^{-1} over the period 158 to 179 days. At the end of this period the average %N in the plant was 3.2% compared with a value of 2.3% (Fig. 3) needed for a crop with the same dry weight (5.6 t ha^{-1}).

During the next 30 days the plant only absorbed N from soil at about 0.72 kg N ha^{-1} d^{-1} (the level of inorganic N remained almost unchanged (Fig. 6)) and so uptake was approximately equal to the apparent mineralization rate (Table 5). The %N gradually declined through dilution from growth but not sufficiently to cause any restriction in growth rate (Fig. 1). Luxury consumption of N thus enabled the plant to maintain maximum growth during a subsequent period when uptake from the soil was severely curtailed.

Nitrogen release

The total amount of soil organic matter varied by a factor of more than three with the soil textural class. The relative constancy in the apparent mineralization rate (Table 5) thus suggests that nearly all the organic matter was 'old' and was decomposing slowly and that amounts of the readily decomposable fraction were similar in all sites[18,24]. A wide range of soil textures and soil moisture contents was also covered by the experiments but the previous cropping was always similar. It may well be therefore that mineralization rates are similar in widely different soils subjected to the same cropping sequence.

Another aspect of N supply that deserves comment is the unexpected finding that N applied as fertilizer 'disappeared' within 30 days or so of application and then reappeared later on in the season. Any explanation invoking fixation of ammonium by clay minerals is excluded by the absence of fixing capacity on these sites. Other workers have observed the sudden disappearance of fertilizer N under conditions where there can be little denitrification or leaching[2,8,14,22]. In addition an apparent enhancement of mineralization following fertilizer application has been noted on several occasions[2,17]. It seems probable that fertilizer N was immobilized, possibly at micro-sites where there was a metabolizable residue from a previous crop, and then released later in the season as a result of further breakdown.

Yield variability

The data in Fig. 1 show that for long periods growth rates could be near maximum on a sand, a sandy loam and a clay soil. Texture *per se* clearly does not limit growth rate.

Final total dry matter yields, however, varied considerably (10.9–18.5 t ha^{-1}) from experiment to experiment even when N fertilizer was applied. Some low yields were caused at least in part by rather low values of the growth rate constant K_2 during the phase of growth when Equation (2) held. For example in experiments 70PO and 71IB (Table 3) it was only 0.19 t ha^{-1} d^{-1} compared with the average for all experiments of 0.25 t ha^{-1} d^{-1}. Some of the differences in yield however resulted from variations in the period for which Equation (2) held before growth rate was seriously impeded. This may well have resulted from lack of nitrogen in experiment 72PO. Evidence was obtained of considerable leaching of nitrate from the subsoil in the experiments 72PO and 72PZ. Although fertilizer N is incorporated in the surface soil and is thus less susceptible to leaching losses than subsoil nitrate considerable quantities of fertilizer N may well have been leached in the wet year of 1972 from experiment 72PO as the PO soil was light and more susceptible to leaching losses than the PZ soil. Moreover during the latter half of growth when Equation (2) no longer held, the %N in the dry matter of plants was less than our estimate (Fig. 3) of that needed to sustain maximum growth. The average %N in the dry matter (foliage plus tubers) for all harvests in experiment 72PO when Equation (2) no longer held was 1.54 compared with the required 1.74. As was argued on p. 167 checks to growth of experiments 69PO, 71PO, 69PZ, 70PZ, 71PZ, 70IB and 71IB could well have resulted from water stress. There were no checks to growth in experiments 70PO and 72PZ. The only other experiment was 72IB and in this case deviations from Equation (2) only occurred in the middle of September (Fig. 1) when incoming radiation begins to fall.

Conclusion

Some if not all the key processes governing N response of potatoes can be described by simple equations with parameter values that are almost constant over a wide range of conditions. These relationships have been combined into a dynamic model for calculating N response throughout the growing season on widely different soils from a few easily obtainable values of parameters. A description of this model and of its reliability is given in the next paper.

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