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Tuberization in potato plants as affected by applications of nitrogen to the roots and leaves

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Zusammenfassung, Résumé p. 56

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Summary

Tuberization can be prevented in water culture experiments with continuous nitrogen supply via the roots. Interruption of the nitrogen supply via the roots induces tuberization; simultaneous sprayings of the leaves with urea cannot delay or prevent tuberization. Nitrogen analyses show that there is no correlation between nitrogen content of the plants and tuberization. The results are discussed in terms of hormonal changes within the roots and shoots caused by the differences in nitrogen nutritional status of the roots.

Introduction

Tuberization and tuber growth are controlled not only by daylength and temperature but also by the mode of nitrogen nutrition. In field experiments, tuberization is delayed by a high supply of nitrogen (Simpson, 1962) but stimulated by nitrogen withdrawal (Burghausen, 1963) or by inhibition of nitrogen uptake as a result of low temperatures (Burt, 1964). In water culture experiments with 20 C and 12 h daylength, tuberization can even be completely prevented by a continuous supply of nitrogen as either nitrate or ammonium via the roots (Krauss & Marschner, 1971, 1976).

The simplest and most obvious interpretation of the effect of nitrogen would be to assume that vegetative growth and protein synthesis are stimulated at the expense of carbohydrate formation and storage when nitrogen is supplied continuously. Thus Werner (1934) postulates that a high concentration of assimilates in the stolon tips is a prerequisite for induction. This view was supported by Headford (1962) and has not yet been disproved, although a number of facts indicate that more is involved in induction than merely a wide ratio of carbohydrates to proteins in the plant in general and stolon tips in particular.

It is now widely accepted that tuberization and tuber growth are controlled by the endogenous level of phytohormones, and that these are influenced by exogenous factors such as daylength, temperature and nitrogen nutrition in such a way that changes in these exogenous factors result in a change in the ratio of the endogenous phytohormones. A ratio of the endogenous phytohormones which favours tuberization is referred to as the 'stimulus' for tuberization (Hammes & Nel, 1975). Whereas the shoot seems to be the acceptor for the 'stimulus' regulated by the daylength (Okazawa & Chapman, 1962), no corresponding information is available about the factor nitrogen nutrition. In the experiments presented here, nitrogen was supplied either to the roots or to the leaves in order to ascertain whether the 'stimulus' regulated by nitrogen nutrition is formed in the roots or in the shoots.

Materials and methods

After sprouting in quartz sand, the plants (*Solanum tuberosum* L. cv. Ostara) were grown in water culture under constant climatic conditions (20 C day and night, 12 h daylength), one plant per plastic container with 5 litres constantly aerated nutrient solution of the following composition: macronutrients (m*M*): K 1.5, Ca 1.0, Mg 0.75, NO_3 3.5, SO_4 0.37, PO_4 0.75; micronutrients (μM): Fe 17.9 (Fetrilon), Mn 3.6, Cu 1.6, Zn 1.5, B 55.5, Mo 1.0.

The plants were precultured for 29 days in this complete nutrient solution; thereafter 5 plants were grown further in the complete solution (continuous nitrogen supply via the roots = cont. N), while 10 plants were transferred into a nitrogen-free nutrient solution (in one experiment, for 21 days; in the other, for 9 days) in which nitrate had been replaced by sulphate (discontinuous nitrogen supply = discont. N). The leaves of 5 of these 10 plants were sprayed twice daily (with a flower sprayer) with a 0.1 % solution of urea.

In order to prevent the effects of high urea concentration on the margins of the leaves, the drops of urea solution formed on the leaf margins were removed by 'Kleenex' tissue. With the exception of some necrosis on the leaf margins, the urea sprayings did not cause any damage to the plants.

At the end of the experiments, the shoots of the urea-treated plants were thoroughly washed by 2 dippings, of 5 minutes each, in distilled water. The roots and shoots of all three treatments were dried at 105 C, and both the total nitrogen content (Kjeldahl, with selenium reaction mixture) and the nitrate content (nitrate-sensitive electrode, type Orion) were determined.

Results

Compared to the plants with cont. N, the shoots of the plants with discont. N were stunted and had smaller leaves (Fig. 1). Additional nitrogen supply in the form of urea via the leaves did not overcome the stunted growth of the plants produced by discont. N (Fig. 1, right), it only delayed or prevented yellowing of the older leaves (senescence). Whereas tuberization did not occur in the plants with cont. N, in the plants with discont. N, including those with additional nitrogen supply as urea via the leaves, tuber formation occurred (Fig. 1) in at least 4 of the 5 plants in each of these two groups.

