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Some observations of patterns of tuber formation and growth in the potato

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Summary

Patterns of tuber formation and growth were studied with the varieties Désirée, Maris Piper and Pentland Crown.

The varieties formed similar numbers of stolons but different numbers of tubers. More tubers were formed at the first node than at any other but Pentland Crown formed fewer tubers over nodes 2–8 than the other varieties. The range of nodes over which tubers formed and competition for photosynthate within a node appeared to be factors controlling the tuber size distribution. The time over which tuber formation occurred was not important.

Measurements of individual tuber growth suggested that some tubers followed an approximately sigmoid curve, some grew linearly and some showed periods of tuber growth interrupted by periods when the tubers grew slowly if at all.

Estimation of the fresh and dry weights of growing tubers using a relationship between the product of tuber axis lengths and the weights of harvested tubers proved most satisfactory.

Introduction

A single potato stem may bear tubers of a wide range of sizes yet the causes of such variation are not understood. There are also considerable varietal differences in the tuber size distribution. Krijthe (1955) assumed that the largest tubers at maturity were the first formed and she found that they were borne on stolons from the third, fourth and fifth nodes from the base of the stem. However Clark (1921) considered that differences in the rate of growth of individual tubers were more important in determining final tuber size than their time of formation, and Gray (1973), measuring growth over a limited period, showed that the tubers with the highest growth rate came from the basal nodes. Furthermore, Moorby (1967a, 1967b, 1968) suggested that individual tubers may show fluctuating growth rates so that the largest tubers at one stage of growth may not be the largest at another.

This paper describes a study of the patterns of tuber formation and growth using three varieties which naturally give different tuber size distributions.

Experiments

All the field experimental work described was carried out on a coarse sandy loam of the Wick Series receiving 251 kg/ha of N, P_2O_5 and K_2O.

Tuber formation

Seed tubers of three sizes, 30–35, 40–45 and 50–55 mm, of each of the three varieties Pentland Crown, Désirée and Maris Piper were planted on 26 April in a randomized block design with three replicates. Plots were 12.2 m long and consisted of three rows 76 cm apart, within which tubers were planted at a spacing of 30 cm. A four-plant sample was removed from each plot three times a week for five weeks, beginning 4 June. One mainstem was taken from each plant as a sub-sample and the numbers of stolons and tubers at each stem node were recorded (nodes were numbered upwards from the parent tuber).

Tuber growth

Experiment 1 (1972). Seed tubers of the two early maincrop varieties Pentland Crown and Maris Piper were selected from each of the two size grades, 35–40 and 50–55 mm, to have three and six sprouts per tuber. This gave four treatments: Pentland Crown three sprouts (T1) and six sprouts (T2), Maris Piper three sprouts (T3) and six sprouts (T4), each of which was replicated six times in a randomized block design.

Tubers were grown in wood-framed boxes with removable glass sides. The panes of glass were covered with a non-toxic Bitumastic paint to exclude the light. Each seed tuber was planted on 4 May on top of a piece of 1 mm nylon mesh which covered 0.03 m^3 of sieved topsoil contained in the lower half of each box. The soil was fertilized with 6.1 g of N, P_2O_5 and K_2O (equivalent to the fertilizer that would be available to a single plant at a population of 41 000 plants/ha receiving 250 kg/ha of each nutrient). The seed tubers were then covered to a depth of 10 cm with vermiculite (grade 3). The soil in the lower half of the boxes was kept moist by applying water through plastic tubes which ran directly from reservoirs on the surface of the vermiculite.

On 14 June the vermiculite was washed out of the boxes to allow observation of tuber formation and growth (Fig. 1) but not all plants had initiated tubers, and where this was so the vermiculite was replaced and was washed out again one week later. A square piece of 5-cm-thick polyester foam, painted black and with a slit in it for the stems was then fitted inside the top of each box to exclude light from the stolons and tubers. Removal of both the polyester foam and the glass sides of the upper half of the growth chamber enabled stolons and tubers to be labelled and measured. Tuber growth was then followed by measuring the three major axes with calipers (Gray, 1973) twice a week for six weeks and thereafter at weekly intervals until 100% senescence on 29 August. Tuber volume (V) was calculated by assuming the tuber to be ellipsoidal in shape and using the equation $V = \frac{4}{3}\pi abc$ where 2a, 2b, 2c are the major

