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Effects of drought on the initiation, yield, and size distribution of tubers of *Solanum tuberosum* L. cv. Bintje

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Zusammenfassung, Résumé p. 498

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Summary

Potato plants were grown in pot assemblies which allowed non-destructive observations.

During tuberization, plants were exposed to dry or wet conditions in the stolon environment and normal or low osmotic potential of the nutrient solution.

Drought in the stolon environment enhanced the initiation of stolons and tubers. Although this treatment caused a minor reduction in yield, more large tubers were produced because there were more large tubers on the early-initiated stolons.

Drought in the root medium did not affect the final number of stolons or tubers initiated, but reduced tuber yield. It inhibited the formation of large tubers on the later-formed stolons.

Drought conditions simultaneously in the stolon and root media slightly stimulated the initiation of stolons and tubers. Furthermore, it reduced the tuber yield and no large tubers were found on the latest-formed stolons. However, there were more large tubers on the early-formed stolons.

Introduction

Because water shortage affects the morphology, development, stolonization, tuberization, growth and productivity of the potato (*Solanum tuberosum* L.) crop, it also affects total and marketable yield and tuber quality (shape, frequency of abnormalities, dry-matter content, size distribution, chemical composition). The effects of water shortage depend on the physiological stage at which the plants are exposed to the stress (Harris, 1978).

Many reports (e.g. de Lis et al., 1964; Singh, 1969; Cavagnaro et al., 1971) indicate that during stolonization and tuberization potato plants are especially sensitive to drought, which then reduces the number of tubers (Salter & Goode, 1967; Steckel & Gray, 1979). Taylor & Rognerud (1959) even stated that availability of water during tuberization determined the final number of tubers. Krug & Wiese (1972), however, found that fewer tubers were initiated when there was drought during early tuberization, but this negative effect was compensated for by less resorption of tubers during the bulking period. Jefferies & MacKerron (1986) found no effect of drought on tuber number when water was withheld at any time from tuber initiation onwards. Cavagnaro et al. (1971) observed that although more tubers were initiated when plants were exposed to water shortage during tuberization, fewer were harvested because of an increase in the number of tubers or incipient tubers that were resorbed. Other reports indicate that there is a clear optimum amount of rainfall or irrigation: more water might result in an increase or in a decrease in the number of tubers harvested (Pätzold & Stricker, 1964; Timm & Flocker, 1966; Harkett & Burton, 1975). Reductions in yield caused by water shortage during stolonization and tuberization can be considerable (e.g. de Lis et al., 1964). In extreme cases abundant water supply before tuberization results in numerous tubers but this leads to such a decrease in the size of individual tubers that the marketable yield is reduced (Harris, 1978). Drought before the foliage is fully expanded reduces leaf size but also prolongs leaf persistence (e.g. Krug & Wiese, 1972; Harris, 1978; van Loon, 1981).

It is useful to discriminate between drought in the area of the basal roots and drought in the stolon region. In the field, water taken up by roots arising from the stems is almost exclusively transported to the aerial plant parts (Kratzke & Palta, 1985). Roots arising from the stolons (or even from tubers themselves) play a very important role in the transport of water to the tubers (Kratzke & Palta, 1985). Moreover, it is commonly believed that tuberization is greatly favoured by moist conditions around the stolon tip or other growing points (Ewing, 1985).

This paper describes research on the effects of drought in the environments of the roots and of the stolons on the dynamics of stolonization and tuberization, and the consequences of these effects for tuber yield and tuber-size distribution.

Materials and methods

Plant material and experimental set-up

Plants were grown from pre-sprouted tubers of cv. Bintje. The fresh weight of the individual mother tubers did not differ by more than 1 g. Mother tubers with one stem were placed on a piece of gauze sited over a hole in a rimmed plate that rested on a container holding 6.5 l nutrient solution (Fig. 1). The roots had to grow through the gauze to reach the solution. In Exp. 1 the solution contained, per litre, 86 mg N, 15 mg P, 137 mg K, 76 mg Ca, 23 mg Mg, 49 mg S, 4.6 mg Fe and all other micro-elements required. In Exp. 2 it contained, per litre, 86 mg N, 62 mg P, 156 mg K, 40 mg Ca, 12 mg Mg, 28 mg S, 4.6 mg Fe and all other micro-elements required. The pH of both solutions was 6.0 and the osmotic potential was -34 kPa; both values were checked regularly. The nutrient solution was not aerated and after an initial growth period it was renewed weekly to ensure that all nutrients were abundantly available. Earlier glasshouse experiments had shown that Mg deficiency could occur during tuber bulking because of limited uptake of Mg by the weak root systems, so $MgSO_4$ (0.2 mol/l) was applied to the foliage in Exp. 2.

Stolons and tubers were constrained within an upper container holding a mixture of equal volumes of coarse sand and agra-perlite (expanded volcanic rock) that was moistened during initial growth to allow normal development of the sprout and initiation of roots and stolons (Fig. 1). The sand of the stolon medium had a pH (in KCl) of approximately 6 and contained only traces of organic matter or nutrients. The stolon medium could be removed easily by a vacuum cleaner to allow stolon and tuber initiation to be observed. The exposure of stolons and tubers to light was kept as short as possible and the medium was renewed after each observation.