Fig. 1. Effect of different nitrogen nutrition on the growth of potato plants. Duration of experiment 21 days. Left: cont. N; centre: discont. N; right: discont. N with simultaneous urea application via the leaves.

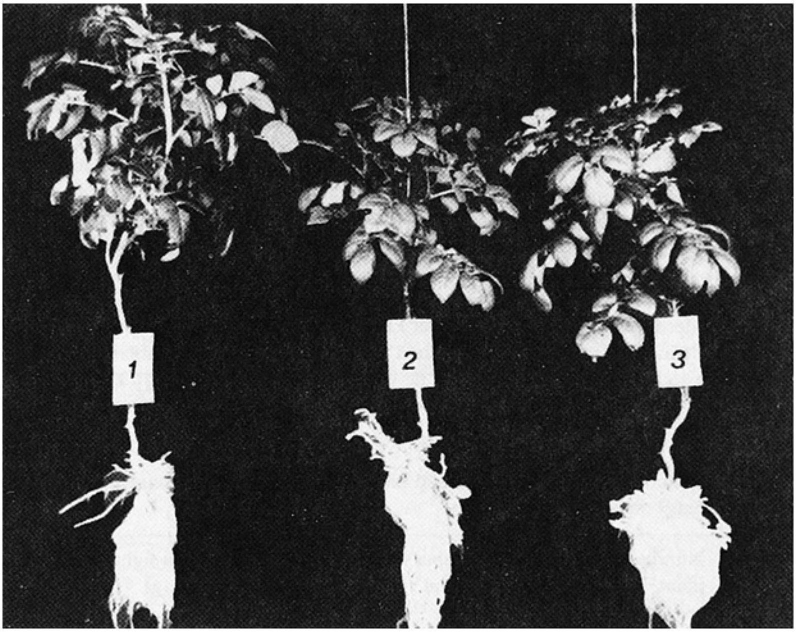

Abb. 1. Auswirkung unterschiedlicher N-Ernährung auf das Wachstum von Kartoffelpflanzen. Versuchsdauer 21 Tage. Links: kont. N; Mitte: diskont. N; Rechts: diskont. N aber gleichzeitig Harnstoff-Blattdüngung.

Fig. 1. Effets de différentes nutritions en azote sur la croissance des plantes de pommes de terre. Durée de l'essai 21 jours. Gauche: N-continu; centre: N-discontinu; droite: N-discontinu avec application simultanée d'urée sur les feuilles.

The total nitrogen content in both roots and shoots was high in the plants with cont. N, and substantial amounts of nitrate were present in the shoots in particular (Table 1). With discont. N, the total nitrogen content and especially the nitrate content dropped sharply during the 3 weeks of nitrogen withdrawal. With additional nitrogen supply as urea via the leaves, it was almost possible to maintain the same level of reduced nitrogen in the leaves as with cont. N. However, there seemed to be no net retranslocation of this leaf-applied nitrogen into the roots.

In order to verify these results, the experiment was repeated but the duration of the treatments was reduced from 21 to 9 days. As can be seen in Fig. 2, the results of the previous experiment could be confirmed in principle: nitrogen withdrawal from the root medium led to a decrease in nitrate content of both roots and shoots, but had scarcely any effect on the amount of reduced nitrogen during the 9 days of nitrogen withdrawal. Additional nitrogen supply as urea via the leaves of plants without

Table 1. Influence of nitrogen nutrition on the content of nitrogen in potato plants (in mg/g dry weight). Age of plants at time of harvest 50 days; duration of treatment 21 days.

Nitrogen nutrition (during treatment)[1]	Total N[2]		Reduced N[5]		Nitrate N[6]	
	shoot[3]	roots[4]	shoot	roots	shoot	roots
+ N (root)	53	41	43	37	10	4
– N	26	31	25	30	1	0.5
– N + urea (via leaves)[7]	40	25	39	25	1	0.3

[1] *Stickstoffernährung (während der Behandlung) - Nutrition en azote (pendant le traitement)*; [2] *Gesamtstickstoff N-total*; [3] *Stengel - Pousse*; [4] *Wurzel - Racine*; [5] *Reduzierter Stickstoff - N-réducteur*; [6] *Nitratstickstoff N-nitrique*; [7] *Harnstoff (über die Blätter) - Urée (via feuilles)*

Tabelle 1. Einfluss unterschiedlicher N-Ernährung auf den N-Gehalt in Kartoffelpflanzen (Angaben in mg/g Trockengewicht). Alter der Pflanzen zum Zeitpunkt der Ernte 50 Tage; Behandlungsdauer 21 Tage.
Tableau 1. Influence de la nutrition en azote sur la quantité d'azote présente dans les plantes de pommes de terre (en mg/g de matière sèche). Age des plantes lors de la récolte 50 jours; durée du traitement 21 jours.

