Potato Res. 24 (1981) 267-278

Effects of a mixture of NAA + BA on numbers and growth rates of tubers of *Solanum tuberosum* L.

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Accepted for publication: 3 March 1981

Zusammenfassung, Résumé p. 276

Additional keywords: tuber initiation, growth regulators, sand-vermiculite units

Summary

A mixture of NAA at 10 mg l^{-1} + BA at 1 mg l^{-1} caused increases in growth rates of treated tubers of potato. Sub-irrigation and foliage sprays with the same mixture caused tuber initiation and increased the growth rates of some of the tubers. In a field study substantial increases in tuber number and final tuber volume per plant were recorded.

Introduction

Tuber yield of a potato plant can be regarded as the summation of three separate processes, stolon development, the proportion of stolons which tuberize and the growth of initiated tubers. Booth (1959) and Kumar & Wareing (1974) have demonstrated that stolon development in *Solanum andigena* L. is regulated by the interaction between endogenous hormones. Numerous reports about the control of tuber initiation have been published (e.g. Gregory, 1956; Lovell & Booth, 1967; Palmer & Smith, 1969) and Moorby (1978) has recently reviewed the subject. According to one hypothesis, tuber initiation may be due to the accumulation of high levels of soluble carbohydrates at stolon tips, according to another, tuberization is hormonally controlled. In the former view there is a 'push' of carbohydrates from the leaves to a passive sink (Edelman, 1963), in the latter there may be a 'pull' by an active sink. The observations of Burt (1964) and of Nösberger & Humphries (1965) that removal of tubers depresses net assimilate rate tend to favour the second view.

The homeostatic control of growth of plants is incompletely understood but there is a general consensus that growth regulating substances are involved.

Potato tubers are the major sinks of a potato plant (Baker & Moorby, 1969) but the mechanism that controls sink strength in tubers has not been established; however the growth of the tuber is primarily the result of cell division and subsequent cell enlargement (Artschwager, 1924; Reeve, Timm & Weaver, 1973a). Phillips (1975) has suggested that sink strength is under the influence of a hormone that regulates cell expansion.

The involvement of several growth regulating substances in tuberization and in

tuber development has been reported (Van Staden & Dimalla, 1976, 1977). Evidence has been found of cytokinin like substances in potato tubers (Anstis & Northcote, 1975) and of gibberellins (Tizio, 1971). However, it is most likely that tuber growth is controlled by a balance of two or more growth regulators. Further, the growth response at any time may depend on hormone concentrations (Webb, Van Staden & Wareing, 1973) or a balance between levels of inhibitors and promoters (Kefeli & Kadyrov, 1971).

There have been two different approaches to the study of growth regulating substances in plants. The first has been by analysis where changes in absolute and relative concentrations of hormones have been measured, the second by exogenous applications of known amounts of growth substances. In the present study, GA (gibberellic acid), NAA (α-naphthaleneacetic acid), BA (N^6 benzyladenine), abscisic acid and ethephon (2-chloroethylphosphonic acid) were tested separately for their effects when applied directly to the tubers; later, mixtures and different concentrations of NAA, BA and GA were tested both by direct and by more general application. The application of each of these substances alone did not produce useful effects (Ahmed, 1978) and only the later experiments are reported here.

Materials and methods

Experiment 1

On 2 August 1976, 34 pre-sprouted tubers of potato cv. Maris Peer, each 40–50 g fresh weight and from which all buds except the apical bud had been removed, were planted separately 10 cm deep in damp quartz sand in 20.3 cm diameter plastic pots. These pots were placed in a Saxcil growth cabinet where temperatures were 18 ± 2 °C (day) and 9 ± 2 °C (night). The relative humidity was maintained between 60–70 %. Day length was 16 hours and light intensity at pot height 22 klux; four 100 W tungsten bulbs were suspended in the cabinet. Pots were irrigated daily. On 27 August, 16 uniform plants, with single shoots 10–15 cm high, were transfered into sand-vermiculite units. (The mother tubers of these single shoots were removed at this stage). Sixteen such units, each containing one plant were placed in a growth cabinet.

