Potato Res. 24 (1981) 279-288

Volume increase of individual tubers of potatoes grown under field conditions

CH. M. S. AHMED and G. R. SAGAR

School of Plant Biology, University College of North Wales, Bangor, Wales

Accepted for publication: 11 March 1981

Zusammenfassung, Résumé p. 287

Additional keywords: variation, sink activity, non-destructive measurement

Summary

Non-destructive observations of the growth of every tuber on nine individual potato plants grown in the field revealed great variation in total number of tubers per plant, total tuber volume per plant and the volumes of individual tubers. The number of tubers was established early but the rates of increase in total and mean tuber volume changed greatly up to a short time before the final harvest. The growth rates of individual tubers on each plant also showed great variation and it was clear that the largest tuber at any one time was not necessarily the largest at a later time. Both the duration of the main period of growth and growth rates varied and acted independently to determine the final size of a tuber.

Introduction

Clark (1921) concluded from serial harvests of potato plants that the rates of growth of individual tubers were more important in determining the final size of tubers than was time of initiation. Krijthe (1955), on the unproven assumption that the largest tuber present at harvest had always been the largest, suggested that the weight of a tuber increased linearly with time and also that rates of increase differed greatly between tubers. Moorby (1968) deduced from the results of $^{14}CO_2$ tracer studies that individual tubers showed different rates of growth relative to each other, such that the largest tuber at any time need not necessarily be the largest on any future occasion. On the other hand Plaisted (1957) reported a logarithmic relationship between mean tuber weight and time. More recently Moorby & Milthorpe (1975) concluded that the rate of increase of total tuber volume per plant (the rate of bulking) is exponential for the first two to three weeks but then becomes almost linear. Similarly, Gray (1973), from short-term experiments, indicated that the change in fresh weight of individual tubers with time during the early stages of growth was linear. He assumed that the largest tuber at the time of initial measurements was the first to be initiated.

Sadler (1961) claimed that tuber fresh weight appeared to follow a sigmoid course with time, but that the slopes and duration of this course differed widely between tubers and were not closely related to relative times of initiation. Hewitson (1967) confirmed the hypothesis of Sadler (1961) and added that the differences in size of tubers at harvest were most closely related to the maximum rate of growth attained and the length of the growing period of individual tubers. More recently Wurr (1977), from measurements of the growth of individual tubers, suggested that some tubers followed an approximately sigmoid curve, some grew linearly and some showed periods of growth interrupted by periods when the tubers grew slowly if at all. Further, he added that the time over which tuber formation occurred was not important. Moorby (1978) has recently reviewed some aspects of this problem.

Too little attention has been devoted to the study of the pattern of growth of individual tubers with time. It was felt, therefore, that a study should be made to find the patterns of growth of individual tubers growing in field conditions, for such a study would seem to be an essential preliminary to understanding the causes of variation in tuber size on the same and on different plants.

Materials and methods

On 7 May 1975 sixteen potato plants (cv. Maris Peer) which were a part of a normal outdoor commercial crop (planted on 25 March 1975) were excavated. Standard commercial seed tubers were used. Single shoots which had emerged on average 27 days previously were transferred to special growth units (Fig. 1). These units consisted of the top 13 cm of plastic pots of 26 cm diameter. The bases of these rings were closed by a sheet of polythene which had a 1-cm^2 hole in the centre. Each unit was placed into a pit which had been prepared on the ridges of the potato field at Pen-y-ffridd Experimental Station, Bangor, N. Wales. The tops of the rings were at soil level. The roots of the selected plants were passed through the hole in the polythene sheet and buried in the soft, wet soil of the pit by slurrying. The upper chamber was then filled with dry sand which in turn was covered with non-absorbent cotton wool. Two notched, polythene-covered hard-boards (30 cm $\times$ 15 cm) were then secured onto the top of the pots to provide a reasonably water-tight cover; the notches allowed the shoots to pass through the cover without damage.