Fig. 1. Illustration of the method of growing plants on a nutrient solution, while constraining the stolons and tubers within a container with a removable sand/perlite mixture.
1: Mother tuber – *Mutterknolle* – *Tubercule-mère*
2: Gauze – *Gaze* – *Gaze*
3: Container with nutrient solution and roots – *Behälter mit Nährlösung und Wurzeln* – *Bac avec solution nutritive et racines*
4: Stolon chamber filled with sand/perlite mixture – *Stolonenkammer mit Sand/Perlit-Mischung gefüllt* – *Bac pour les stolons, rempli d'un mélange sable/perlite*
5: Saucer with ring – *Schale mit Ring* – *Soucoupe cerclée*
6: Stick to support the shoot – *Stab zur Befestigung des Triebs* – *Tuteur*

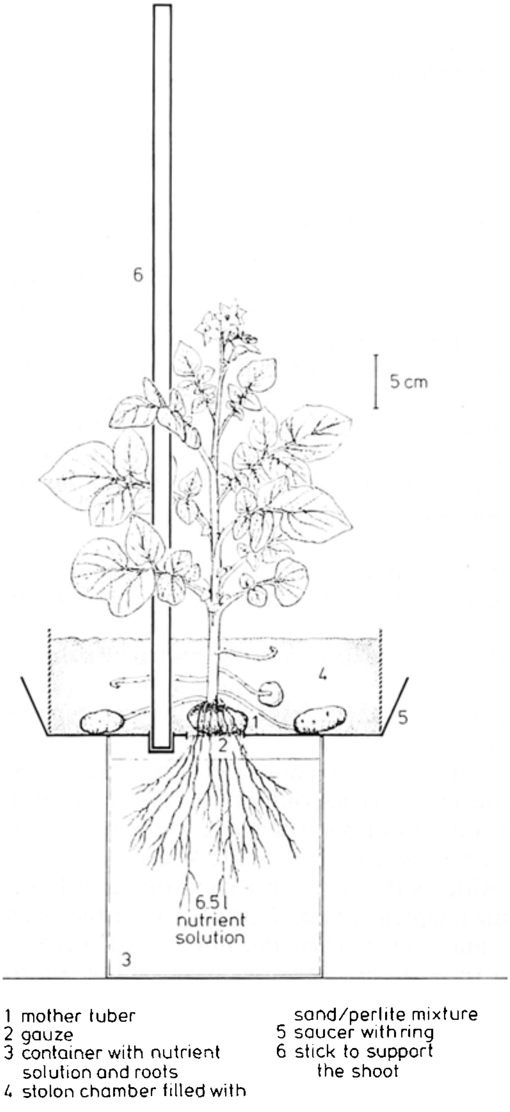

Abb. 1. Illustration der Methode zur Anzucht von Pflanzen auf Nährlösung, bei Begrenzung des Wachstums von Stolonen und Knollen innerhalb eines Behälters mit auswechselbarer Sand/Perlit-Mischung.
Fig. 1. Illustration de la méthode utilisée pour la croissance des plantes sur solution nutritive, de telle sorte que les stolons et les tubercules soient retenus dans un bac contenant un mélange sable/perlite changeable.

Table 1. Climate control in Exps. 1 and 2.

	Exp. 1 (growth chamber)	Exp. 2 (glasshouse)
Duration of photosynthetically active radiation (h)	12	14
Day temperature (°C)	20	18
Duration of day temperature (h)	12	14
Night temperature (°C)	15	12
Photoperiod (h)	14	14
Relative humidity (%)	75	75

Tabelle 1. Klima-Kontrolle in den Versuchen 1 und 2.
Tableau 1. Conditions climatiques dans les expérimentations 1 et 2.

Growing conditions and treatments
Two experiments with the same treatments were carried out; one in a growth chamber (Exp. 1) and the other in a glasshouse (Exp. 2). The physiological age of the mother tubers was similar in both experiments. Table 1 shows the main climatic conditions. These conditions allow good induction of tuberization of cv. Bintje. Light intensity was approximately 100 W m^{-2} (400–700 nm) in Exp. 1 and variable in Exp. 2. There was hardly any inter-plant competition for light. In Exp. 2 natural light was supplemented on dull days. The light intensity was relatively high during the 11 days of drought treatment in Exp. 2. The treatments could therefore be regarded as detrimental. In Exp. 1 the photoperiod was extended by 2 h by incandescent bulbs which burnt 1 h before and 1 h after the basic light period. Minimum illuminance during the supplementary photoperiod was 100 lx.

The treatments were as follows:
– control: wet sand/perlite mixture, normal osmotic potential (code WN)
– 'drought' in root medium: wet sand/perlite mixture, low osmotic potential of nutrient solution (code WL)
– 'drought' in stolon medium: dry sand/perlite mixture, normal nutrient solution (code DN)
– 'drought' in both root and stolon media: dry sand/perlite mixture, low osmotic potential of nutrient solution (code DL).