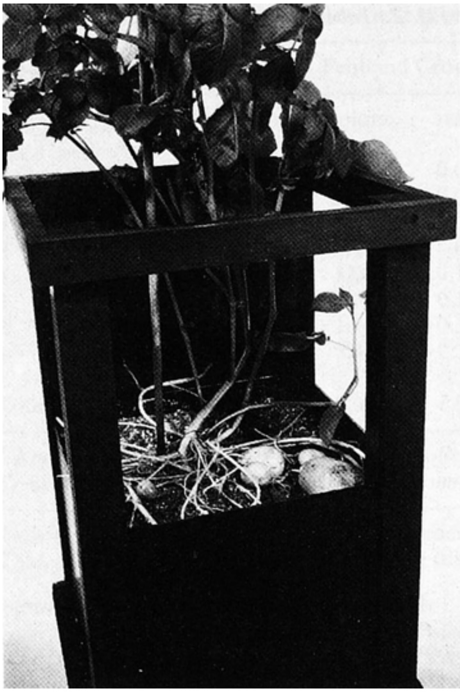


Fig. 1. Tubers grown in a wood-framed box.

Abb. 1. Knollenwachstum in einer Kiste aus Holzlatten.
Fig. 1. Tubercules produits en caisses de bois.

axes measurements (cm). The plants were watered regularly throughout growth to avoid any stress which might affect tuber growth.

Experiment 2 (1973). In the field, tops of potato ridges 76 cm apart were removed and approximately 2.5 cm depth of Levington compost was added to the flat surface. Sixty single-sprouted Désirée seed tubers graded 35–40 mm were then planted 61 cm apart within each row with the bases of their sprouts level with the top of the compost. Each tuber was covered with a 61 cm × 61 cm square of black polythene with a hole cut in it for the sprout. Until root growth was established the compost and surrounding soil were kept moist by watering. Once tubers had formed under the polythene they were tagged (Fig. 2) and measured on ten of the plants at weekly intervals.

In order to estimate fresh and dry weights of tubers, five non-tagged plants were harvested each week and their tubers were measured and weighed fresh and after drying at 100 °C for 48 hours. The relationships between the product of the tuber axis lengths and tuber fresh and dry weights were determined each week by linear regression and these were then used to estimate the weights of the tubers which had been tagged and measured.

Experiment 3 (1974). The growth of individual tubers of the variety Désirée was followed in the field using the same technique as in 1973 except that the rows were

Fig. 2. Tubers grown under black polythene.

Abb. 2. Knollenwachstum unter schwarzem Polythen.
Fig. 2. Tubercules produits sous film polyéthylène noir.

152 cm apart to aid access to the plants that were measured. The tubers on ten plants were tagged and measured throughout the season, and tuber fresh and dry weights were estimated as in Experiment 2.

Results

Tuber formation

The number of tubers formed per node was not affected by seed tuber size. It did vary with time, but the varietal ranking was not affected by the time of sampling. Typical data are presented in Table 1 showing the mean number of stolons and tubers at each node, for each variety, over the last seven harvests, together with the appropriate standard errors of the means at each node.

All the varieties initiated most of their tubers at the first node but Pentland Crown formed fewer of its tubers over nodes 2–8 than Désirée and Maris Piper. This uneven distribution of tubers may well explain why the control of tuber size in Pentland Crown proves so difficult, yet as Table 1 shows, there was no shortage of potential tuber sites (stolons). Although some tubers (less than 10%) were inevitably lost during sampling there were still many more stolons produced than tubers, particularly

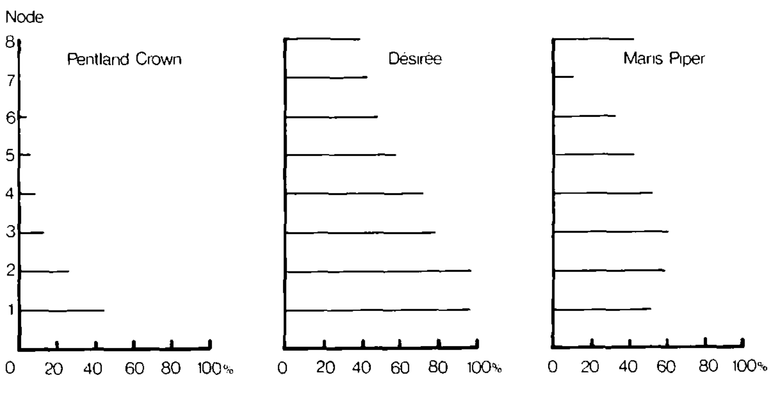
Table 1. Average numbers of stolons and tubers formed per node on each stem.