To examine the tubers, the sand was extracted at intervals of 2–3 weeks with a

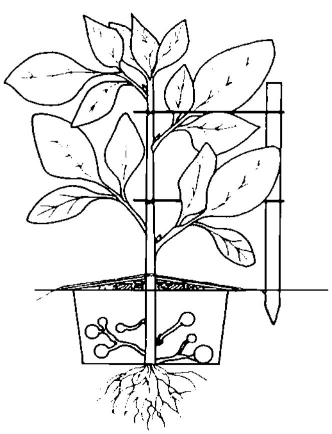

Fig. 1. A growth unit. See text for details

Abb. 1. Ein Spezialbehälter. Einzelheiten siehe im Text.
Fig. 1. Une unité de croissance. Voir le texte pour plus de détail.

domestic vacuum cleaner. The sand was replaced after the appropriate observations had been made. Tubers were identified by using plastic covered rings of different colours which were secured onto the stolons.

Tubers were measured by using dividers. Since tubers are approximately ellipsoidal, volume was calculated as $(a \times b^2 \times \pi)/6$ where a is length of tuber and b its mean maximum diameter (Hewitson, 1967). Measurement of tubers was continued until the death of the above-ground parts of the mother plants.

Results

Total tuber volume per plant

Of 16 plants selected, 9 survived until harvest time. These plants were fully tuberized within four weeks of transfer into the growth units. Plants 1, 8, 6 and 5 produced the greater final total tuber volumes (Fig. 2), all four plants having similar rates and patterns of bulking. Plants 7, 2 and 9 produced lower final total tuber volumes; their rates of bulking declined early, indeed bulking had virtually stopped after 16 weeks. Plant 3 produced only one tuber which grew slowly throughout. At first the tubers of plant 4 bulked slowly but the rate later increased to yield a final total tuber volume intermediate between plants 7 and 5. The number of tubers per plant varied from one to twelve (Table 1).

Mean volume per tuber

The final mean volumes per tuber of plants 5, 4, 6 and 8 were greater than those of plants 1, 2, 9 and 7 with 3 intermediate (Fig. 3). The differences were not established by week 14 when only 5 and 1 were at all clearly different from the others. Plant 5 showed an approximately linear growth rate per tuber from week 7 to week 16 but plants 4, 6 and 8 showed marked increases in rate of growth per tuber over the period week 14 to week 16 when the tubers of plants 2, 9 and 7 had apparently ceased growth. The single

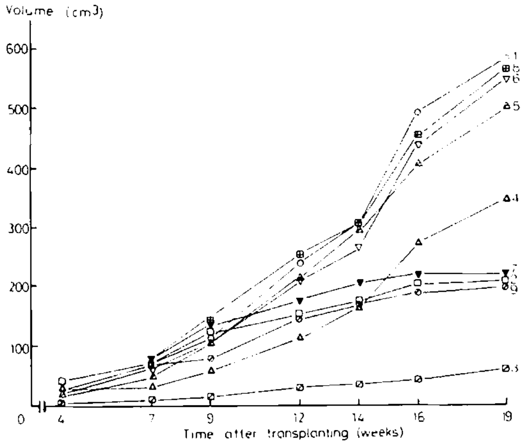

Fig. 2. The cumulative total tuber volumes of the nine plants. The numbers refer to the plants identified in Table 1.

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

Abb. 2. Die steigenden Gesamt-Volumen der Knollen der 9 Pflanzen. Die Zahlen beziehen sich auf die in Tabelle 1 aufgeführten Pflanzen.
Fig. 2. Les volumes cumulés de tubercules des neuf plantes. Les numéros font référence aux plantes identifiées dans le tableau 1.