Table 2. Influence of nitrogen nutrition on tuberization and tuber weight. Age of plants at time of harvest 39 days; duration of treatment 9 days.

Nitrogen nutrition (during treatment)[1]	Number of tubers/ plant[2]		Tuber weight/ plant[3] (g)		Tuber weight/ tuber[4] (g)	
	$\bar{x}$ mean[5]	standard deviation[6] s_x	$\bar{x}$	s_x	$\bar{x}$	s_x
+ N (root)	–	–		–		-
– N	4.2	5.2	0.8	0.6	0.2	0.1
– N + urea (via leaves)[7]	16.6	17.6	2.0	2.2	0.1	0.03

[1, 7] *Siehe Tabelle 1 - Voir tableau 1*; [2] *Zahl der Knollen/Pflanze Nombre de tubercules par plante*; [3] *Knollengewicht/Pflanze - Poids des tubercules par plante*; [4] *Knollengewicht/Knolle Poids des tubercule par tubercule*; [5] *Mittelwert - Moyenne*; [6] *Standardabweichung - Ecart type*

Tabelle 2. Einfluss unterschiedlicher N-Ernährung auf Knolleninduktion und Knollengewicht. Alter der Pflanzen zum Zeitpunkt der Ernte 39 Tage; Behandlungsdauer 9 Tage.
Tableau 2. Influence de la nutrition en azote sur l'induction de la tubérisation et le poids des tubercules. Age des plantes à la récolte 39 jours; durée du traitement 9 jours.

nitrogen in the root medium led to a higher nitrogen content in the shoots than in plants with cont. N.

Despite the increase in nitrogen content of the shoots and the almost unaffected nitrogen content of the roots (Fig. 2), tuberization was not delayed or prevented by spraying the leaves with urea (Table 2). By contrast, the number of tubers per plant was increased in comparison to plants with discont. N. In this experiment, as well, no tuberization took place in the plants with cont. N.

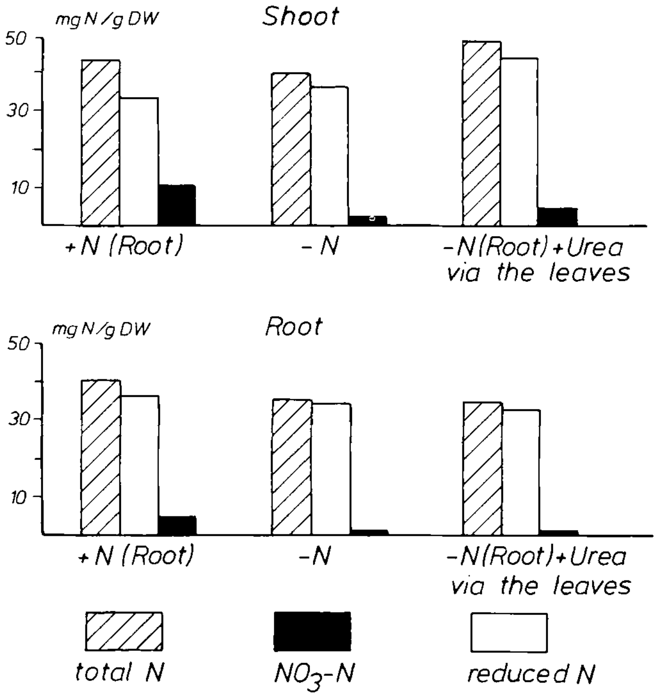

Fig. 2. Influence of different nitrogen nutrition on nitrogen content of potato plants. Age of plants at time of harvest 39 days; duration of treatment 9 days.

mg N/g DW	*mg N/g Trockengewicht*	*mg N/g de matière sèche*
Shoot	*Stengel*	*Pousse*
Root	*Wurzel*	*Racine*
Urea via the leaves	*Harnstoff über die Blätter*	*Urée via les feuilles*
Reduced N	*Reduzierter N*	*N-réducteur*

Abb. 2. Einfluss unterschiedlicher N-Ernährung auf den N-Gehalt in Kartoffelpflanzen. Alter der Pflanzen zum Zeitpunkt der Ernte 39 Tage; Behandlungsdauer 9 Tage.

