BIOLOGIA PLANTARUM (PRAHA)

20 (4) : 248—255, 1978

Mathematical Description of Nitrogen and Phosphorus Accumulation in Developing Barley Kernels

L. NÁTR*†, P. APEL** and IVANA KOUSALOVÁ*

*Cereal Research Institute, Kroměříž,
and **Zentralinstitut für Genetik und Kulturpflanzenforschung, Gatersleben

Abstract. The changes of kernel nitrogen (N), phosphorus (P) and dry weight (DW) were determined during the time period from 10 days after anthesis till maturity in three spring barley strains. The plants were cultivated under field conditions in Gatersleben (German D.R.) and Kroměříž (Czechoslovakia). The course of N, P and DW changes was described by Richard's comprehensive growth function $dW/dt = aW^m + bW$, where W is the amount of N, P or dry matter per kernel, a, b, m are coefficients. The integral of this function was used and several parameters calculated. There was a remarkable synchrony between N or P and total dry matter accumulation in the kernels. Thus, the N or P concentration per unit kernel dry weight was relatively constant during the investigated period and with few exceptions corresponded to 80% to 100% of the final value. However, considerable differences between strains, years or places of cultivation were found.

Changes of the mineral nutrient content in the plant and its individual organs are brought about by changes in external conditions and by their interaction with physiological processes. Hence, data on the mineral composition of plant tissue are often needed to explain the causal relationship between the factor under study and the results obtained. The cereal kernel is often used in studies on the source-sink relationship and represents the most important plant product for human nutrition (*e.g.* CERNING 1970, JENNER 1974, SEILER-KELBITSCH *et al.* 1974). So a precise description of the growing kernels is of prime interest in biological research.

APEL *et al.* (1975) first introduced the mathematical expression by Richards' growth function for a description of dry matter changes of wheat grain. This procedure was further used for analysing the relationship between the amount of carbohydrate in the stem and kernel growth rate (APEL 1976, APEL and NÁTR 1976).

In this paper, a similar procedure was used for the description of the course of nitrogen (N) and phosphorus (P) accumulation in the kernels of three spring barley strains.

Received October 11, 1976; accepted December 15, 1977

Addresses: *767 41 Kroměříž, Czechoslovakia. **4325 Gatersleben, DDR.
† *New permanent address*: Department of Plant Physiology, Charles University, Viničná 5, 128 44 Praha 2, Czechoslovakia.

Material and Methods

The spring barley plants (*Hordeum vulgare* L.) were cultivated with 5 cm × 25 cm spacing in 1975 in the experimental fields in Gatersleben and in 1974 and 1975 in Kroměříž. The strains used: Diamant: a highly productive short-stemmed and early maturing cultivar. Ametyst: a recent cultivar selected on the Diamant basis. Very productive, short stem with good lodging resistance. KM 1192: a new line (selected in the Cereal Research Institute by J. Lekeš and L. Zeniščeva) with high productivity and complex disease resistance. For further description of the strains used see Kopecký *et al.* (1975).

During anthesis, about 200 ears of similar growth stage were marked. At regular 5 day intervals from the 10th day after anthesis samples of 15 ears were collected till maturity. For each sample, kernel dry weight was determined and used for further calculations.

In the kernels of each sample the total N and P content was determined (Nátr and Purš 1969) and the N and P amount per kernel calculated. From these values growth curves were calculated.

As a basis for description of N and P accumulation in the kernel Richards' comprehensive growth function was used (Richards 1959, 1969): $\mathrm{d}W/\mathrm{d}t = aW^m + bW$, where W is the amount of N or P in the kernel (μg kernel^{-1}), a, b, m are coefficients.

For calculation, the integral of this function was used:

$$W_{(t)} = \left[\left(\frac{a}{b} + W_0^{1-m}\right)\mathrm{e}^{bt(1-m)} - \frac{a}{b}\right]^{\frac{1}{1-m}}$$

The coefficients a, b, m, W_0 were calculated from empirical data.

Apel *et al.* (1975) give full information on the calculation procedure for kernel growth (precisely: kernel dry weight changes). In the same way, the changes in the amounts of N and P in the kernel were calculated.