Node[1]	Désirée		Pentland Crown		Maris Piper		S.E. mean[4]	
	stolons[2]	tubers[3]	stolons	tubers	stolons	tubers	stolons	tubers
8	0.11	0.04	0.02	0.00	0.01	0.00	± 0.013	± 0.008
7	0.26	0.11	0.11	0.00	0.12	0.01	± 0.023	± 0.012
6	0.58	0.27	0.35	0.01	0.43	0.14	± 0.038	± 0.023
5	0.84	0.47	0.80	0.05	0.90	0.38	± 0.043	± 0.032
4	0.99	0.71	1.06	0.10	1.08	0.57	± 0.047	± 0.043
3	0.84	0.65	1.08	0.14	1.15	0.70	± 0.047	± 0.048
2	0.81	0.78	1.16	0.30	1.21	0.70	± 0.045	± 0.052
1	5.17	4.96	5.42	2.36	4.68	2.31	± 0.169	± 0.161
Total[5]	9.60	7.99	10.00	2.96	9.58	4.81	± 0.250	± 0.219

[1] *Knoten – Noeud;* [2] *Stolon – Stolons;* [3] *Knollen – Tubercules;* [4] *Standardfehler des Mittelwertes – Erreur standard de la valeur moyenne;* [5] *Gesamt – Total*

Tabelle 1. Mittelwerte der pro Knoten an jedem Stengel gebildeten Stolonen und Knollen.
Tableau 1. Nombre moyen de stolons et de tubercules formés par noeud sur chaque tige.

Fig. 3. The number of tubers per node expressed as a percentage of the number of stolons per node.