Fig. 2. Influence de différentes nutritions en azote sur la quantité d'azote présente dans les plantes de pommes de terre. Age des plantes à la récolte 39 jours; durée du traitement 9 jours.

Discussion

Judging from the results obtained in the present study, it can be assumed that nitrogen nutrition does not influence tuberization and tuber growth directly via the protein or carbohydrate metabolism of the plants, as postulated by Werner (1934).

After 9 days of nitrogen withdrawal, the content of reduced nitrogen in the plants with discont. N was practically the same as in the plants with cont. N (see Fig. 2). When urea was applied to the leaves during the nitrogen withdrawal period, the nitrogen content of the leaves was even higher than in plants with cont. N; nevertheless, tuberization still took place after this urea treatment (Fig. 1, Table 2). It is unlikely that there are interferences between the effect of nitrogen applications to the roots and to the leaves on tuberization, and between the different forms of nitrogen (nitrate versus urea), since tuberization is prevented by both nitrate and ammonium when they are supplied continuously to the roots (Krauss & Marschner, 1976).

It is, therefore, much more likely that nitrogen nutrition regulates tuberization by changing the endogenous phytohormone level in the different organs of the potato plant.

Little information is available about the regulatory mechanism of the exogenous factors which influence tuberization.

Regarding the factor daylength, it could be demonstrated that the leaves are the site of reception (Leopold, 1964). However, the shoot not only represents the site of reception, but the 'stimulus' for tuberization is also formed in these organs (Hammes & Beyers 1973). As demonstrated by Chapman (1958), this 'stimulus' can be transferred by grafting.

With respect to the factor nitrogen nutrition, no such investigation has yet been made. If the shoot is likewise the site from which the 'stimulus' for tuberization comes, then it must receive information about the state of nitrogen nutrition from the roots, since tuberization is only a response to the regime of nitrogen supplied via the root (Table 2).

'Nitrogen deficiency theory'

When nitrogen is withdrawn from the nutrient solution, the root translocates insufficient nitrogen in reduced form as amino or amide nitrogen into the shoot. The latter reacts to the nitrogen deficiency by forming the 'stimulus'.

According to this theory, the root exclusively acts as the organ for uptake and translocation. It does not convert the nitrogen nutritional status into hormonal information. This assumption is contradicted by two results of the present study:

a) tuberization cannot be delayed by means of urea application via the leaves during the period of nitrogen withdrawal;

b) after 9 days of nitrogen withdrawal, only the nitrate content, but not the reduced nitrogen content of the shoots was decreased, i.e., nitrogen deficiency did not occur.

Furthermore, the stunted shoot growth of the plants without nitrogen in the root medium could not be overcome by urea application to the leaves (Fig. 1). It can, therefore, be assumed that, under conditions of nitrogen deficiency in the root region, a substance in the roots which is essential for normal shoot development fails to be produced.

'Ageing theory'

As a result of nitrogen withdrawal, the cytokinin activity in the xylem exudate of potato plants decreases sharply (Sattelmacher & Marschner, 1978b). It can, therefore, be assumed that nitrogen withdrawal leads to a decrease in cytokinin supply from the roots to the shoots of intact plants as well. This view is also supported by the decrease in cytokinin activity in the shoots of non-induced plants during the period of nitrogen withdrawal (Sattelmacher & Marschner, 1978a).

A reduced supply of cytokinins from the roots could accelerate the ageing of the shoot (Sitton et al., 1967; Goldbach et al., 1975; Krauss & Marschner, 1976). As is well known, this brings about an increase in ABA content in the leaves, while the GA content drops (Chin & Beevers, 1970; Rajagopal & Rao, 1974). Increase in ABA and decrease in GA content are both factors which favour tuberization or always accompany it (Hammes & Nel, 1975; Krauss & Marschner, 1976).

On the basis of these results, the following model would seem to be conceivable: nitrogen withdrawal reduces the cytokinin supply from the roots to the shoot. The 'physiological ageing' of the plant is thus accelerated – the GA content drops, the ABA content rises. This 'stimulus' is translocated basipetally into the stolons and here it causes tuberization.