The stolon medium was air-dry (0 % water; dry) or contained 5 % water (w/w; wet). The root medium consisted of the normal nutrient solution (see above; osmotic potential −34 kPa) or the same nutrient solution plus sufficient polyethylene glycol (P.E.G.; mol. wt. 400) to produce an osmotic potential of −102 kPa.

Every swollen tip more than twice as wide as the first- or second-order stolon to which it was attached, was designated an incipient tuber. Treatments started when the first incipient tubers were observed and ended when the number of incipient tubers became constant. Before and after tuberization all plants received the control treatment. Both experiments were laid out as randomized block designs with 12 replicates.

To accommodate plant variation in date of tuberization in Exp. 1, the timing of the start and the end of the treatments were determined individually for each plant.

This was not necessary in Exp. 2. The duration of the treatments was variable, but averaged ca. 6 weeks in Exp. 1, and only 11 days for all plants in Exp. 2 where the plants remained very small, showed an early, prompt and uniform tuberization and senesced early.

Observations

Stolon and tuber initiation were recorded approximately twice a week. Stolons were tagged with numbered rings. Tuber sites could be identified per stolon by designating the tip of each first-order stolon site 1, the tip of the second-order stolon closest to the stem site 2, the tip of the second-order stolon second closest to the stem site 3, etc.

At the final and destructive harvest, leaf area was measured with a Li-Cor 3100 area meter. Other data recorded at final harvest were: length of the stolons, site and fresh weight of the tubers, and plant height. The tubers were then individually chopped and together with the stolons and shoots, dried to constant weight in forced ventilated ovens at 105 °C. The dry weight was then determined.

Data were evaluated using standard statistical procedures for a 2^2 factorial design.

Results

The first stolons appeared several weeks before tuber initiation. Stolons continued to be initiated until the end of the tuber initiation period. Those initiated early grew very long and were likely to form many second-order stolons, especially in Exp. 1. Later-formed stolons were much shorter and did not branch. The period between initiation of a stolon and the swelling of its tip also decreased the later a stolon was formed. A dry stolon medium (D vs W in the treatment descriptions) significantly increased the number of stolons in Exp. 1 ($P<0.01$) (Fig. 2a) and in Exp. 2 ($P<0.05$) (Fig. 2b), especially at the higher osmotic potential in the root medium (DN). Only in Exp. 2 did the low osmotic potential of the nutrient solution (L vs N) have a slightly significant, negative effect on the final number of stolons ($P<0.10$). The interaction between drought in the stolon medium and drought in the root medium was not significant in either experiment. Even though the duration of the treatments differed between the experiments, the effects were similar.

A dry stolon medium (D vs W) stimulated the formation of second-order stolons, thus increasing the number of potential tuber sites.

In Exp. 1 (Fig. 3a) the appearance of new incipient tubers was boosted by a dry stolon medium (D vs W) and by a low osmotic potential of the solution (L vs N) in the first two weeks. In the latter case, however, the curve levelled off earlier in time. At the end of the tuberization period, the dry stolon medium (D vs W) was found to have had a positive, significant effect on tuber number ($P<0.01$). The osmotic potential of the nutrient solution did not significantly affect the final number of tubers. The final values suggest an interaction between stolon drought and root drought but it was not significant.

In Exp. 2 the trends were similar (Fig. 3b), although the duration of the treatments was shorter and the final numbers of tubers were much lower. The difference between DL and the control (WN) was smaller than in Exp. 1. Nevertheless, no significant interaction between stolon drought and root drought was observed. At the final observation, the effect of drought was significant in both the stolon medium (D vs W)

Fig. 2. Effect of stolon and root drought treatments on number of stolons per plant in a growth chamber experiment (Exp. 1; Fig. 2a) and a glasshouse experiment (Exp. 2; Fig. 2b). Bars indicate standard error of the mean at the date of the final observation.

o =WN – control (i.e. wet sand/perlite mixture and normal osmotic potential of nutrient solution) – *Kontrolle (feuchte Sand/Perlit-Mischung und normales osmotisches Potential der Nährlösung) – Témoin (mélange sable/perlite humide et potentiel osmotique normal de la solution nutritive).*
• =WL – drought in root medium (wet sand/perlite mixture and low osmotic potential of nutrient solution) – *Trockenheit im Wurzelmedium (feuchte Sand/Perlit-Mischung und normales osmotisches Potential der Nährlösung) – Sécheresse du milieu racinaire (mélange sable/perlite humide et faible potentiel osmotique de la solution nutritive).*
× = DN – drought in stolon medium (dry sand/perlite mixture and normal osmotic potential of nutrient solution) – *Trockenheit im Stolonenmedium (trockene Sand/Perlit-Mischung und niedriges osmotisches Potential der Nährlösung) – Sécheresse au niveau des stolons (mélange sable/perlite sec et potentiel osmotique normal de la solution nutritive).*
+ = DL – drought in both stolon and root media (dry sand/perlite mixture and low osmotic potential of nutrient solution) – *Trockenheit sowohl im Stolonen- als auch im Wurzelmedium (trockene Sand/Perlit-Mischung und niedriges osmotisches Potential der Nährlösung) – Sécheresse au niveau des stolons et des racines (mélange sable/perlite sec et faible potentiel osmotique de la solution nutritive).*
↓ start of treatment – *Beginn der Behandlung – Début du traitement;* ↑ end of treatment – *Ende der Behandlung – Fin du traitement.*