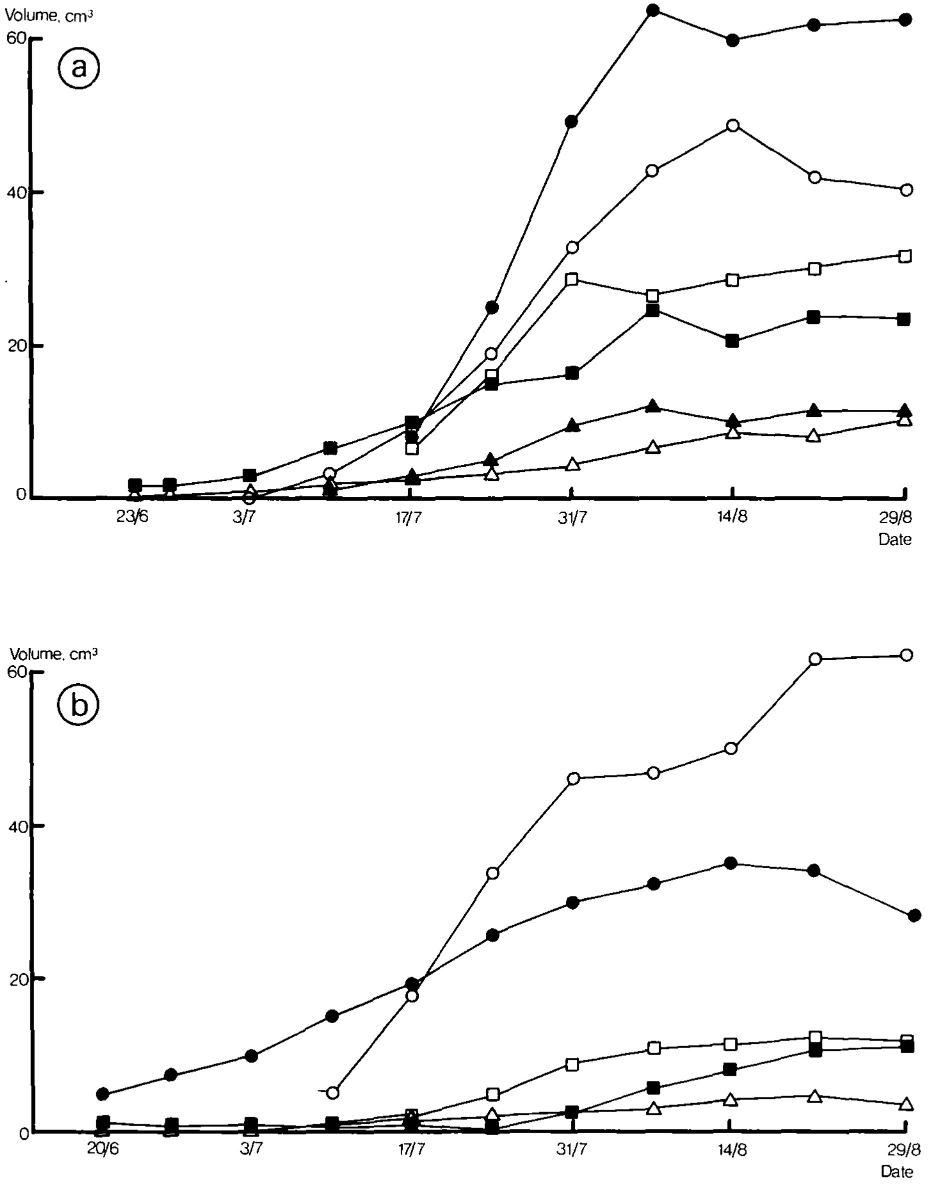


Node – *Knoten – Noeud*

Abb. 3. Knollenzahl pro Knoten ausgedrückt in Prozent der Stolonen pro Knoten.
Fig. 3. Nombre de tubercules par noeud exprimé en % du nombre de stolons par noeud.

with the variety Pentland Crown. In fact Fig. 3 shows that the number of tubers at a node expressed as a percentage of the number of stolons, varies considerably within and between varieties.

Fig. 4. The growth of some tubers on a single plant of Pentland Crown (a) and Maris Piper (b).



Volume – *Volumen* – *Volume*; Date – *Datum* – *Date*

Abb. 4. Wachstum einiger Knollen einer Einzelpflanze von Pentland Crown (a) und Maris Piper (b).
Fig. 4. Croissance de quelques tubercules sur un pied de Pentland Crown (a) et de Maris Piper (b).

Tuber growth

Experiment 1. Unfortunately the node of origin of individual stolons could not be determined because they occupied a very compact zone at the base of each stem. In addition those plants which had not initiated tubers when the vermiculite was first washed out, then formed many tubers which were too close to the stems to be measured. Nevertheless it was possible to follow the growth of several tubers on each treatment. The largest average rates of growth from the first to the last measurement were 3.30, 1.81, 1.06 and 1.14 cm^3/day for T1, T2, T3 and T4, respectively.

The growth rates of Pentland Crown tubers (T1 and T2) were greater than those of Maris Piper (T3 and T4), a situation which corresponds with field experience, Pentland Crown producing fewer tubers which grow to be individually larger.

It seems from the growth of individual tubers shown in Fig. 4a and 4b that some tubers followed an approximately sigmoid curve, some grew linearly and some showed periods of tuber growth interrupted by periods when the tubers grew slowly if at all.

Experiment 2. The system of estimating fresh and dry weights of measured tubers in Experiments 2 and 3 using the relationship between the product of the tuber axis lengths and the fresh and dry weights of harvested tubers was quite satisfactory. The values of the parameters p and q for the first and last measurements in each year are shown in Table 2 together with the coefficient of determination (R^2) which shows the 'goodness of fit'. The regressions accounted for a minimum of 96% of the variation

Table 2. The values of the parameters p and q and the coefficient of determination (R^2) used to describe the linear relationship ($y = p + qx$) between the product of the major axes of a tuber and its fresh and dry weights. y = tuber weight (g); x = product of major axes (cm^3).