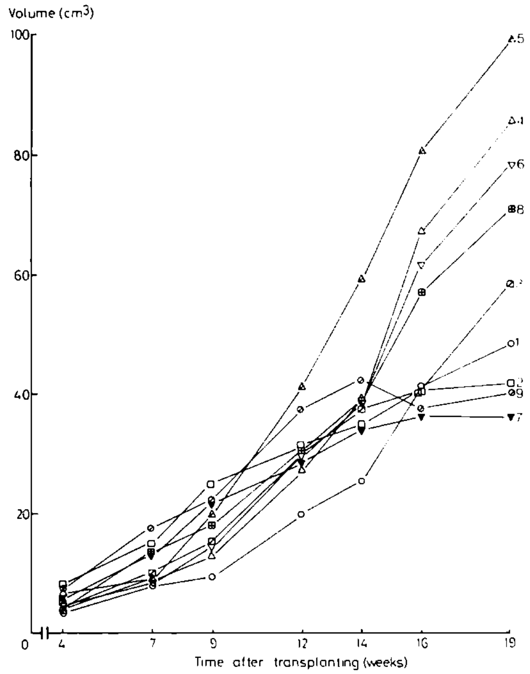

Fig. 3. Mean volume per tuber for the nine plants. The identification number of each plant is given.

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

Abb. 3. Durchschnittliches Volumen pro Knolle der neun Pflanzen. Die Nummer jeder Pflanze ist angegeben.
Fig. 3. Volume moyen par tubercule pour les neuf plantes. Chaque plante est identifiée par son numéro.

tuber on plant 3 grew only slowly up to week 9, more rapidly from week 9 to week 14 and then even more rapidly up to week 19.

The growth in volume of individual tubers
Plant 5. Tubers T2 and T4 which were the largest after 19 weeks, were smaller than tubers T1 and T3 at 4 weeks and 7 weeks (Fig. 4a). The differences in final tuber size were associated with different rates of bulking over the period 4 to 19 weeks.
Plant 6. Differences in final tuber size were not clearly established until close to harvest time. Tubers T3 and T4 which were smaller than T1 and T2 at weeks 9 and 14 then showed sudden increases in growth rates and reached similar sizes to T1 and T2 that had been increasing in volume steadily over a much longer period. The latter tubers

Table 1. Total number of tubers on each plant.

Plant No[1]	1	2	3	4	5	6	7	8	9
Number of tubers[2]	12	5	1	4	5	7	6	8	5

[1] *Nummer der Pflanze - Numéro de la plante;* [2] *Knollenzahl - Nombre de tubercules*

Tabelle 1. Zahl der Knollen an jeder Pflanze.
Tableau 1. Nombre total de tubercules de chaque plante.

had ceased growth by week 16 (Fig. 4b). The smaller tubers T6 and T5 although present at week 4 grew very slowly up to harvest.

Plant 4. The patterns of growth of T1 and T2 were similar (Fig. 4c). Tubers T3 and T4 were larger throughout and although T4 was finally the largest, the difference was established over the period 9 and 12 weeks after observations began.

Plant 8. The final volume of each tuber was a reflection of both differences in size at week 4 and in the rates of bulking (Fig. 4d). Acceleration of rates of bulking over the period 14 to 16 weeks was evident in some (e.g. T1, T4 and T8) but not all tubers. Tubers T2, T6 and T8 which were largest at 19 weeks could not be distinguished from the rest at week 7 but all three bulked at higher rates thereafter.

Plant 1. The larger (T8, T1, T9, T3 and T11) and the smaller tubers (T7, T6, T10 and T4) at week 19 were clearly distinguishable by week 12 (Fig. 4e). Growth rates of tubers T1, T9, T3 and T11 were similar after week 14 but T8 showed a very marked increase in growth rate between weeks 14 and 16. Of the smaller tubers, T5 and T2 were initiated very late.

Plant 2. The largest tuber at week 19 (T1) was the smallest at week 4 (Fig. 4f). The larger tubers at week 4 (T4 and T3) showed reduced growth rates after week 9 when T1 was growing most rapidly. Tuber T2 grew very slowly from week 4 to the time of harvest.