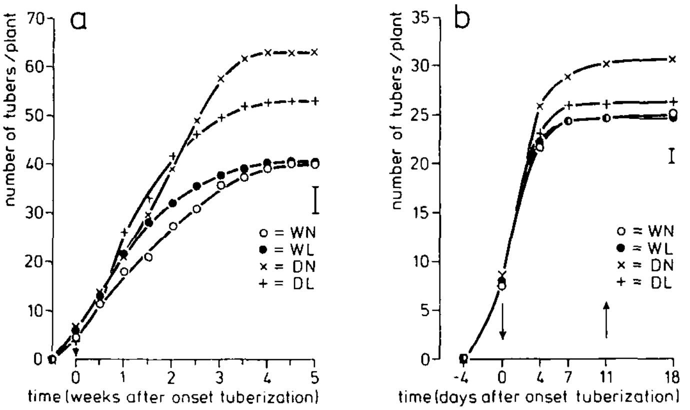

Abb. 2. Einfluss von Wurzel- und Stolonen-Behandlungen auf die Zahl der Stolonen pro Pflanze in einem Klimakammer-Experiment (Exp. 1; Abb. 2a) und einem Gewächshaus-Experiment (Exp. 2; Abb. 2b). Säulen zeigen den Standardfehler des Mittelwertes für die Daten der letzten Erhebung.
Fig. 2. Effets de différentes conditions de sécheresse sur stolons et racines, sur le nombre de stolons par plante dans un essai en salle de culture (exp. 1, fig. 2a) et un essai en serre (exp. 2; fig. 2b). L'erreur-type de la moyenne de la valeur finale est indiquée par les barres.

($P<0.05$) and in the root medium (L vs N) ($P<0.10$).

In these experiments with two types of drought it was observed that a dry stolon medium (D vs W) increased the number of stolons formed and the number of tubers

Fig. 3. Effect of stolon and root drought treatments (coded as in Fig. 2) on number of tubers per plant in a growth chamber experiment (Exp. 1; Fig. 3a) and a glasshouse experiment (Exp. 2; Fig. 3b). Note that the scales on the y-axes are different.
↓ start of treatment – *Beginn der Behandlung – Début du traitement;* ↑ end of treatment – *Ende der Behandlung – Fin du traitement.* Bars indicate standard error of the mean at date of final observation – *Die Säulen zeigen den Standardfehler des Mittelwertes für die letzten Erhebungsdaten – L'erreur-type de la moyenne de la valeur finale est indiquée par les barres.*

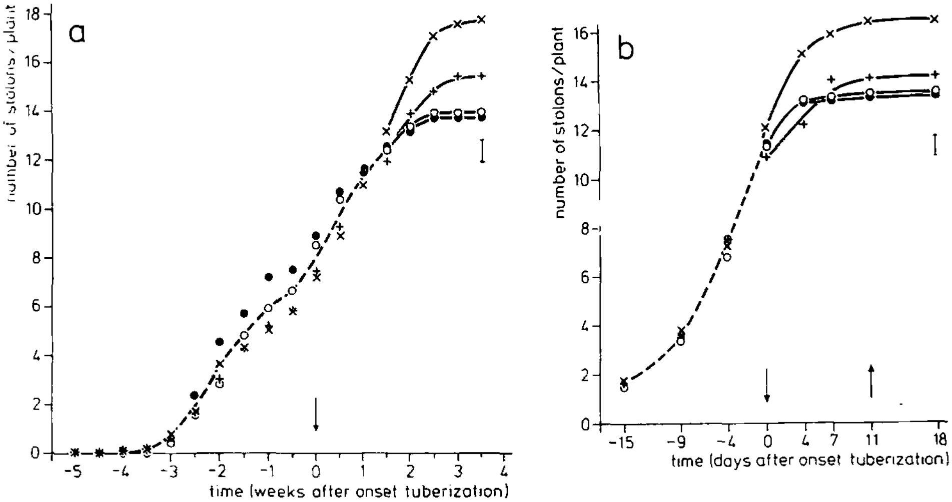

Abb. 3. Einfluss von Wurzel- und Stolonen-Behandlungen mit Trockenheit (Bezeichnungen wie in Abb. 2) auf die Zahl der Knollen pro Pflanze in einem Klimakammer-Experiment (Exp. 1; Abb. 3a) und einem Gewächshaus-Experiment (Exp. 2; Abb. 3b). Die Skalen auf den y-Achsen sind unterschiedlich.
Fig. 3. Effets de différentes conditions de sécheresse sur stolons et racines (comme décrit fig. 2) sur le nombre de tubercules par plante dans un essai en salle de culture (exp. 1, fig. 3a) et un essai en serre (exp. 2; fig. 3b).

initiated. The osmotic potential of the nutrient solution (L vs N) did not significantly affect the final number of stolons or tubers although DL tended to result in fewer stolons and tubers than DN in both experiments. Although several statistical procedures and designs were tried this interaction between stolon drought and root drought could not be proved to be significant.