The following values were derived from the function and used for comparisons:

1. $W_{(t)}$ — the calculated N or P amount at time t between anthesis and maturity (μg kernel^{-1}).
2. W' — the absolute rate of changes of N or P (μg kernel^{-1} d^{-1}).
3. $W_{\max}$ — the computed saturation level for the curve of N or P amount in kernel. These data are nearly identical with the mean value of the last two or three samplings (μg kernel^{-1}).
4. $W'_{\max}$ — maximum absolute growth rate (μg kernel^{-1} d^{-1}). These data give the maximum rate of N or P accumulation in kernels. Similarly, $W'_{W10\%}$, $W'_{W50\%}$, and $W'_{W90\%}$ indicate the rate of accumulation at the time when the amount of N or P reaches 10%, 50% or 90%, respectively, of the final amount at maturity.
5. RGR — the course of relative growth rate (μg μg^{-1}).
6. $\overline{\mathrm{RGR}}$ — the mean RGR for the time period between $W_{10\%}$ and $W_{90\%}$ (μg μg^{-1}).
7. $D_{W10\%}$, $D_{W50\%}$, and $D_{W90\%}$: the number of days from anthesis till the time when the N or P amount reaches 10%, 50%, 90%, respectively, of the final value (day).

TABLE 1

The coefficient m of the equation of growth function representing the accumulation of dry matter [mg kernel^{-1}], nitrogen and phosphorus [μg kernel^{-1}] and some calculated values in the kernels of three spring barley strains grown in 1974 at Kroměříž and in 1975 at Kroměříž (Kr) and Gatersleben (Ga).

$D_{W'max}$: time period from anthesis till the day when W'_{max} was reached (day), $W_{W'max}/W_{max}$: the amount accumulated at $D_{W'max}$ in % of the final maximum value

		m			$D_{W'max}$			$W_{W'max}/W_{max}$		
		dry m.	N	P	dry m.	N	P	dry m.	N	P
	Diamant	1.812	1.548	1.276	23.58	25.62	23.74	48.1	45.1	41.3
Kr 74	Ametyst	1.774	1.921	1.198	23.85	26.05	23.15	47.7	49.2	40.2
	KM 1192	1.904	1.755	1.453	23.13	22.21	23.82	49.0	47.5	43.8
	Diamant	1.413	2.261	1.380	13.85	18.06	14.70	43.3	52.4	42.8
Kr 75	Ametyst	1.201	1.000	1.000	15.93	13.68	11.38	40.2	36.8	36.8
	KM 1192	1.359	1.000	1.399	14.73	15.66	15.17	42.6	36.8	43.1
	Diamant	2.285	3.596	1.998	13.34	17.15	13.38	52.6	61.1	50.0
Ga 75	Ametyst	1.227	1.000	1.000	10.40	11.25	10.74	40.6	36.8	36.8
	KM 1192	2.307	1.000	2.239	14.13	12.48	15.38	52.8	36.8	52.2

8. $W_{10\%}$, $W_{50\%}$ and $W_{90\%}$ — 10%, 50% and 90%, respectively, of the W_{max} (μg kernel^{-1}).
9. $W_{W'max}$ — the amount of N or P in kernel (μg kernel^{-1}) at the time when W'_{max} is reached. Similarly, $D_{W'max}$ indicates the number of days from anthesis till the time when W'_{max} is reached.
10. W/W_{max} — the course of "norm" growth rate, *i.e.* the amount of N or P expressed in percent of the final amount.

For better comparison, the data on N and P amount in kernels are followed by data on kernel dry weight (mg kernel^{-1}).

Results

There is an apparent similarity in the course of the total kernel dry weight and the N or P amount in the kernel (Fig. 1). The same holds for the growth rate curves. However, when examining the individual features in more detail, distinct differences become apparent.

Of the four growth coefficients, that of m is of special interest. If $m = 2$, then $W_{W'max} = W_{50\%}$ and the rate curve is symmetrical. If $1 < m < 2$, then the maximum value of the rate curve of the factor under study (dry weight, N or P amount) is reached before its value equals 50% of its final (maximum) value.

The m values for dry weight and N (Table 1) indicate, that m for N is smaller than m for dry weight in all the three experiments for the strain KM 1192 only. With the cultivars Ametyst and Diamant, there are no consistent differences between m values for dry weight and for N. On the other hand, the m values for P are always smaller than or equal to those for dry weight. This indicates that the decrease in the rate of P accumulation in all strains and that of N in KM 1192 begins earlier than the decrease in the rate of dry matter accumulation.