Plant 7. All the tubers grew over the period 4 to 7 weeks but after this only tubers T4 and T5 continued to increase in volume. They were the smallest at week 7 but the largest at week 19 (Fig. 4g).

Plant 9. All three tubers grew throughout the period 4 to 16 weeks (Fig. 4h). Final sizes of tubers reflected different volumes at week 4 and different rates of increase in volume thereafter.

Plant 3. The single tuber increased in volume at a slow but constant rate from week 4 to week 19 (Fig. 3). The final volume of this single tuber was similar to that of the larger tubers on other plants.

Discussion

Hewitson (1967) thoroughly examined the technique used to obtain non-destructive measurements of tuber growth. In the present study tuber numbers and volumes were similar to those of plants left to grow undisturbed in the same field.

The nine plants which reached harvest in the field were of the same variety, every mother tuber was planted in the same field on the same day and each of the selected plants had a single shoot. Mother tubers of these plants were detached before the shoots were transplanted. On simple theoretical grounds tuber production ought to have been relatively uniform. In fact it was not. Every mean value hides a very large variance.

Total tuber volume per plant at harvest (Fig. 2) has two components, the number of tubers (Table 1) and the mean tuber volume (Fig. 3). Both these parameters varied greatly. Although in some of the plants (1, 8 and 6) total tuber volume seemed to be positively related to the number of tubers on the plant, this correlation did not hold for all plants. The number of tubers on each plant was determined early and numbers did not change significantly during the period of observation. Conversely, the rates of