The sand-vermiculite units (Fig. 1) were containers with vermiculite (in which the roots grew) in the lower half separated from an upper half containing dry sand (in which stolons and tubers grew). They have been described in detail by Hewitson (1967) and the same general procedures were followed in the present studies. In brief, 26 cm diameter, dark green plastic buckets with a 2.5 cm^2 hole in the centre of the base were selected and half of a 30.5 cm long, 2.5 cm diameter wick (WK) made from water-absorbent cottonwool was passed through the hole of each bucket. Into the bucket a 12-cm-deep layer of vermiculite (V), which had been sieved to remove all particles less than 2 mm and which had been soaked in Long Ashton nutrient solution, was introduced. Over the layer of vermiculite a fitted sheet of polythene (PS) with a 1-cm^2 hole in the centre was laid. The roots of a plant were threaded through this hole and planted into the vermiculite. The polythene sheet was secured to the bucket, the upper chamber of which was then filled with dry sand (SD) (washed, coarse concrete gravel, size grade 1/8 to dust).

The units were supported on troughs (123 cm × 10 cm × 5 cm) containing nutrient

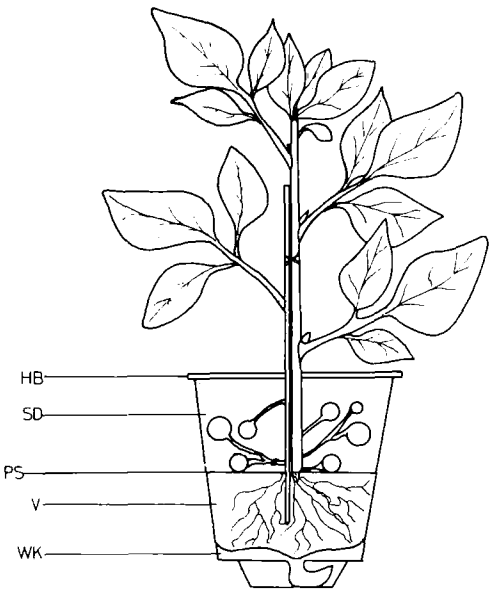


Fig. 1. The growth units used for sand-vermiculite culture of potatoes in the growth cabinet. SD, air-dry sand; HB, hardboard covers; PS, polythene sheet; V, vermiculite; WK, wick.

Abb. 1. Spezialbehälter, die für die Sand-Vermiculite-Kultur von Kartoffeln in den Vegetationskabinen benutzt wurden. SD, lufttrockener Sand; HB, feste Dechel; PS, Polythenefolie; V, Vermiculite; WK, Pfropfen.

Fig. 1. Les unités de croissance utilisées pour la culture des pommes de terre en pots contenant du sable et de la vermiculite. SD, sable sec; HB, couvercle dur; PS, film en polyéthylène; V, vermiculite; WK, mèche.

solution and the exposed ends of the wicks were in contact with the solution. The troughs were filled daily with Long Ashton solution during the first week after the plants were transferred. Later, de-ionized water was added daily but the troughs were cleaned and refilled with fresh nutrient solution every two weeks.

To examine the tubers, the sand was extracted with a domestic vacuum cleaner. The sand was replaced after appropriate observations had been made. Tubers were identified by using plastic-covered rings of different colours and secured onto the stolons. Tubers were measured by using dividers and volume was calculated as $(a \times b^2 \times \pi)/6$, where a is length of the tuber and b is the mean diameter of the tuber (Hewitson, 1967).

From the sixteen units, twelve were selected for treatment with NAA and BA in different combinations (Table 1).

Tuber volumes were measured 0, 1 and 2 weeks before 11 October when the two fastest and the two slowest growing tubers on each plant were identified, placed individually into separate plastic weighting boats (8 cm × 6 cm × 2 cm deep) and covered with absorbent cotton wool. After this, 25 cm^3 of the appropriate solution was added dropwise to the cotton wool. The weighing boat was then covered by another (inverted) in which a small slit had been made, to allow the stolon to pass through. This treatment unit was then secured to the polythene sheet at the interphase between sand and vermiculite. Two days later the treatments were discontinued. On 18 and 25 October the dimensions of all the tubers on each plant were determined.