However, there are still several observations which are difficult to fit into this simple picture of the 'ageing theory' directed by the cytokinin supply from the roots. Application of kinetin to the leaves does not prevent tuberization under conditions of discont. N and, simultaneously with tuberization, the cytokinin activity in the shoot is increased (Sattelmacher & Marschner, 1978b).

Even though, according to the results obtained with other factors that control tuberization (Okazawa & Chapman, 1962; Hammes & Beyers, 1973), the assumption that the stimulus comes from the shoot also for the factor nitrogen nutrition appears justified, the possibility that this 'stimulus' is formed in the roots still cannot be ruled out.

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Zusammenfassung

Unterschiedliche Wirkung von Stickstoffzufuhr über die Wurzeln und über die Blätter auf die Knolleninduktion bei Kartoffeln

In Wasserkulturversuchen mit Kartoffelpflanzen (*Solanum tuberosum* L., Sorte 'Ostara') wurde unter kontrollierten Umweltbedingungen (12 h Tageslänge, 20 C Tag und Nacht) der Einfluss von Stickstoffzufuhr über die Wurzeln bzw. über die Sprosse untersucht. Ein Teil der Pflanzen wuchs während der gesamten Versuchsdauer in vollständiger Nährlösung (kont. N), ein anderer wurde für 21 (Versuch 1) bzw. 9 (Versuch 2) Tage in Nährlösungen ohne Stickstoff (diskont. N) übertragen. Bei der Hälfte dieser Pflanzen in der Nährlösung ohne Stickstoff erfolgte Besprühen der Blätter mit Harnstofflösungen.

Verglichen mit den Pflanzen bei kont. N zeigten die Pflanzen beider Varianten mit diskont. N (± Harnstoff über die Sprosse) ein gestauchtes Wachstum (Abb. 1). Bei kont. N über die Wurzeln wurde die Knolleninduktion verhindert, bei diskont. N trat Knolleninduktion ein, auch bei gleichzeitiger Behandlung der Sprosse mit Harnstoff (Abb. 1 und Tabelle 2). Zwischen der Knolleninduktion und dem Gehalt der Pflanze an Gesamt-Stickstoff, Nitrat- und reduziertem Stickstoff bestanden keine Korrelationen (Abb. 1, 2 und Tabellen 1, 2).

Die Ergebnisse lassen vermuten, dass der die Knolleninduktion auslösende 'Stimulus' zwar aus dem Spross kommt, der Spross aber die Information über den speziellen Stickstoffernährungszustand der Wurzeln durch Verschiebungen im Spektrum der wurzelbürtigen Phytohormone erhält.

Résumé

Effets de l'apport d'azote par les racines et par les feuilles sur la formation des tubercules de la pomme de terre

L'influence de l'apport d'azote par les racines et par les feuilles de la pomme de terre (*Solanum tuberosum* L., variété 'Ostara') a été étudiée avec des essais en hydroculture, dans un environnement contrôlé (longueur du jour 12 h, et 20 C jour et nuit). Une partie des plantes a été maintenue pendant toute la période d'essai dans une solution nutritive complète (N-continu); et l'autre partie a été transférée pendant 21 jours (essai 1) et 9 jours (essai 2) dans des solutions nutritives sans azote (N-discontinu). Sur la moitié des plantes cultivées dans le milieu sans azote, les feuilles ont été aspergées avec une solution d'urée.

Les plantes cultivées dans les deux variantes N-discontinu (application de ± d'urée sur les pousses) présentent une croissance moins élancée que celles cultivées en N-continu (fig. 1). Lors de l'apport continu d'azote aux racines il n'y a pas d'induction de la tubérisation (fig. 1, tableau 2). Par l'apport discontinu d'azote, l'induction de la tubérisation eut lieu, malgré l'application d'urée sur les pousses.

Il n'a pas été observé de corrélation entre l'induction de la tubérisation et la teneur totale d'azote, de nitrate, et d'azote réducteur des plantes (fig. 1, 2 et tableaux 1, 2).

Les résultats laissent présumer que le déclanchement du 'stimulus' de l'induction de la tubérisation provient de la pousse. Cependant, l'information arrive à la pousse par un changement du spectre des phytohormones, qui est causé par la nutrition particulière des racines en azote.

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