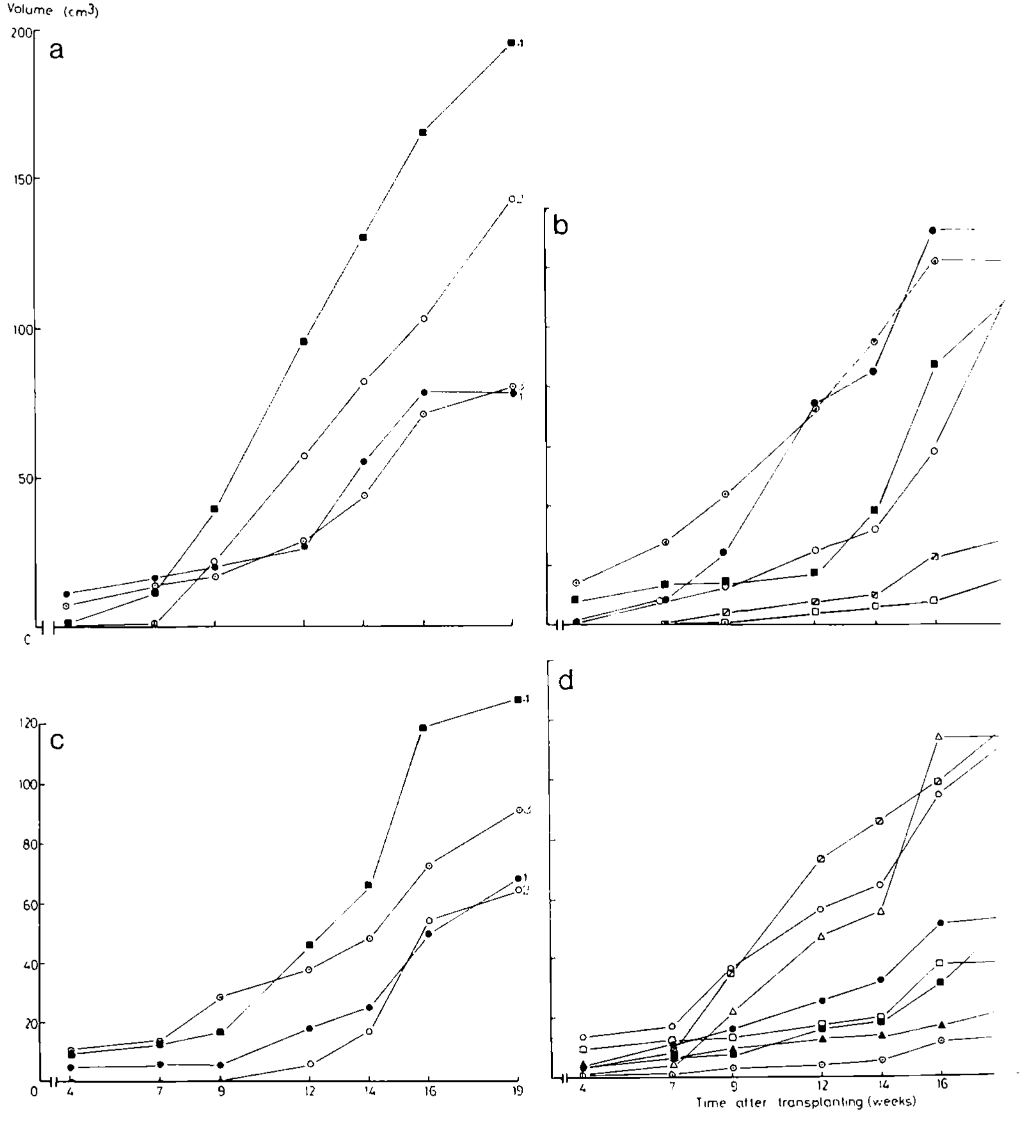

Fig. 4. The growth in volume of individual tubers on each of the nine plants. (a) plant 5, (b) plant 6, (c) plant 4, (d) plant 8, (e) plant 1, (f) plant 2, (g) plant 7, (h) plant 9. The numbers identify each tuber.