Experiment 2

On 10 November 1976, 34 pre-sprouted tubers of potato (cv. Maris Peer) were planted in sand in a growth cabinet (see Expt. 1 for details). On 22 December, sixteen uniform plants were transferred into growth units which were supported on troughs containing mineral nutrients (Expt. 1). The dimensions of all the tubers on all these plants were measured three, four and five weeks after transfer to the units. Twelve units were selected for the experiment which had four treatments in its design: (i) control; (ii) direct application of hormones to the tubers; (iii) application of hormones by sub-irrigation; (iv) foliage application of hormones. Solution No 6 (Table 1) was used.

On 25 January 1977 the treatments were given. Control plants were supported on a trough containing only distilled water. The method of direct treatment of the hormones to the tubers was similar to that described for Expt. 1. Units receiving the sub-irrigation treatment were supported on separate plastic bowls (each 17 cm diameter and 6 cm deep) containing 800 cm^3 of solution. To spray the plants, Hills All Purpose Hand Sprayer No 34 was used. Spraying was done outside the growth cabinet at a rate of approximately 50 cm^3 per plant. On return to the growth cabinet the sprayed plants were supported on a trough filled with distilled water. Direct treatment of hormones to the selected tubers ceased on 27 January while irrigation and daily foliage spray treatments were both continued for one week. Tubers were subsequently measured on 1 and 8 February.

Experiment 3

Eighty-four pre-sprouted tubers, 40–50 g fresh weight of cv. Maris Peer from which all buds except the apical bud had been removed were, on 24 March 1977, planted 15 cm deep and 30 cm apart in an area prepared for a standard commercial potato crop. The 84 plants were divided into sets of four plants to allow three replicates of seven treatments.

Table 1. Concentrations of NAA and BA in the six mixtures used to treat the selected potato tubers. All solutions contained 0.01 % Tween 20.

Solution No[1]	Concentration[2] (mg l^{-1})	
	NAA	BA
1 (control[3])	0	+ 0
2	1	+ 10
3	5	+ 10
4	10	+ 10
5	10	+ 5
6	10	+ 1

[1] *Nummer der Lösung - Numéro de la solution;* [2] *Konzentration - Concentration;* [3] *Kontrolle - Témoin*

Tabelle 1. Konzentrationen von NAA und BA, in den sechs Mischungen, die zur Behandlung der ausgesuchten Kartoffelknollen benutzt wurden. Alle Lösungen enthielten 0,01 % Tween 20.
Tableau 1. Concentrations de NAA et BA dans les six mélanges utilisés pour traiter les tubercules de pommes de terre choisis. Toutes les solutions contiennent 0,01 % de Tween 20.