Date[1]	Fresh weight[2]			Dry weight[3]		
	p	q	R^2	p	q	R^2
23-7-73	-0.02	0.59	0.993	-0.104	0.082	0.991
17-9-73	-0.91	0.55	0.995	-1.529	0.132	0.982
22-7-74	0.02	0.55	0.999	-0.008	0.075	0.999
23-9-74	-1.34	0.58	0.996	-0.827	0.116	0.992

[1] *Datum – Date;* [2] *Frischgewicht – Poids frais;* [3] *Trockengewicht – Poids secs*

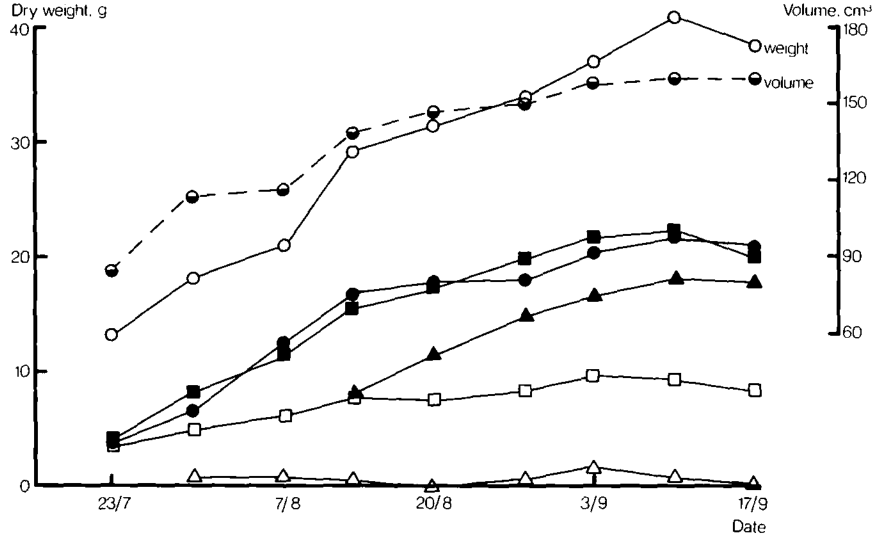
Tabelle 2. Werte der Parameter p und q und des Bestimmtheitsmasses (R^2), die verwendet wurden, um das lineare Verhältnis ($y = p + qx$) zwischen dem Produkt der Hauptachsen einer Knolle und ihrem Frisch- und Trockengewicht zu beschreiben. y = Knollengewicht (g); x = Produkt der Hauptachsen (cm^3).

Tableau 2. Valeurs des paramètres p et q et du coefficient de détermination R^2, utilisés pour décrire la relation linéaire ($y = p + qx$) entre le produit des axes principaux du tubercule et les poids frais et secs. y = poids du tubercule; x = produit des axes principaux.

in fresh weight and 94% of the variation in dry weight and in most weeks accounted for 98% of the variation. There was no consistent change in the slopes of the regression lines for fresh weight but those for dry weight showed a steady increase over time indicating an increase in the specific gravity of the tubers associated with increasing dry-matter content.

Measurements were made from 23 July to 17 September but tuber growth over this period was disappointing and not many tubers grew extensively. This is illustrated by Fig. 5 which shows the changes in dry weight of tubers on a single plant. Tuber dry weights in general increased throughout the season and though there were fluctuations in the rate at which this occurred, these changes tended to be consistent among tubers on the same plant suggesting that they were caused by environmental stress. Fluctuations in fresh weight were more common but these were not necessarily accompanied by similar changes in dry weight, presumably because moisture stress frequently results in temporary water loss from the tuber and a subsequent rise in tuber dry-matter percentage (Wurr & Allen, 1974). Fig. 5 shows that changes in volume followed a similar pattern to changes in dry weight of the largest tuber.