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

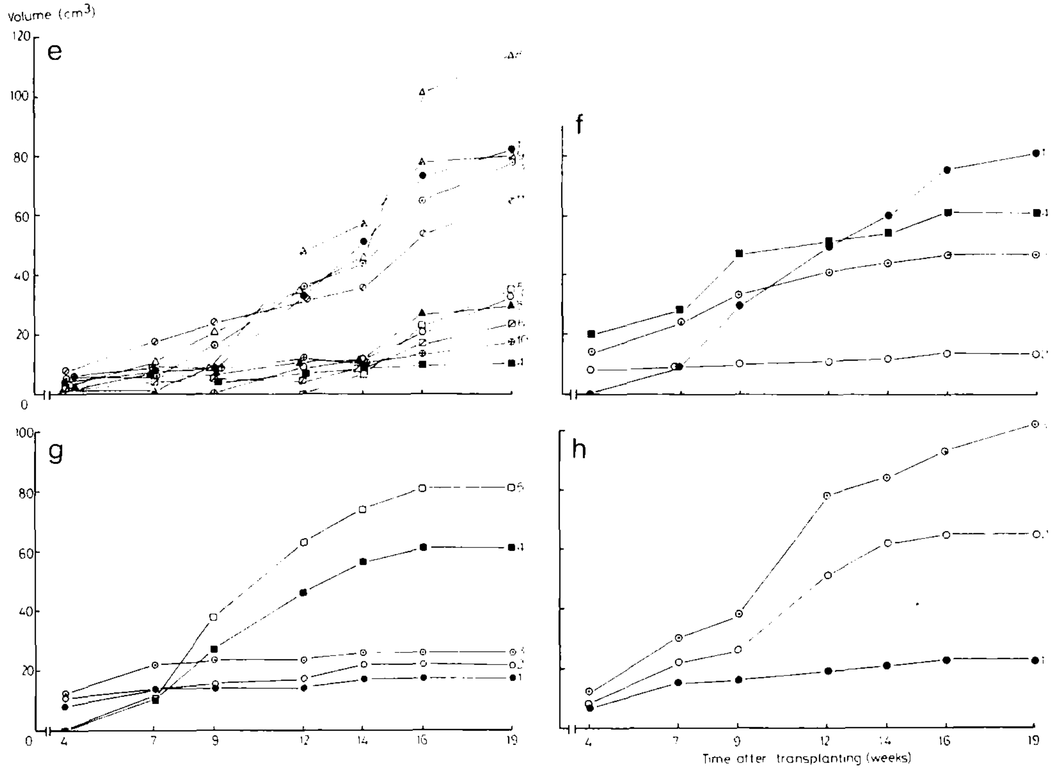

Abb. 4. Die Volumenzunahme von Einzelknollen von jeder der neun Pflanzen. (a) Pflanze 5, (b) Pflanze 6, (c) Pflanze 4, (d) Pflanze 8, (e) Pflanze 1, (f) Pflanze 2, (g) Pflanze 7, (h) Pflanze 9. Die Zahlen kennzeichnen jede Knolle.
Fig. 4. La croissance en volume de chaque tubercule de chacune des neuf plantes. (a) plante 5, (b) plante 6, (c) plante 4, (d) plante 8, (e) plante 1, (f) plante 2, (g) plante 7, (h) plante 9. Les numéros identifient chaque tubercule.

increase in total and mean tuber volumes per plant did change frequently and sometimes dramatically over the fifteen weeks of study. The patterns of increase were such that the final value of the total tuber volume of plants could not have been predicted until three weeks before maturity and, of the mean tuber volume per plant, even later. The dangers of extrapolation from sequential harvests are clearly exposed.

Fig. 4a–4h show the behaviour of different tubers on single plants during the period of growth. Krijthe (1955) assumed that the largest tuber at harvest had always been the largest. The results from the present study do not agree with her assumption but rather with the suggestion by Moorby (1968) that individual tubers showed different rates of growth relative to each other, such that the largest tuber at any time need not necessarily be the largest on any future occasion. Different tubers on these field-grown plants followed different courses of growth patterns at different times. Similar results have been reported by Wurr (1977).

Theoretically, the volume of an individual tuber at harvest could be determined by several factors, namely, time of initiation and of onset of tuber growth, rate of growth, duration of the main period of growth and the time of cessation of growth. Each of these factors plays a vital role in tuber growth but from these studies none of them could be singled out as independently responsible for the variation in final tuber size. Hence, variation in final size of a tuber on a potato plant appeared to be affected by more than one factor or by some factor not measured. The time of initiation, the time of onset of growth and the time of cessation of growth are important because the main period of growth is determined by them. However, careful examination revealed that the differences in the final tuber sizes were most obviously affected by a combination of growth rates and the duration of the main period of growth, the larger the differences in these two factors the greater the variation in final tuber size. From serial harvests of potato plants, Clark (1921) concluded that the growth rates of individual tubers were very important in determining final tuber size.

To understand, at least in part, the causes of differences in tuber size at harvest it becomes essential to trace the factor or factors controlling the growth rate of a tuber. Moorby (1968) pointed out that certain leaves or groups of leaves might be responsible for the filling of particular tubers. Indeed, vascular association between leaves and other organs has been demonstrated in a number of crop plants (Wardlaw, 1968); similarly, Gray & Smith (1973) suggested that there is a high degree of vascular continuity between tubers and the supplying leaves; although vascular bundles from one leaf are not necessarily restricted to only one side of the stem (Artschwager, 1918).

Over the period of observations it seems likely that increase in tuber volume was due primarily to increases in cell size, partly through the import of assimilates and partly through the intake of water. The tubers were physiological sinks and the capacity of a sink is a function of (a) its size, (b) its activity and (c) the availability of supplies of assimilates, minerals and water. If, for the present study, the sink is regarded as total tuber volume, variation between plants must be explicable in terms of one or more of these components. The availability of supplies of assimilates (which was not studied directly) is determined by the size of the photosynthetic system, the rate of photosynthesis and the efficiency of the transport system between leaves and tubers. The efficiency of the transport system has been described by Milthorpe & Moorby (1969). If the vascular system between tubers and leaves was responsible for overall control of growth rate and eventually the final size of tubers, then changes in growth rates of individual tubers on the same plant ought to be synchronous; they were not. If the size of the photosynthetic system was a primary determinant of tuber size then there would be a relationship between rate of tuber bulking and leaf area present during bulking. However, Burt (1961) and Borah & Milthorpe (1962) failed to find such a relationship. Vascularisation and the size of the photosynthetic system do not appear to account for the variation studied.