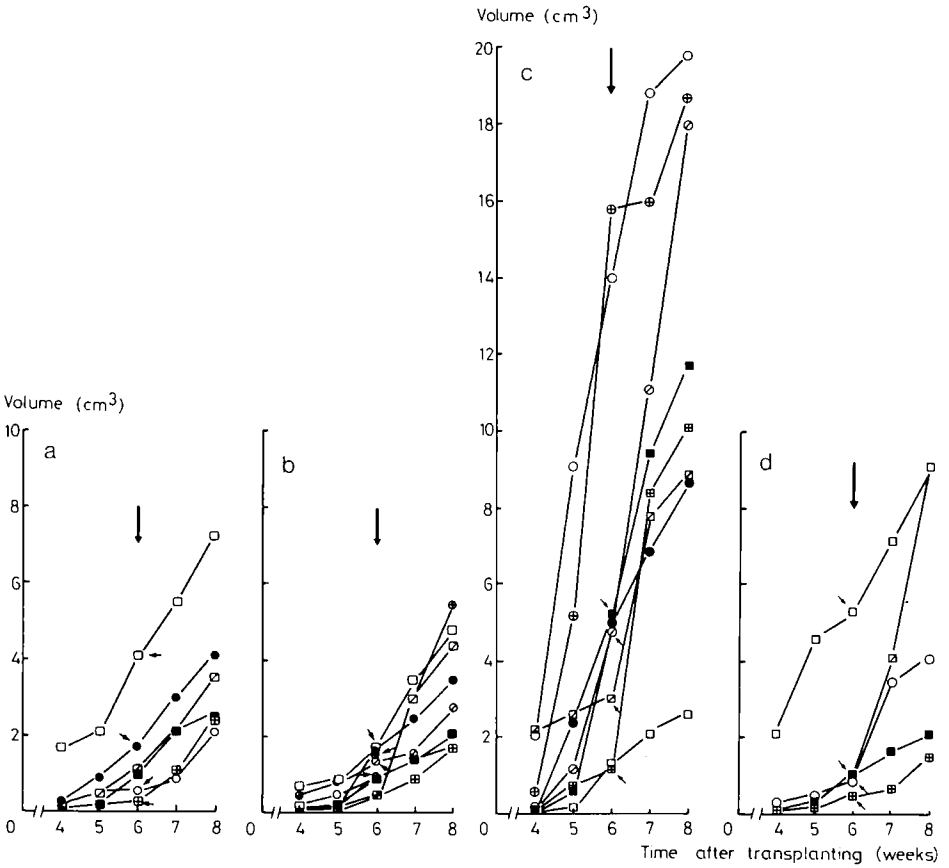


Fig. 2. The effects of distilled water (plants a & b) or a mixture of 10 mg l^{-1} NAA + 1 mg l^{-1} BA (plants c & d) given to four selected tubers on each plant. The small arrows indicate the tubers which were treated. The large arrow shows the time of treatment.

Volume (cm^3) - *Volumen - Volume*
Time after transplanting (weeks) - *Zeit nach dem Umpflanzen (Wochen) - Durée après transplantation (semaines)*

Abb. 2. Einfluss von destilliertem Wasser (Pflanzen a & b) oder einer Mischung von 10 mg l^{-1} NAA und 1 mg l^{-1} BA (Pflanzen c & d), auf 4 ausgesuchte Knollen von jeder Pflanze. Die kleinen Pfeile zeigen die behandelten Knollen. Der grosse Pfeil zeigt den Zeitpunkt der Behandlung.
Fig. 2. Effets de l'application d'eau distillée (plantes a & b) ou d'un mélange de 10 mg l^{-1} de NAA + 1 mg l^{-1} BA (plantes c & d) sur quatre tubercules choisis par plante. Les petites flêches indiquent les tubercules qui sont traités. La grande flêche montre la date du traitement.