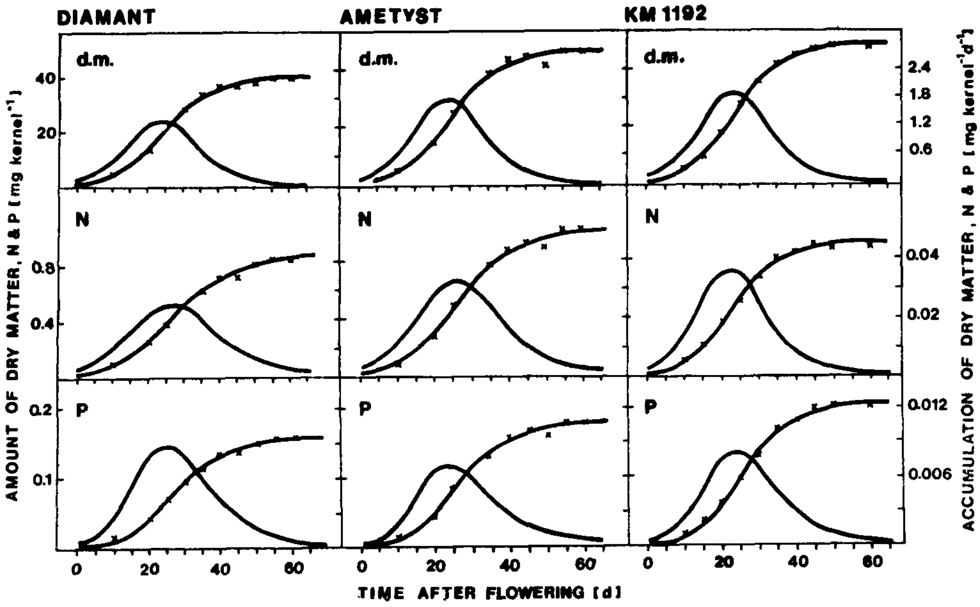

Fig. 1. Dry matter, N and P [mg kernel^{-1}] amount (crosses) and the rate of dry matter, N and P [mg kernel^{-1}d^{-1}] accumulation (———) in three spring barley strains grown in 1974 at Kroměříž. The curves correspond to the equations calculated on the basis of experimental data (×). For further details see material and methods.

The same conclusion may be derived from data on the amount of N or P expressed in percent of the maximum value, *i.e.* $W_{W'\max}/W_{\max} \cdot 100$ (Table 1).

The majority of our data indicate that about 50% of the final dry matter is already accumulated in the kernels at the time when maximum growth rate is reached. The values for N and P amounts obviously lead to the same conclusion as given above on the basis of the evaluation of the *m* coefficients.

There is remarkable variability, especially for N content, when strains in one year and one place are compared, *e.g.* Gatersleben 1975 $W_{W'\max}/W_{\max} \cdot$ 100 value for Diamant is 61.1% and that for the other two strains: 36.8%. Similarly, the same strain shows very different values in different years and places: *e.g.* Diamant: Kroměříž 1974: 45.1%, Kroměříž 1975: 52.4%, Gatersleben 1975: 61.1%.

The differences are even greater as regards the time period $D_{W'\max}$ (Table 1). Even with relatively small differences in maximum values ($W_{\max}$) of dry weight and N and P amounts, the maximum rates (W') were reached in about 23 days in 1974 (Kroměříž) while this period was shorter by nearly 10 days in 1975 (Gatersleben).

The Diamant cultivar is known for its smaller grains. The same is true of our data: final kernel weight was always smaller in Diamant as compared with Ametyst and KM 1192 (Fig. 1). Similar differences were found in N and P amounts in kernels. In one year and at one place, the cultivar differences in kernel dry weight and those in N or P amount are very similar. For better comparison of the course of total dry matter and N and P accumulation, the "norm" values indicating $W/W_{\max}$ ratio seem to be more