Many tubers remained small (<0.5 g dry matter) and the positive effect of the dry stolon medium (D vs W) on tuber initiation did not result in more tubers larger than 0.5 g (Table 2). In both experiments there was a significant reduction in the number of these tubers, attributable to the addition of P.E.G. to the root medium (L). Drought did not reduce the number of harvestable tubers by reducing the number of tubers initiated, but by reducing the number of tubers that grew to a certain minimum size.

The tuber weight (Table 2) from the control of 105 g for Exp. 1, is a usual value for this type of experiment, but that of 44 g in Exp. 2 was due to the poor vegetative

Table 2. Effect of stolon and root drought treatments (as coded in Fig. 2) on the average number of tubers that exceeded a dry-matter weight of 0.50 g, and the relative tuber yield, in a growth chamber experiment (Exp. 1) and a glasshouse experiment (Exp. 2).

	Exp. 1	Exp. 2
Number of tubers/plant (>0.50 g dry matter)		
WN	18.7	11.9
WL	16.2	8.4
DN	18.3	12.7
DL	13.8	8.8
Stolon drought[a]	n.s.	n.s.
Root drought	*	**
Stolon drought × root drought	n.s.	n.s.
Relative tuber yield (%)		
WN	100[b]	100[c]
WL	80	70
DN	96	94
DL	72	84
Stolon drought	n.s.	n.s.
Root drought	*	*
Stolon drought × root drought	n.s.	n.s.

[a] n.s. not significant – *Nicht signifikant* – *Non significatif*
* $0.01 < P \leq 0.05$.
** $P \leq 0.01$.
[b] 100 % = 105 g dry matter – *Trockenmasse* – *Matière sèche.*
[c] 100 % = 44 g dry matter.

Tabelle 2. Einfluss von Behandlungen mit Wurzel- und Stolonen-Trockenheit (wie in Abb. 2 erläutert) auf die durchschnittliche Zahl von Knollen, welche ein Trockenmasse-Gewicht von 0,50 g überschritten, und auf den relativen Knollenertrag, in einem Klimakammer-Experiment (Exp. 1) und einem Gewächshaus-Experiment (exp. 2).

Tableau 2. Effets de différentes conditions de sécheresse sur stolons et racines (comme décrit dans la fig. 2) sur le nombre moyen des tubercules, d'un poids de matière sèche supérieur à 0,50 g, et le rendement relatif en tubercules, dans un essai en salle de culture (exp. 1) et un essai en serre (exp. 2).

development, the very early tuber set and the early and fast, but normal looking senescence at the end of a growth period that was approximately 40 days shorter than in Exp. 1. The relative tuber yield was greatly reduced by a low osmotic potential of the nutrient solution (L vs N) in both experiments. The effects of a dry stolon medium (D vs W) on tuber yield were not significant.

Shoot development was also influenced by stolon and root drought. The data are not presented for reasons of space, but the effects will be described briefly.

Leaf area was reduced by the drought treatment in the root medium (L vs N), especially in Exp. 2. After the treatments were stopped, there was considerable regrowth of the foliage but this was not accompanied by second growth of tubers. The newly-formed leaves were dark green and shiny and were more persistent than the top leaves of the control and of treatment DN, consequently differences in leaf area between

Fig. 4. Effect of stolon and root drought treatments (as coded in Fig. 2) on the percentage of the total tuber dry matter present in three classes of dry weight in a growth chamber experiment (Exp. 1; Fig. 4a) and a glasshouse experiment (Exp. 2; Fig. 4b). Class sizes are 0–8, 8–16 and >16 g in Exp. 1 and 0–4, 4–8 and >8 g in Exp. 2.

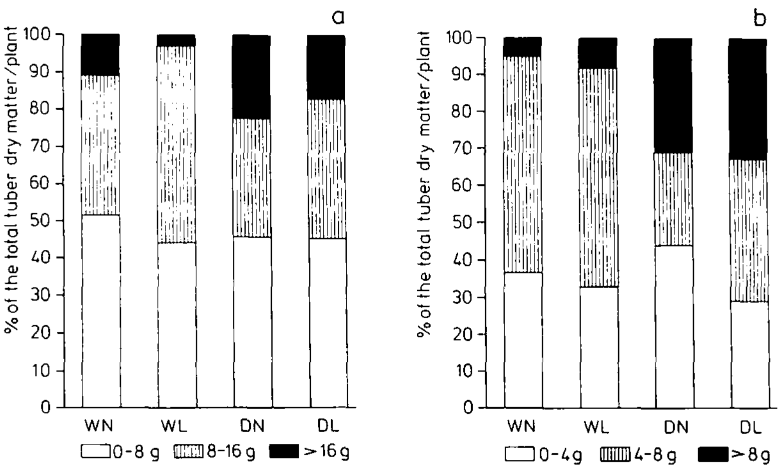

Abb. 4. Einfluss von Wurzel- und Stolonen-Behandlungen mit Trockenheit (Bezeichnungen wie in Abb. 2) auf den Prozentsatz und die Knollen-Gesamttrockenmasse in drei Trockengewichts-Klassen in einem Klimakammer-Experiment (Exp. 1; Abb. 4a) und einem Gewächshaus-Experiment (Exp. 2; Abb. 4b). Klassengrössen sind 0–8, 8–16 und >16 g in Exp. 1 und 0–4, 4–8 und >8 g in Exp. 2.