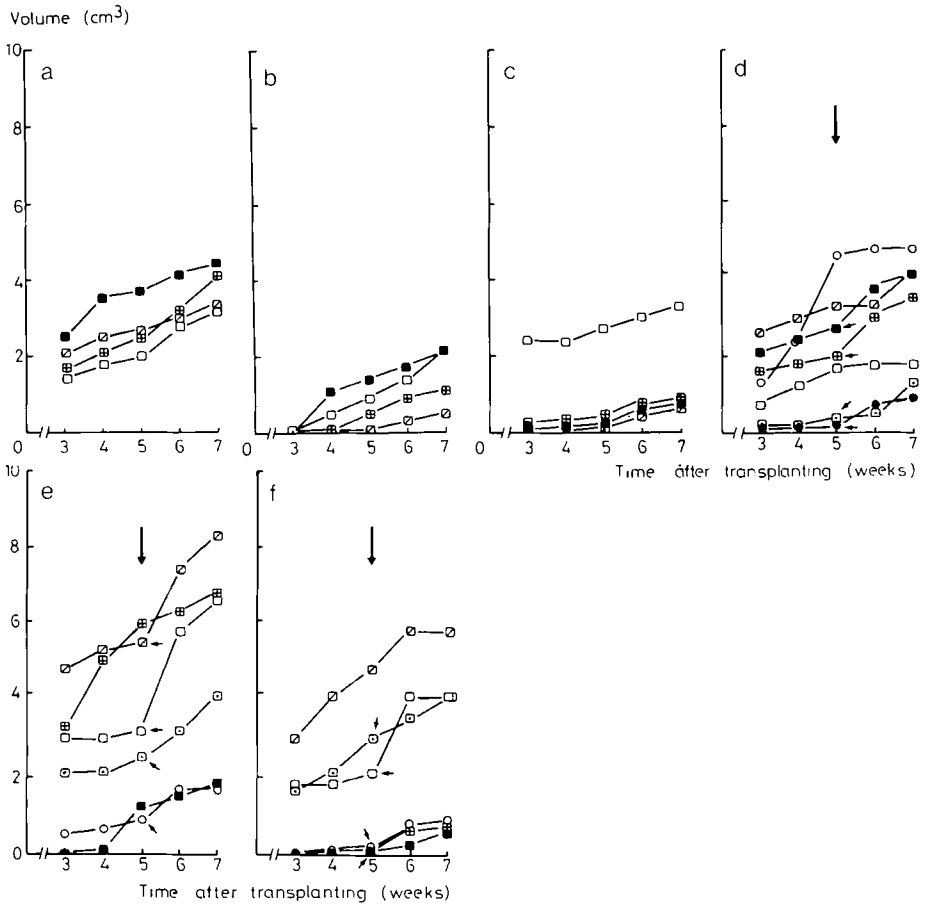
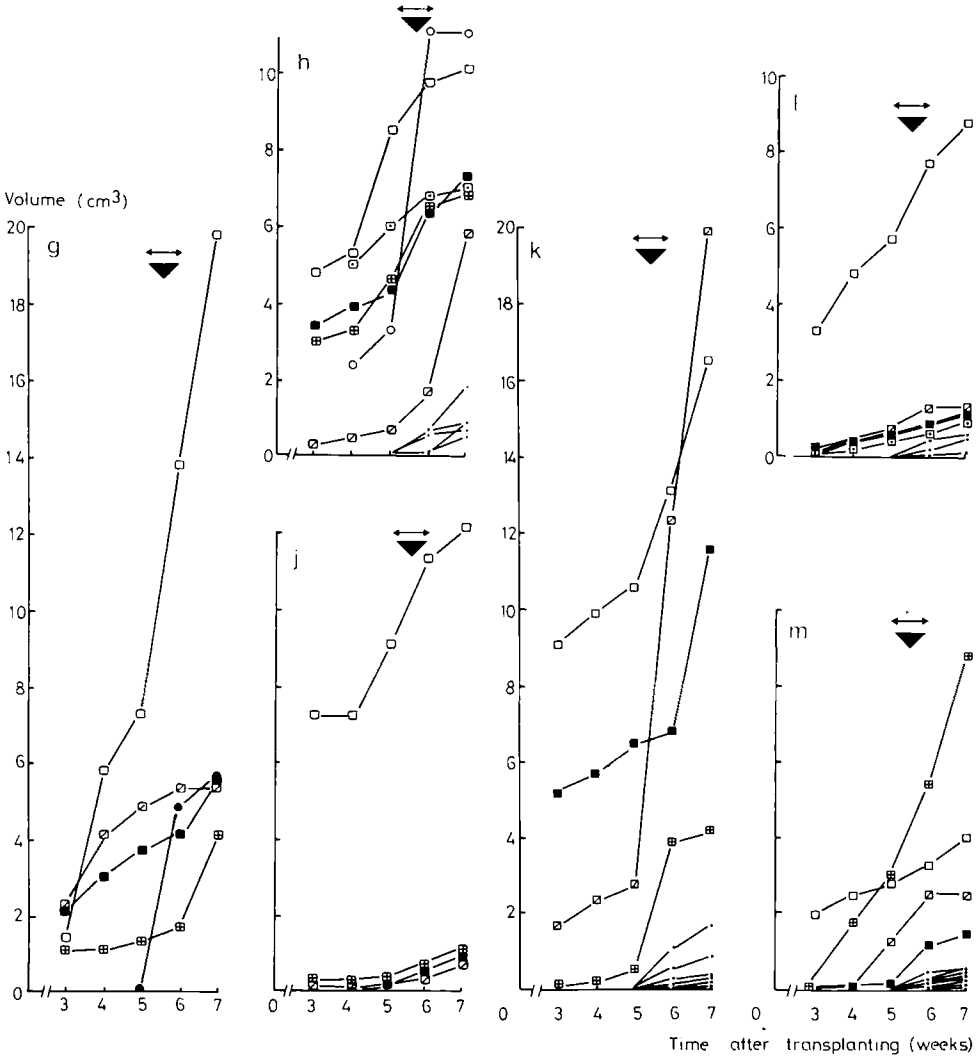