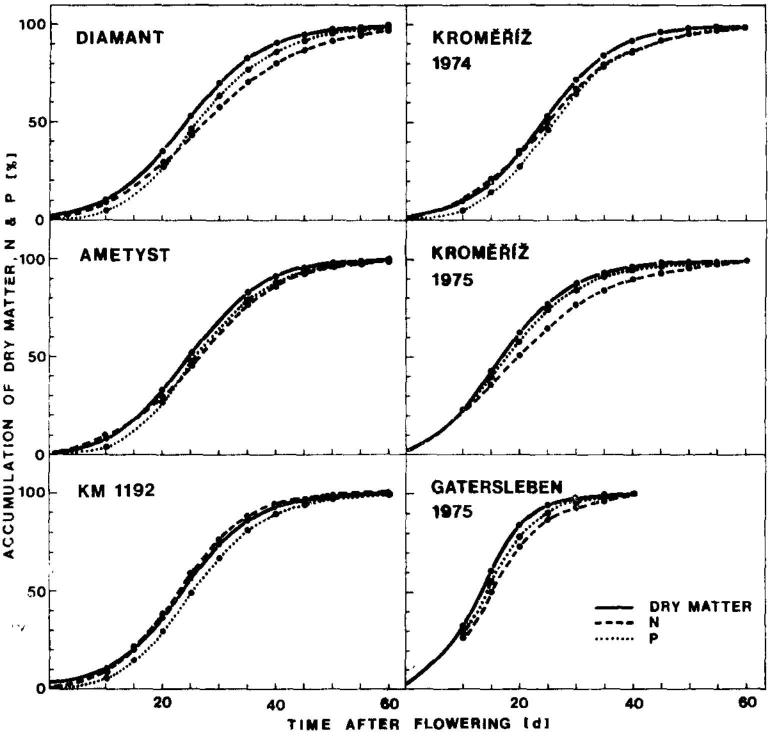

Fig. 2. The course of dry matter (full line), N (dashed line) and P (dotted line) accumulation in the kernels of spring barley Diamant, Ametyst and KM 1192 grown in 1974 at Kroměříž (left) and mean values of three strains grown at Kroměříž 1974 and 1975 and at Gatersleben in 1975 (right). The values are given in % of the maximum value at maturity: $(W/W_{max}) \times 100$.

suitable. In 1974, the curve of dry matter accumulation is practically identical with that of N amount for the KM 1192 (Fig. 2). For Diamant and Ametyst, the dry matter accumulation preceded the N accumulation. Similar time shift is apparent for P accumulation.

The "norm" values make it possible to compare mean values of all strains in the individual experiments. The curves (Fig. 2) indicate that relatively more dry matter — expressed in per cent of the final value — than N or P is accumulated in the kernel at any moment of the whole filling period. In other words, at any time moment W/W_{max} for dry weight is greater than W/W_{max} for N or P. (It should be noted that this conclusion need not be reliable for the very early period of kernel growth as the first sampling was carried out 10 days after anthesis in the experiments.) Hence, there must be a relatively higher rate of N and P accumulation than that of dry weight during the final stage of grain filling.

All these changes are well documented by changes in the N and P concentration in kernel dry matter. The calculated data on dry weight and N, P amounts in the kernel were used for computing the N and P concentration in % of dry matter (Fig. 3). The computed data agree reasonably well with the experimental ones. But the curve constructed from the computed values is more regular and smooth. The same computed values were further used

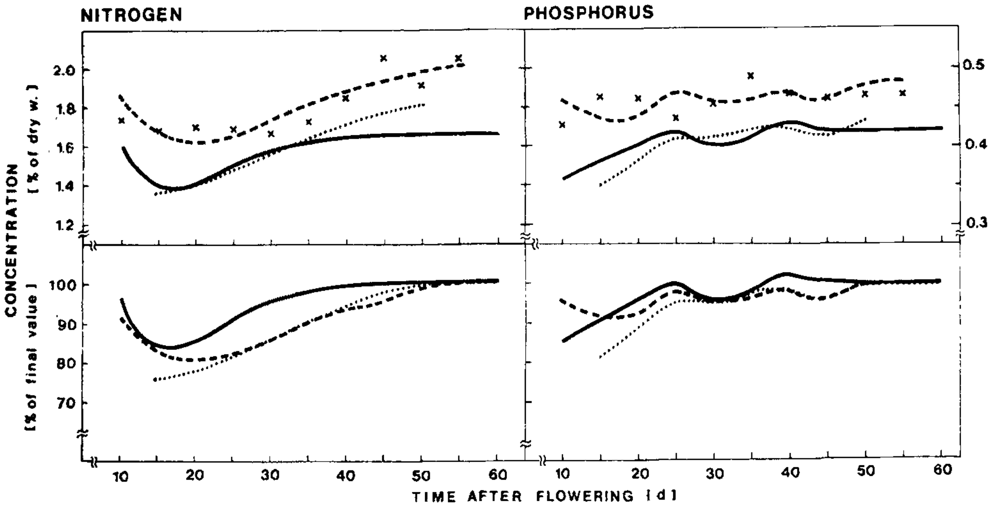

Fig. 3. The N and P concentration in % of dry matter during the filling period and in % of the final value at maturity (= 100%) of three barley strains grown at Kroměříž in 1975. Diamant (full line), Ametyst (dotted line) and KM 1192 (dashed line). The curves correspond to the values calculated from growth functions for dry matter and N, P accumulation. Experimental (measured) data for KM 1192 indicated by ×.