Such arguments turn attention to the tubers themselves as the governors of their own volume increase. Sink size is not of primary importance because subsequent increase in volume is not related to size (except when tubers reach their maximum potential size – when increase stops). Hence, sink activity remains as the most likely component responsible for variation between tubers and between plants. An experimental approach to this possibility is described by Ahmed & Sagar (1981).

Zusammenfassung

Volumenzunahme einzelner Knollen von Kartoffelpflanzen, die unter Feldbedingungen wuchsen

Viele Jahre wurden zur Ernte die Variationen in der Knollenzahl und -grösse zwischen und an Einzelpflanzen beobachtet. Die Ursachen für diese Variationen sind schwer verständlich und einer der Gründe ist der Mangel an Information über die Art wie die Einzelknollen während der Periode des Knollenwachstums wachsen. Die vorliegende Arbeit umfasst die Messung des Volumens aller Knollen von 9 Pflanzen, die in speziellen Gefässen im Feld gewachsen waren, zu 7 verschiedenen Terminen zwischen der Knollenbildung und dem Absterben des Krautes. Die Spezialbehälter hatten einen mit Sand gefüllten oberen Plastikring, in dem die Stolonen und Knollen wuchsen. Der Sand wurde in Zeitabständen entfernt und wieder aufgefüllt, um ein nicht störendes Messen des Volumens der Einzelknollen zu gestatten. Die Wurzeln der Pflanzen entwickelten sich im natürlichen Ackerboden unter dem Ring (Abb. 1).

Die Zahl der Knollen/Pflanze schwankte zwischen 1 und 12 (Tab. 1) und das Volumen aller Knollen/Pflanze von 60 bis 600 cm^3 (Abb. 2). Die Muster der Grössenzunahme variierten. Vier Pflanzen zeigten im allgemeinen eine lineare Zunahme des Volumens, drei eine reduzierte Zunahme in der Mitte des Grössenwachstums und eine steigerte – nach einem langsamen Beginn – die Zunahme (Abb. 2). Die Steigerung im durchschnittlichen Knollenvolumen/Pflanze variierte ebenfalls (Abb. 3), aber infolge der Unterschiede in der Zahl der Knollen/Pflanze, war die Rangfolge der Pflanzen nicht die selbe wie beim Gesamtvolumen. Abb. 4 (a–h) zeigt die Volumenzunahme von Einzelknollen. Die Variation schliesst fast alle theoretischen Möglichkeiten ein (verschiedene Startzeiten, verschiedene Zuwachsraten im Volumen, verschiedene Daten des Wachstumsstillstandes).

In der Diskussion werden einige der möglichen Gründe für die Variabilität innerhalb der Pflanze geprüft und es wird versucht, den Schluss zu ziehen, dass die Einzelknollen wahrscheinlich ihr Wachstum selbst bestimmen.

Résumé

Augmentation individuelle du volume de tubercules de pommes de terre cultivées dans les conditions du champ

La variation du nombre et de la taille des tubercules d'une même plante et de différentes plantes au moment de la récolte a été observée depuis de nombreuses années. Les causes de variation sont mal comprises, en particulier parce que l'on manque d'informations sur la croissance de chaque tubercule pris individuellement tout au long de la période de végétation. Cette publication décrit les travaux de mesure du volume de tous les tubercules de neuf plantes cultivées dans des unités spéciales disposées dans le champ; les mesures ont été effectuées à 7 dates entre la tubérisation et le défanage.