Fig. 3. The effects of a mixture of 10 mg l^{-1} NAA + 1 mg l^{-1} BA given to four selected tubers (plants d-f), to roots (plants g-j) or sprayed onto the haulm (plants k-m) on tuber growth and initiation of tubers. Control (plants a-c). Small arrows on (d)-(f) indicate the tubers which were treated. Large arrows show the dates of treatment.

Volume (cm^3), Time after transplanting (weeks) - *Siehe Abb. 2 - Voir Fig. 2*

Abb. 3. Einfluss einer Mischung von 10 mg l^{-1} NAA und 1 mg l^{-1} BA nach Applikation auf 4 ausgesuchte Knollen (Pflanzen d-f), auf Wurzeln (Pflanzen g-j) oder nach Spritzung der Stengel (Pflanzen k-m) auf das Knollenwachstum und die Knollenbildung. Kontrolle (Pflanzen a-c). Kleine Pfeile auf (d)-(f) bezeichnen die behandelten Knollen. Grosse Pfeile zeigen die Behandlungsdaten.

Fig. 3. Effets de l'application d'un mélange de 10 mg l^{-1} de NAA et 1 mg l^{-1} de BA sur quatre tubercules choisis (plantes d-f), sur les racines (plantes g-j) ou sur le feuillage (plantes k-m): effet sur la croissance et l'initiation des tubercules. Témoins (plantes a-c). Les petites flêches sur (d)-(f) indiquent les tubercules qui ont été traités. Les grandes flêches montrent les dates de traitement.



Beginning on 12 May 1977 the foliage of plants was sprayed with either distilled water plus 0.01 % Tween 20 or a mixture of NAA (10 mg l^{-1}) and BA (1 mg l^{-1}) with 0.01 % Tween 20. Sprays were given on 0, 1, 3 or 7 days for one week and on each occasion 50 cm^3 of the appropriate liquid was given to each plant. Drift was prevented. All the plants were harvested individually on 24 June and the data on tuber number and volume were analysed with Duncan's Multiple Range Test (Duncan, 1955).

Results

Experiment 1

On control plants (Fig. 2a & b) none of the eight nominated tubers showed any marked change in growth rates after receiving the treatment and similar nil responses were recorded for all the other treatments except 10 mg l^{-1} NAA + 1 mg l^{-1} BA. However, six of the eight tubers treated with the latter mixture showed increased growth rates after the treatment (Fig. 2c & d).

Experiment 2

On the control plants (Fig. 3a–c) all tubers grew slowly from the time of first recording up to the end of the experiment. By contrast, eleven of the twelve tubers treated directly with the hormone mixture showed increased growth rates after the treatment (Fig. 3d–f). Sub-irrigation with the growth regulator mixture did not cause changes in the growth rates of all the tubers that were established before the treatment began although a few tubers did show increased growth rates during the week after treatment was withdrawn (Fig. 3g–j). However, on one plant one new tuber and on another five new tubers were initiated during the treatment period. The third plant showed no response to treatment. Foliage treatments did not show consistent changes in the

Table 2. The results of the field study where the mixture of NAA (10 mg l^{-1}) and BA (1 mg l^{-1}) was sprayed onto the foliage of potato plants.

NAA + BA (mg l^{-1})	Number of times treated per week[1]	Mean number of tubers per plant at harvest[2]	Mean total volume of tubers per plant at harvest[3] (cm)
0 + 0	0	11.7 cd*	405.5 c
0 + 0	1	9.0 d	549.1 c
0 + 0	3	7.9 d	538.5 c
0 + 0	7	10.3 d	448.9 c
10 + 1	1	17.7 bc	474.6 bc
10 + 1	3	20.7 ab	684.7 ab
10 + 1	7	25.9 a	843.3 a