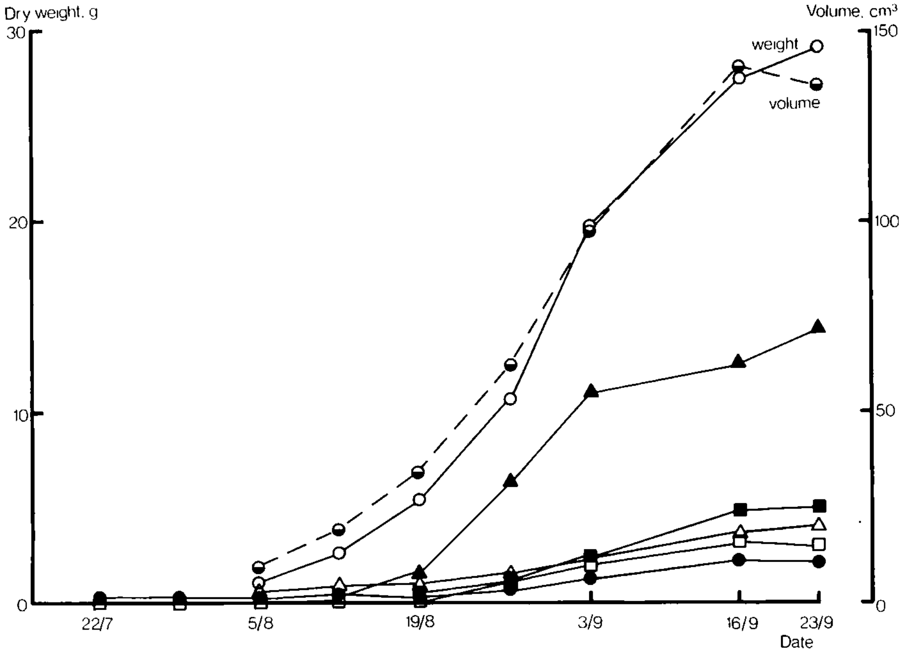
Fig. 5. The changes in dry weight of tubers on a single plant of Désirée (1973). Changes in the volume of the largest tuber are also included.



Dry weight – *Trockengewicht – Poids de matière sèche;* Weight – *Gewicht – Poids;* Volume – *Volumen – Volume;* Date – *Datum – Date*

Abb. 5. Aenderungen im Trockengewicht der Knollen einer Einzelpflanze von Désirée (1973). Aenderungen im Volumen der grössten Knolle sind mit einbegriffen.
Fig. 5. Evolution du poids sec des tubercules sur un pied de Désirée (1973). L'évolution du volume du tubercule le plus gros est incluse.

Fig. 6. The changes in dry weight of tubers on a single plant of Désirée (1974). Changes in the volume of the largest tuber are also included.



Dry weight, Weight, Volume, Date: *siehe Abb. 5 - voir Fig. 5*

Abb. 6. Aenderungen im Trockengewicht der Knollen einer Einzelpflanze von Désirée (1974). Aenderungen im Volumen der grössten Knolle sind mit einbegriffen.
Fig. 6. Evolution du poids sec des tubercules sur un pied de Désirée (1974). L'évolution du volume du tubercule le plus gros est incluse.

Experiment 3. The dry weights of the tubers either increased at a rate that was reasonably constant throughout the season or at a rate that initially increased and then declined as illustrated by Fig. 6. There was little evidence that tubers showed periods of growth interrupted by periods when they grew slowly if at all. It is interesting that the largest tuber in Fig. 6 decreased in volume during the last week but its dry weight still increased because of increasing dry-matter content.

Discussion

The object of this series of experiments was to study how patterns of tuber formation and growth contribute to the variation in tuber size found on an individual plant.

Examination of the patterns of tuber formation in the varieties Maris Piper, Désirée and Pentland Crown showed that there were considerable differences between the varieties. Although Pentland Crown tended to form fewer and therefore larger tubers than the other two varieties, all of the varieties formed similar numbers of stolons. This suggests that there is no shortage of potential tuber sites on a variety like Pentland Crown, but that some control (probably hormonal) over tuber initiation limits the number of stolons which form tubers. Furthermore Pentland Crown formed nearly 80% of its tubers at the first node and hardly any after the fifth while the other varieties formed a lower proportion at the first node and continued to produce tubers up to the seventh and eighth nodes. The time taken for the number of tubers formed to reach a maximum was 7 days in all three varieties. This is unusually short, Krijthe (1955) finding that in her experiments over 3 years, tuber formation generally took 2–3 weeks; and it is quite possible that weather conditions at the time of stolon and tuber formation may have affected the results presented here.

Measurements of tuber growth were made (in Experiments 1–3) but unfortunately it was not possible to classify the growth of individual tubers according to the node from which the stolon originated. Normal field grown plants give distinct nodes, although it is only possible to distinguish these by using destructive harvests. There is a need for a technique which would produce plants similar to those growing in a crop, yet which would permit the classification of tuber positions and the measurement of tuber growth.

Measurements made in Experiment 1 were of tuber size only, whereas in Experiments 2 and 3 it was also possible to estimate the fresh and dry weights of measured tubers. There was no inconsistency between the use of size and weight parameters other than the changes in dry matter content associated with moisture stress which have already been described. Tuber size calculated as the product of the three major axes could be used to give an accurate indication of tuber fresh and dry weights.