Fig. 4. Effets de différentes conditions de sécheresse sur stolons et racines (comme décrit dans la fig. 2) sur le pourcentage de la matière sèche totale des tubercules dans trois classes de poids sec, dans un essai en salle de culture (exp. 1; fig. 4a) et un essai en serre (exp. 2; fig. 4b). La largeur des classes est 0–8, 8–16 et >16 g dans l'exp. 1 et 0–4, 4–8 et > 8 g dans l'exp. 2).

treatments of Exp. 2 were smaller at final harvest than shortly after treatments began. In both experiments, plant height was significantly reduced by a low osmotic potential (L vs N) ($P<0.05$). However, dry weight of the shoot was not affected by drought in the root medium (L vs N). A dry stolon medium (D vs W) did not affect the shoot dry weight in Exp. 1, but it was increased in Exp. 2 ($P<0.01$).

The effects on tuber-size distribution were remarkable. We divided the tubers into three classes (Fig. 4) according to their dry weight and depending on the yield of the experiment. In Exp. 1 (Fig. 4a), the relative yields of the small tubers were not affected by the treatments. Significantly fewer medium-sized tubers were produced by a dry stolon medium (D vs W) ($P<0.10$) but more large tubers were produced ($P<0.10$) The contrast in dry-matter yield between the two largest sizes was highly significant ($P<0.01$), suggesting that a dry stolon medium (D) caused relatively more dry matter to be invested in large tubers. Low osmotic potential (L vs N) tended to increase the proportion of medium-sized tubers. The effect of drought in the stolon medium (D vs W) was greater in Exp. 2 (Fig. 4b): again there was a shift towards the larger sizes when the stolons were subjected to dry conditions. In both experiments even the absolute yields of the largest fraction were significantly higher for the plants exposed to a dry stolon medium during tuberization. This was true whether data were analysed according to the normal distribution or the Poisson distribution. Depending on experiment and type of analysis the level of significance ranged from 0.10 to 0.01.

The frequent observations enabled us to categorize the stolons and tubers according to their time of initiation (Fig. 5). In Exp. 1 almost all the large tubers were located either on the stolons initiated earliest (numbers 1–5) or on those initiated latest (numbers ≥ 11). Only two large tubers were found in the intermediate group of stolons. Moreover, there were clear differences between treatments: a dry stolon medium (D vs W) significantly increased the absolute yield of large tubers on the oldest stolons ($P<0.05$), whereas low osmotic potential (L) lowered this yield but not significantly. Large tubers on the oldest stolons were found only on sites 2 and higher.

Only in the DL treatment did large tubers occur in the middle group of stolons. In the group of late-initiated stolons large tubers were found only when the osmotic

Fig. 5. Effect of stolon and root drought conditions (as coded in Fig. 2) on the distribution of the largest tubers (as total tuber dry matter/plant) over the different groups of stolons in a growth chamber experiment (Exp. 1; Fig. 5a) and a glasshouse experiment (Exp. 2; Fig. 5b). Stolons are grouped according to their date of first observation. Bars indicate standard error of the mean.

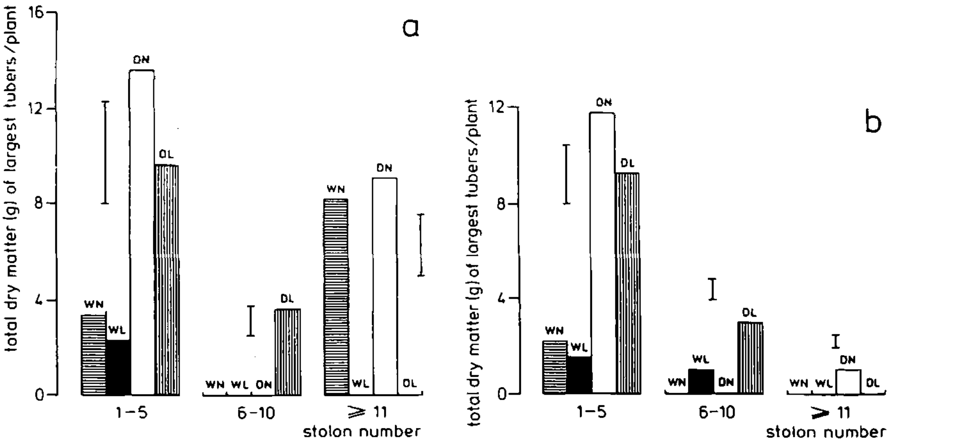

Abb. 5. Einfluss von Trockenbedingungen auf Wurzeln und Stolonen (Bezeichnungen wie in Abb. 2) auf die Verteilung der grössten Knollen (als Gesamttrockenmasse der Knollen/Pflanze) über die verschiedenen Stolonengruppen in einem Klimakammer-Experiment (Exp. 1; Abb. 5a) und einem Gewächshaus-Experiment (Exp. 2; Abb. 5b). Die Stolonen sind entsprechend ihrer Daten der ersten Beobachtung gruppiert. Säulen zeigen den Standardfehler des Mittelwertes.