* Values in a column sharing a common letter do not differ significantly at the 5 % level of probability (Duncan, 1955) - *Werte in einer Reihe, die durch den selben Buchstaben gekennzeichnet sind, unterscheiden sich nicht signifikant auf dem 5 % Wahrscheinlichkeitsgrad (Duncan, 1955) - Les valeurs d'une même colonne qui sont suivies de la même lettre ne sont pas significativement différentes au seuil de probabilité 5 % (Duncan, 1955).*

[1] *Anzahl der Behandlungen pro Woche - Nombre d'applications par semaine;* [2] *Durchschnittliche Zahl der Knollen/Pflanze bei der Ernte - Nombre moyen de tubercules par plante à la récolte;* [3] *Durchschnittliches Gesamtvolumen (cm^3) der Knollen/Pflanze bei der Ernte - Volume total moyen de tubercules par plante à la récolte*

Tabelle 2. Ergebnisse der Feldversuche, in denen die Mischung aus NAA (10 mg l^{-1}) und BA (1 mg l^{-1}) auf die Kartoffelblätter gesprüht wurde.

Tableau 2. Résultats des études de plein champ dans lesquels le mélange de NAA (10 mg l^{-1}) et BA (1 mg l^{-1}) a été pulvérisé sur le feuillage de plantes de pommes de terre.

growth rates of tubers initiated before the treatment began but seven new tubers were initiated on one plant, three new tubers on a second, and ten new tubers on the third during the period of treatment (Fig. 3k–m).

Experiment 3

In general, control plants produced fewer tubers than did plants sprayed with the growth regulator mixture (Table 2). Plants which received three or seven sprays of the mixture had significantly more tubers per plant than did any of the plants in the control treatments. Mean tuber volume per plant followed similar trends, the more frequent spray treatments of the mixture increasing volume yield significantly. In general mean volume per tuber was decreased by spraying the mixture.

Discussion

During the past two decades it has become clear that several of the processes involved in the growth and development of the potato can be influenced by exogenous applications of growth regulating substances and there has emerged a body of evidence which suggests that each process is controlled by an interplay of these substances.

The increase in growth rates of slow growing tubers supplied directly and exogenously with the mixture of NAA (10 mg l^{-1}) + BA (1 mg l^{-1}) in solution (Expt. 1) allows the suggestion that a tuber which is growing slowly has a sub-optimal endogenous balance of growth regulating substances.

A potato tuber, attached to the haulm and the root system of a whole plant via the stolon is made up of cells which are either meristematic, enlarging, differentiating, storing or almost dormant. Presumably, according to current hypotheses, it is fair to suggest that each of these aspects of cellular activity is under the control of growth regulating substances. Very short term increases in the volume of a potato tuber must be due primarily to increases in the size (volume) of individual cells. Auxin (IAA) is known to be involved in cell extension in many tissues (Bonner, Bandurski & Millerd, 1953). Similarly, gibberellic acid is widely believed to be involved in the enlargement of cells (Wareing & Phillips, 1976). Yet in the present study it was the combination of an auxin (NAA) and a cytokinin (BA) which promoted the rate of increase in volume. Cytokinins are believed to be involved in cell division; indeed Osborne (1962) reported that tissue cultures of tobacco required both auxin and kinetin before continuous culture was possible. It seems reasonable to suggest that in the present studies acceleration of volume increase following exogenous applications of an auxin and a cytokinin may have been the result of increasing both meristematic activity and the rate of cell enlargement.

Rather unexpectedly the same mixture of growth regulating substances either sprayed onto the leaves or applied to the roots by irrigation also caused some increases in the rates of tuber growth (Expt. 2). This observation leads to questions about the mobility of effective growth regulators. The simplest hypothesis is one where the NAA and BA, sprayed onto leaves and penetrating into them, were loaded into the phloem transport system and carried by mass flow to the tubers where they were unloaded and then transported to dividing and enlarging cells. Similarly the root applied mixture

may have been taken up by the epidermal cells of the roots, transported across the cortex, endodermis and pericycle of the root, loaded into the xylem (actively or passively) where it may have gone directly to the tuber or indirectly via the leaves and, with subsequent re-export, via the phloem. An alternative hypothesis can be constructed - one where NAA and BA, wherever applied, do not have their effects in the tuber at all, but rather in say the leaves. It would be very rewarding to use ^{14}C-labelled NAA and BA to follow the patterns of distribution of these compounds after they have been supplied exogenously. The sites of synthesis and the patterns of distribution of endogenous growth regulating substances have not been studied in the present work.