During the course of this work more than 500 tubers were measured over a period of at least six weeks and the growth measurements which were made indicated that growth may be broadly classified into three types, though the latter two are probably variations of one basic type and cover a gradation of growth patterns shown by a population of tubers. Indeed it is sometimes difficult to decide into exactly which category a tuber should be put because it may show features of one or more types of growth pattern. The most common type is that of growth following a sigmoid curve as described by Milthorpe (1963). The second type is that where there was approximately linear growth over the whole period. This tended to be confined to small tubers and suggests that it is probably Milthorpe's sigmoid growth curve with a very shallow slope. The third type involved a basically sigmoid pattern but with discontinuous growth and was only clearly found in Experiment 1 on plants grown in boxes. There is however other good circumstantial evidence that irregular patterns of tuber growth might occur.

Artschwager (1918) showed that vascular bundles from individual leaves were not necessarily entirely restricted to the same side of the stem and that anastomoses of the vascular bundles occurred at the nodes. Nevertheless directional transport of assimilates has been demonstrated by Gray & Smith (1973), and Chapman (1958), on a plant consisting of one main stem divided above ground into two branches, showed that when one branch of the plant was subjected to short days and the other to long days tubers were formed on the short day side only. This suggests that leaves and nodes bearing stolons on the same sides of the stem are limited by a common vascular transport system and if this is so then tuber growth might be expected to follow the development and senescence of those leaves particularly when they are on lower nodes which become progressively more shaded and begin to become senescent in mid-season. This would be likely to slow down tuber growth until another more productive leaf higher in the canopy could take over. In addition the collapse of potato haulm in mid-July to August is almost certain to lead to a very heavy shading of one side of the plant and a consequent reduction in the growth of tubers fed by those leaves.

Whatever the exact patterns of tuber growth, collectively they are responsible for the tuber size distributions which occur. Data from another experiment in 1973 shows that at maturity the variance of tuber size (measured in cm) produced by the varieties Désirée, Pentland Crown and Maris Piper, planted at the same spacing, were 0.50 ($\pm$ 0.010), 0.59 ($\pm$ 0.016) and 0.34 ($\pm$ 0.009), respectively. In view of the size of the standard deviations involved it is clear that these variances can be regarded as being quite distinct. The variances certainly agree with a visual assessment of the size distribution which each variety typically produces, but do not fully explain varietal differences in the numbers of tubers shown in Table 1. Désirée and Maris Piper both initiated tubers over a wide range of nodes and during the period in question Désirée formed more tubers than Maris Piper, yet had a much larger variance. The difference in tuber numbers is largely attributable to the first node and many of these are probably resorbed. At maturity Maris Piper usually has more tubers than Désirée.

The tuber size distributions produced by each variety obviously depend on competition for the products of photosynthesis and this occurs at two levels: between and within nodes. The proportion of the total number of tubers at each node represents competition between nodes and the number of tubers formed at each node expressed as a percentage of the number of stolons (Fig. 3) represents competition within a node. In Pentland Crown node 1 dominated the other nodes while in Désirée and Maris Piper node 1 was again dominant but the wide range of nodes bearing tubers, and the fact that competition within nodes was much more even, seems likely to be responsible for their tubers being of more even size.

It seems likely that differences between varieties in the position of tuber formation may affect the subsequent tuber size distribution, but it is not clear to what extent individual patterns of tuber growth are also affected by the position of the tuber on the stem. Before the causes of variation in tuber size can be properly understood there needs to be an investigation of tuber formation and growth using techniques which allow the classification of tuber growth in relation to the position on the stem of the stolon bearing the tuber. Such work would be most valuable because tuber growth patterns probably affect other tuber characteristics such as tuber specific gravity, cell size, starch content and suitability for cooking.

Acknowledgments

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Zusammenfassung

Einige Beobachtungen zum Muster der Knollenbildung und des Knollenwachstums der Kartoffel

In einer Reihe von Versuchen, bei denen die Sorten Désirée, Maris Piper und Pentland Crown verwendet wurden, wurden die Muster der Knollenbildung und das Knollenwachstum untersucht. Diese 3 Sorten haben bei gleichem Pflanzenabstand eine unterschiedliche Verteilung der Knollengrösse; Pentland Crown neigt zur Produktion grosser Knollen, Maris Piper bringt viele kleinere Knollen und Désirée liegt dazwischen.