Les unités spéciales (fig. 1) ont un anneau supérieur rempli de sable dans lequel poussent les stolons et les tubercules. Le sable est enlevé, puis remplacé pour permettre une mesure non destructive du volume de chaque tubercule. Les racines des plantes se développent dans le sol du champ, en-dessous des anneaux.

Le nombre de tubercules par plant a varié de 1 à 12 (tableau 1) et le volume total de tubercules par plante s'est étendu de 60 à 600 cm^3 (fig. 2). Les façons de tubériser ont également varié. Les vitesses de croissance en volume de 4 plantes ont été tout le temps linéaires, celles de 3 plantes ont été réduites pendant la moitié de la tubérisation, et celle d'une plante a augmenté après un départ lent (fig. 2). Les vitesses de croissance du volume moyen des tubercules par plante ont été aussi très variables (fig. 3), mais à cause des différences de nombre de tubercules par plante, l'ordre des plantes n'était pas le même que pour le volume brut. La fig. 4 (a–h) montre l'augmentation de volume des tubercules pris individuellement. La variation inclut presque toutes les possibilités théoriques (différentes dates d'initiation, différentes vitesses de croissance de volume, différentes dates de fin de croissance).

Dans la discussion, plusieurs des causes possibles de variabilité intra-plante sont examinées et il est suggéré que chaque tubercule détermine très probablement sa propre croissance.

References

Ahmed, Ch. M. S. & G. R. Sagar, 1981. Effects of a mixture of NAA + BA on tuber number and growth rates of tubers of *Solanum tuberosum* L. *Potato Res.* 24: 267–278.

Artschwager, E. F., 1918. Anatomy of the potato plant with special reference to the ontogeny of the vascular system. *J. agric. Res.* 14: 221–252.

Borah, M. N. & F. L. Milthorpe, 1962. Growth of the potato as influenced by temperature. *Indian J. Pl. Physiol.* 5: 53–72.

Burt, R. L., 1961. Some effects of temperature on the growth and development of the potato. Ph.D. thesis, University of Nottingham.

Clark, C. F., 1921. Development of tubers in the potato. *Bull. U.S. Dept. Agric.* No. 958.

Gray, D., 1973. The growth of individual tubers. *Potato Res.* 16: 80–84.

Gray, D. & Smith, D. J., 1973. The pattern of assimilate movement in potato plants. *Potato Res.* 16: 293–295.

Hewitson, J. F., 1967. Translocation in the potato with special reference to variation in tuber size. Ph.D. thesis, University of Wales.

Krijthe, N., 1955. Observations on formation and growth of tubers on the potato plant. *Neth. J. agric. Sci.* 3: 291–304.

Milthorpe, F. L. & J. Moorby, 1969. Vascular transport and its significance in plant growth. *A. Rev. Pl. Physiol.* 20: 117–138.

Moorby, J., 1968. The influence of carbohydrates and mineral nutrient supply on the growth of potato tubers. *Ann. Bot.* 32: 57–68.

Moorby, J., 1978. The physiology of growth and tuber yield. In: P. M. Harris (Ed.), The potato crop, the scientific basis for improvement, pp. 153–194. Chapman and Hall, London.

Moorby, J. & F. L. Milthorpe, 1975. Potato. In: L. T. Evans (Ed.), Crop physiology, some case histories, pp. 225–257. Cambridge University Press, London.

Plaisted, P. H., 1957. Growth of the potato tuber. *Pl. Physiol.* 32: 445–453.

Sadler, E., 1961. Factors influencing the development of sprouts of the potato. Ph.D. Thesis, University of Nottingham.

Wardlaw, I. F., 1968. The control and pattern of movement of carbohydrates in plants. *Bot. Rev.* 34: 79–105.

Wurr, D. C. E., 1977. Some observations of patterns of tuber formation and growth in potato. *Potato Res.* 20: 63–75.