The present work was done to study increase in volume of growing tubers. Not only was tuber volume increase affected by the mixture of NAA and BA but new tubers were also initiated in a significant number of those plants whose leaves were sprayed with the mixture.

The field study (Expt. 3) merits repetition on a larger scale and with more cultivars. If the results are confirmed some exciting possibilities may emerge. It is a possible that carefully timed sprays of the appropriate mixture might be used to control the time of tuberization, the rate of tuber growth or indeed the number of tubers produced by a plant. Such developments might be particularly useful in the production of both early and seed potatoes. In the latter case cultivars producing few large tubers might be made to produce more smaller ones. It is emphasized that departure from the stated doses and ratio of the two growth substances resulted in the loss of the effects reported.

Zusammenfassung

Einfluss eines Gemisches von NAA + BA auf Knollenzahl und Wachstumsrate von Knollen von Solanum tuberosum L

Die Faktoren, die die Knollenbildung und Wachstumsrate bestimmen, sind wenig bekannt. Die äusserliche Anwendung verschiedener Wachstumsregulatoren, die getrennt auf Einzelknollen von Pflanzen, die in Spezialbehältern wuchsen (Abb. 1), aufgetragen wurden, brachte wenig Ergebnisse, die kommerziell nützlich sein konnten. Eine Mischung aus NAA (10 mg/l) und BA (1 mg/l), in der selben Weise angewendet, schien jedoch das Wachstum der meisten behandelten Knollen zu fördern (Abb. 2). In einem 2. Versuch wurde die gleiche Mischung direkt auf ausgesuchte Knollen gegeben und es zeigte sich wieder eine Wachstumssteigerung bei einigen (Abb. 3d-f). Wurden die Wurzeln mit dieser Mischung behandelt, so beschleunigte sich das Wachstum einiger Knollen und in zwei von drei Pflanzen wurde das Wachstum des Knollenansatzes gefördert (Abb. 3g-j). Blattspritzungen führten zu einer starken Knollenbildung (Abb. 3k-m). In einem dritten Versuch wurden pro Woche 3 oder 7 Mal die Stengel gespritzt und das führte zu einem signifikanten Anstieg in der Knollenzahl und im Gesamtknollenvolumen/Pflanze (Tab. 2). Abweichungen von den genannten Konzentrationen oder im Verhältnis der beiden Wachstumsregulatoren ergaben einen Wirkungsverlust. Der Wirkungsmechanismus ist noch nicht geklärt.

Résumé

Effets d'un mélange de NAA + BA sur le nombre et la croissance des tubercules de Solanum tuberosum L.

Les facteurs qui contrôlent la tubérisation et la croissance des tubercules ne sont pas très bien compris. Plusieurs substances régulatrices de la croissance ont été appliquées seules sur des tubercules de plantes cultivées dans des unités spéciales (fig. 1), mais peu d'information commercialement utilisable n'a pû en être tiré. Toutefois, un mélange de NAA (10 mg l^{-1}) plus BA (1 mg l^{-1}) appliqué de la même façon semble stimuler la croissance de la plupart des tubercules traités (fig. 2). Dans une seconde expérimentation, des applications du même mélange, faites encore directement sur les tubercules sélectionnés, favorisent la croissance de certains d'entre eux. Appliqué sur les racines, le mélange favorise la croissance de quelques tubercules ainsi que le début de tubérisation sur deux ou trois plantes (fig. 3g-j). Pulvérisé sur le feuillage, le mélange provoque une importante tubérisation (fig. 3k-m). Dans une troisième expérimentation en plein champ, la pulvérisation sur le feuillage trois à sept fois en une semaine conduit à des accroissements significatifs du nombre de tubercules (tableau 2). Lorsqu'on s'écarte des concentrations établies ou du rapport des deux substances de croissance, ces effets disparaissent. Les mécanismes impliqués ne sont pas compris.

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