Um die Knollenbildung zu verfolgen, wurden dreimal in der Woche Proben der wachsenden Pflanzen genommen und die Zahl der Stolonen und Knollen pro Nodium gezählt (Tabelle 1).

Um das Wachstum der Einzelknollen in Kisten (Fig. 1) und im Feld unter Polythenfolie (Fig. 2) zu verfolgen, wurden die drei Hauptachsen gemessen und daraus das Volumen (in der Annahme, dass die Knolle ein Ellipsoid ist) oder das Gewicht errechnet (wobei das lineare Verhältnis zwischen dem Produkt der Knollenachsen und dem Frisch- und Trockengewicht von Knollen verwendet wurde, die unter gleichen Bedingungen gewachsen waren und jede Woche geerntet wurden, wenn die Messungen gemacht wurden). Diese Technik erwies sich als befriedigend und in Tabelle 2 sind die Werte der Parameter für die erste und letzte Messung in jedem Jahr zusammen mit den entsprechenden Bestimmtheitsmassen angegeben.

Die Sorten bildeten die gleiche Anzahl von Stolonen aber unterschiedliche Knollenzahlen. Am ersten Knoten wurden mehr Knollen als an irgend einem anderen gebildet, aber Pentland Crown bildete an den Nodien 2–8 weniger Knollen als die anderen Sorten. Das Verhältnis der Gesamtzahl der Knollen pro Nodium und der Knollenzahl pro Nodium ausgedrückt in Prozent der Stolonenzahl (Fig. 3) unterschied sich zwischen den Sorten beträchtlich und ist vielleicht für die unterschiedliche Verteilung der Knollengrössen verantwortlich. Die Zeit der Knollenbildung war bei allen Sorten gleich.

In den Versuchen über das Knollenwachstum wurden mehr als 500 Knollen gemessen und einige sind in Fig. 4–6 dargestellt. Es sieht so aus, als ob einige Knollen einer ungefähr S-förmigen Kurve folgten, einige wuchsen linear und einige zeigten Perioden des Wachstums, die durch Perioden unterbrochen waren, in denen die Knollen wenn überhaupt nur langsam wuchsen.

Résumé

Quelques types de tubérisation et de croissance observés chez la pomme de terre

Des types de tubérisation et de croissance ont été étudiés au cours d'une expérimentation de variétés portant sur Désirée, Maris Piper et Pentland Crown.

Plantées à la même densité, ces variétés donnent différentes répartitions de calibre.

Pentland Crown tend à produire de gros tubercules; Maris Piper produit un grand nombre de petits tubercules et Désirée est intermédiaire.

La tubérisation a été suivie en prélevant des échantillons en cours de végétation 3 fois par semaine et en enregistrant le nombre de stolons et de tubercules formés à chaque noeud (tableau 1).

Le grossissement de chaque tubercule, en caisses de bois (fig. 1), et au champ sous polyéthylène (fig. 2), a été suivi en mesurant les trois axes principaux et en transformant ces mesures

en volume (on suppose que le tubercule est un ellipsoïde), ou en poids (en utilisant la relation linéaire entre produit des axes et poids frais et sec des tubercules cultivés dans des conditions identiques et récoltés chaque semaine).

Cette technique donne satisfaction et les valeurs des paramètres pour les premières et dernières mesures de chaque année sont indiquées dans le tableau 2 avec les coefficients de détermination appropriés.

Les variétés forment un nombre de stolons similaire mais un nombre de tubercules différents.

Des tubercules plus nombreux se sont formés au premier noeud, mais Pentland Crown présentait moins de tubercules aux noeuds 2–8 que les autres variétés.

Le rapport du nombre de tubercules par noeud et du nombre de tubercules formés à chaque noeud, exprimé en pourcentage du nombre de stolons (fig. 3) différait considérablement d'une variété à l'autre. La répartition des calibres de ces variétés a probablement été influencé. L'époque de tubérisation était la même pour chacune d'entre elles.

Au cours de cette expérimentation, plus de 500 tubercules ont été mesurés (fig. 4–6). Pour certains tubercules, il apparaît que la courbe tubérisation s'apparente à une sigmoïde. Pour d'autres, la croissance est linéaire, parfois interrompue par des périodes de croissance ralentie.

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