Fig. 5. Effets de différentes conditions de sécheresse sur stolons et racines (comme décrit dans la fig. 2) sur la répartition des plus gros tubercules (en matière sèche totale/plante) au niveau des différents groupes de stolons, dans un essai en salle de culture (exp. 1; fig. 5a) et un essai en serre (exp. 2; fig. 5b). Les stolons sont groupés en fonction de leur date d'apparition. L'erreur-type de la moyenne est indiquée par les barres.

potential was normal (N) and almost always on site 1.

Data for Exp. 2 were similar (Fig. 5b). Early-initiated stolons yielded significantly more large tubers when the stolon medium was dry (D) ($P < 0.01$), whereas there was a small, non-significant negative effect of a low osmotic potential (L). Large tubers occurred in the middle group of stolons only if the osmotic potential was low. The opposite was true for the youngest stolons. In this experiment there were few tubers on stolons 6 and higher and almost all the large tubers were found on site 1.

Although date of initiation of the stolon and site on the stolon played an important role in determining the final size of the tuber, in both experiments it appeared that the date of initiation of the *tuber* was of minor importance for its chances of growing or for its final size. The period between initiation and tuberization of a stolon was shorter the later a stolon was initiated. Moreover, the largest tubers of a stolon were often not the ones that were initiated first. Large tubers were initiated 0–29 days after the initiation of the stolon on which they were located.

Discussion

The method described is elegant because it allows both frequent non-destructive observations and the conditions of the different plant organs to be varied independently. There are some disadvantages:

– plants grown in this way proved to be sensitive to pathogens that usually are fairly harmless, e.g. some *Clostridium* spp. (cf. Hooker, 1981);

– plant-to-plant variation may become extremely large if plants are not tended carefully during emergence;

– the root systems may become weak shortly after the start of the bulking period; this weakening is usually faster than in the field where root systems also appear to stop growing and start to deteriorate after tuberization (Steckel & Gray, 1979; Harris, 1983);

– because of the frequent removal of the stolon medium, the stolon roots were not viable, therefore, all minerals had to be taken up by the roots in the nutrient solution. Thus the stolons and tubers had to compete with the shoot for nutrients, too. This is especially important for calcium nutrition;

– the ring that encloses the stolon chamber induces thigmomorphosis and stereotropism when the early, long stolons reach the edge of the stolon chamber;

– extreme care is needed when removing the stolon medium by means of a vacuum cleaner because plant growth may be adversely affected by frequent handling (cf. Stuff et al., 1979).

Our results contradict those in many other reports, partly because of differences in the definition of a tuber (cf. Fig. 3 and Table 2). Apparently, drought causes a reduction in number of harvestable tubers by its effect on tuber growth rather than on tuberization. Moreover, this effect of drought is induced by the restricted uptake of water by basal roots. To induce tuberization it is not necessary to have a moist medium around the stolon tips or to have uptake of water by stolon roots. The effects of drought were recognizable even after a short treatment (Exp. 2). First signs of reaction of the plants were visible very soon after the start of treatments (Figs. 2 and 3).

Another surprising result is the positive effect of a dry stolon medium on the frequency of large tubers. The total tuber yield was somewhat lower, yet the yield of largest tubers was higher for DN in both experiments. Apparently, the yield of large tubers is not only stimulated when the total yield is boosted but can also be affected by manipulating the factors that influence the dry-matter distribution. Results suggest that the pattern of dry-matter distribution within the stolon system at least partly depends on environmental factors during the period of tuberization. In both experiments, when the stolon medium was dry during tuberization the number of large tubers on early-initiated stolons was especially high.

These effects of a dry stolon medium might be brought about by effects on:
- the gas composition within it (concentrations of ethylene, CO_2 or O_2)
- the intensity of contact between it and the stolon tips
- its bulk density
- its temperature (mainly in Exp. 2)
- the induction of root formation on stolons.

The effects of drought in the root medium accord with most of the results in the literature if a certain minimum tuber size is taken into account. The lack of significant interactions between drought in the root medium and drought in the stolon medium is striking. Two separate physiological mechanisms might be involved. However, DL was consistently lower both for stolon number and tuber number. Probably, the plant needs to take up sufficient water by the roots to be able to profit from the stimulating effect of a dry stolon medium on stolon and tuber initiation. The relevance of a dry stolon medium for tuber initiation, yield and quality needs further investigation.

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Zusammenfassung

Einfluss von Trockenheit auf Knolleninitiierung, Knollenertrag und Knollengrössen-Verteilung von Solanum tuberosum L. (Sorte Bintje)

In zwei Experimenten unter kontrollierten Bedingungen (Tabelle 1) wurden Pflanzenentwicklung, Knollenertrag und Knollengrössen-Verteilung von *Solanum tuberosum* L. (Sorte Bintje) untersucht. Das speziell entwickelte Verfahren (Abb. 1) erlaubte fortwährende, nicht-destruktive Beobachtungen der Stolonenbildung und der Knolleninitiierung und ermöglichte separate Variierung der Wasserverfügbarkeit in der Umgebung von Wurzeln und Stolonen.