for calculating the relative values of N and P concentration. It is obvious (Fig. 3) that both N and P concentrations prove differences among cultivars. To compare them, relative values are more convenient. The ratio $W_{\max}$ for N or P/$W_{\max}$ for dry weight represents 100% for each strain and all concentrations were expressed in % of this ratio for the whole filling period (Fig. 3). It may be deduced from the curves (Fig. 3) that there are no considerable changes of N concentration in the kernels during the final stages of the filling period. As stated above (Fig. 3) a slight increase in N concentration seems to be a general feature of a maturing grain. However more experiments are needed to analyse the changes of N concentration because of the rather small variations. Most values obtained correspond to 80 to 100% of N concentration when expressed in per cent of the concentration at maturity (= 100%). The curve for P concentration (Fig. 3) shows even less changes for a longer period before maturity when compared with N concentration.

Discussion

Several remarkable papers were published on various characteristics of developing barley kernels by Harlan in the early twenties. Harlan (1920) investigated not only the course of dry matter accumulation in the kernels, but also the ash content. It may be deduced from his data that changes of N content during the whole filling period are quite small except for the first days after anthesis. His data on daily changes of N amount in the kernel (in Table 3, Harlan and Anthony 1920) show that the mean N concentration 15 to 20, 10 to 15, 5 to 10 and 1 to 5 days before full maturity were 2.12%, 2.05%, 2.07%, and 2.04% of dry weight respectively. A similar conclusion may be drawn from the more recent paper by MacGregor *et al.* (1971) who indicated that the course of ash content (mg kernel^{-1}) generally corresponds to the course of total kernel dry weight. It may be computed from their Fig. 2 that there are practically no changes of N concentration from the 30th day after anthesis till maturity. It seems (especially Figs. 1 and 3) that our results are consistent with the above indicated conclusion about a relative stability of N concentration in the developing kernel (see also IVANKO 1971).

However, when analysing differences among cultivars of N accumulation in the kernel RHODES and MATHERS (1974) found that during the time period from the 17th to the 38th day after anthesis the rate of N accumulation in the cultivar Hiproly was markedly higher than in the cultivar Maris Mink, the latter having at maturity by 50% N less than Hiproly. In this case there must have been a great difference in the course of N concentration because of relatively smaller differences in both accumulation rate and final weight of kernel dry matter.

Even though the N and dry matter accumulation are generally synchronized, a more detailed quantitative analysis reveals significant differences. In the experiments at Kroměříž in 1974, the kernel dry weight of all the three strains reached on the 40th day after anthesis more than 90% of the final value. On the same day, the accumulation of N reached 87%, 93.5% and 101.5% in Diamant, Ametyst and KM 1192, respectively. These differences between cultivars may be caused especially by differences in the interaction between strain and environment because of the variations in the individual years. For example in 1975 at Kroměříž (compare the above given data from 1974), the N accumulation in all the three strains reached more than 90% of the final amount already on the 35th day, when Diamant reached the maximum with 98% and both Ametyst and KM 1192 only 90%.

No physiological processes are known that stimulate an absolute synchrony of carbohydrate accumulation and that of individual elements. The opposite could be expected: taking into account the different sources of photosynthate and mineral elements accumulated in the kernels (PAVLOV *et al.* 1971, DALLING *et al.* 1975) one could assume the possibility of inducing different changes in dry matter and N accumulation. It should be emphasized that the total amount of N was analysed in our experiments. The concentration of different N compounds may vary widely. Thus IVANKO (1971) found that from the 10th to the 43rd day after anthesis the protein content of barley kernels increased from 2.83% to 7.69% (on a kernel dry matter basis), while the amount of non-protein N (per total N) decreased from 58.52 to 26.72%.

There is little information about the course of P accumulation in the cereal kernels. ABERNETHY *et al.* (1973) found a rather rapid increase in P amount of wheat kernels shortly after anthesis followed by stagnation and final decrease. On the other hand, all our results indicate that the course of P accumulation follows that of N and dry matter, *i.e.* that the P amount per kernel steadily — though at various rates — increases till full maturity.

A precise mathematical desciption of kernel growth is very suitable for the evaluation of the effects of various factors on both accumulation rate and final dry weight (APEL 1976). The same is expected when using the method of growth function calculation for the course of mineral elements accumulation in the kernels. The basic characteristics of N and P changes in the developing kernels are presented in this paper. The dependence of these characteristics on both exogenous and endogenous factors will be analysed.

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