Die Stolonen-Initiierung wurde durch ein trockenes Stolonen-Medium gefördert, während Trockenheit in der Wurzelumgebung die Stolonenbildung kaum beeinflusste (Abb. 2). Ebenso wurde Knolleninitiierung durch Trockenheit im Stolonenmedium stimuliert, während eingeschränkte Wasseraufnahme durch die basalen Wurzeln kaum Einfluss auf die Knollenbildung hatte (Abb. 3).

Nicht alle Knollen wuchsen bis zu substanzieller Grösse. Trockenheit im Wurzelmedium reduzierte die Zahl der Knollen, die ein endgültiges Trockengewicht über 0,50 g erreichten (Tabelle 2). Der Feuchtigkeitsgehalt des Stolonenmediums hatte hingegen keinen Einfluss auf diese Zahl. Trockenheit im Wurzelmedium reduzierte auch den Gesamtertrag an Knollentrockenmasse erheblich. Ein trockenes Stolonenmedium hatte lediglich einen geringen Einfluss (Tabelle 2). Offensichtlich reduziert Trockenheit die Zahl der Knollen durch Reduktion des Knollenwachstums und nicht durch Beeinflussung der Knollenbildung, und ist nur bei trockenen Verhältnissen im Wurzelbereich effektiv.

Ein trockenes Stolonenmedium während der Knollenbildung induziert einen Schub an Trockenmasse für höhere Knollengrössen: In beiden Versuchen ergab sich eine höhere Proportion des gesamten Knollenertrages in der höchsten Klasse für Knollengrössen (Abb. 4). Wurden die Wurzeln trockenen Verhältnissen ausgesetzt, wurde relativ mehr Trockenmasse in den mittelgrossen Knollen festgelegt (Abb. 4). Der beobachtete positive Effekt eines trockenen Stolonenmediums wurde durch einen Anstieg der Zahl grosser Knollen an früh-initiierten Stolonen verursacht (Abb. 5). Trockenheit im Wurzelmedium ergab weniger grössere Knollen an den spät-initiierten Stolonen (Abb. 5). Der Einfluss von Trockenheit im Wurzelmedium stimmt mit den meisten Literaturdaten überein. Der Einfluss eines trockenen Stolonenmediums ist dagegen bemerkenswert und bedarf weiterer Untersuchung.

Résumé

Effets de la sécheresse sur l'initiation des tubercules, le rendement et la répartition des calibres de Solanum tuberosum L. variété Bintje

Les effets de la sécheresse sur le développement de la plante, le rendement en tubercules et la répartition des calibres de *Solanum tuberosum* L. variété Bintje sont étudiés dans deux expérimentations en conditions controlées (tableau 1).

Le dispositif spécial utilié (fig. 1) permet des observations non destructives fréquentes de la formation des stolons et de l'initiation des tubercules et rend possible des variations séparées de la disponibilité en eau au niveau des racines et des stolons.

Un milieu sec au niveau des stolons favorise leur initiation tandis que des conditions sèches au niveau racinaire l'affecte (fig. 2). L'initiation des tubercules est stimulée par des conditions sèches au niveau des stolons tandis qu'une absorption d'eau réduite des racines de la base n'a aucun effet sur la tubérisation (fig. 3).

Tous les tubercules n'atteignent pas un calibre important. Une sécheresse au niveau du milieu racinaire réduit le nombre de tubercules de poids sec final supérieur à 0,50 g (tableau 2) mais le degré d'humidité au niveau des stolons n'a aucun effet sur ce nombre. Une sécheresse du milieu racinaire diminue également fortement le rendement total en matière sèche des tubercules. Une sécheresse uniquement au niveau des stolons n'a qu'un effet mineur (tableau 2). Apparemment, la sécheresse diminue le nombre de tubercules en réduisant le grossissement des tubercules et non pas en modifiant la tubérisation, et n'a d'effet que si les racines sont soumises aux conditions sèches.

Un milieu sec au niveau des stolons durant la tubérisation induit un déplacement de la matière sèche vers les tubercules les plus gros: dans les deux expérimentations une plus grande proportion du rendement total en tubercules a été observée dans la classe des calibres les plus gros (fig. 4). Lorsque les racines sont soumises à des conditions sèches une quantité relativement plus importante de matière sèche est accumulée dans les tubercules de moyen calibre (fig. 4). L'effet positif observé dans le cas d'un milieu sec au niveau des stolons est la cause d'une augmentation du nombre de gros tubercules sur les stolons initiés précocement (fig. 5). Une sécheresse du milieu racinaire a pour conséquence un faible nombre de gros tubercules formés sur les stolons initiés tardivement (fig. 5). Les effets d'une sécheresse racinaire concordent avec la plupart des données mentionnées dans la littérature. Les effets d'une sécheresse au niveau des stolons sont cependant singuliers et nécessitent des investigations complémentaires.

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