The influence of early soil moisture stress on tuber numbers in potato

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Summary

The relationship between water shortage and tuber initiation and development in the cv. Maris Piper was examined in glasshouse experiments with several severities of water-stress induced by withholding water at different stages of plant growth. There was a direct reduction in tuber numbers per stem with increasing duration of water stress in plants deprived of water from the time when 50 % of plants had emerged but not when water was withheld from the time of onset of initiation. Using the data from both years a statistically significant negative correlation was established between tuber number per stem and the number of days of soil moisture potential < −25 kPa.

Introduction

There have been several reports included in the reviews by Salter & Goode (1967) and by van Loon (1981), that tuber number in the potato crop is affected by soil moisture in the early part of the growing season. In some of these reports the effect has been identified as a response to irrigation at stages that are ill-defined in relation to tuber development, e.g. before flowering (Brouwer, 1959), so that results conflict (compare Edmundson, 1938; Robins & Domingo, 1956 and Brouwer, 1959 with Taylor & Rognerud, 1959 and Llewelyn, 1962) depending on whether the growing conditions for the non-irrigated crop were in fact dry and on when the treatments were imposed. Nevertheless, Salter & Goode (1967) concluded that 'a plentiful supply of water before tuber initiation increases the number of tubers per plant'. Van Loon (1981) emphasized the depression in tuber number due to drought rather than an increase due to ample water supply when he wrote, 'Dry soil conditions at the beginning of tuberisation...' and '...in the period of tuber initiation result in a relatively limited number of tubers per plant'.

In the work reviewed by Salter & Goode (1967) and by van Loon (1981) the various authors did not always make clear what constituted wet or dry soil conditions and there was no attempt to quantify the relationship between water supply and tuber number. Similarly, the time at which tuber number is influenced has not been made clear. Several authors reported the effects of irrigation before flowering (Brouwer & Martin, 1956; North, 1960), perhaps following Clark (1921) in believing that the time of flowering coincides with that of tuber initiation. While such a coincidence may

occur the statement is not a valid generalization; for example, Steineck (1958) emphasised the importance of adequate water supply during stolon formation some 3 weeks after emergence and well before flowering. Llewelyn (1962) claimed, in an unsupported statement that the number of tubers produced declined in proportion to the length of time before watering started.

Allen (1972) investigated the effects on yield of row width, seed size and seed spacing, and found linear relationships between tuber number and stem density but in the 3 cultivars examined the absolute values differed greatly between years. Allen (1978) ascribed the difference between seasons to 'the extent of water supply at tuber initiation' but he was not able to quantify the relationship. Although it is generally accepted that early water stress depresses final tuber number, it is necessary to quantify the relationship before tuber numbers can be predicted. In turn, prediction is not possible until the plant's sensitive period to water stress has been better defined.

The work reported here was designed to identify the sensitive period and to provide quantitative data that might be used in a model of potato development and growth.

Materials and methods

Experiments were done in 1982 and 1983 in a ventilated and unheated glasshouse to allow control of the soil water conditions. Temperatures were not recorded but they did not differ greatly from outside temperatures. In both years the plants were grown singly in containers (34 cm wide and 51 cm long) in a compost of 3 parts peat to 1 part sand with added nutrients. The compost was 28 cm deep and the volume per plant was 48.5 l.

Experiment 1

In Experiment 1, unsprouted seed tubers (35 – 40 mm), cv. Maris Piper, were planted on 7 April 1982 at a depth of 12 cm in containers spaced to give a plant density of 2.45 m^{-2}. The plants for each of the treatments (Table 1a, and below) were arranged randomly within each of three replicate blocks. The numbers exceed those needed for the treatment harvests by sufficient to allow for periodic destructive harvests to monitor plant development.

Soil water potential (ψ soil) was monitored daily using porous-cup soil moisture tensiometers (Soil Moisture Equipment Corp., California, USA) fitted with either Bourdon gauges or mercury manometers; porous pots were centred in the containers at 15 cm depth. The containers were watered lightly to offset evaporation from the soil surface until the plants emerged. Thereafter they were watered lightly, daily whenever soil water potential fell below -10 kPa except during the periods of imposed drought.

The intention was to phase the relief of water stress in different treatments so that the steps between treatments $A_0 - A_1$, $A_1 - A_2$ etc. would have equal areas beneath a curve of ψ soil plotted against time i.e. there would be equal-sized steps in the time-integral of soil water potential. This intention was not achieved (Fig. 1a) but the attempts to implement it explains the uneven time intervals between the relief of stress in the several treatments.

In each block one plant was assigned to each of the treatments A_1, A_2, A_3, B_1, B_2, C_1, C_2 and two plants to the treatments U, A_4, B_3, C_3. The extra plants in these

Table 1. Summary of treatments.

Treat-ment	Beginning of period when water withheld	Duration of dry period (days)	Minimum measured Ψ soil[2] (kPa)	Number of days with Ψ soil -25 kPa
(a) Treatments imposed in 1982				
U	– (unstressed)	–	–7	0
A_1	50 % emergence (34 DAP[1])	24	–48	2
A_2	50 % emergence (34 DAP)	28	–69	6
A_3	50 % emergence (34 DAP)	33	–70	11
A_4	50 % emergence (34 DAP)	38	–70	15
B_1	tuber initiation (58 DAP)	10	–57	6
B_2	tuber initiation (58 DAP)	15	–63	11
B_3	tuber initiation (58 DAP)	21	–65	17
C_1	small tuber stage (70 DAP)	10	–65	5
C_2	small tuber stage (70 DAP)	13	–71	8
C_3	small tuber stage (70 DAP)	20	–73	15
(b) Treatments imposed in 1983				
U	– (unstressed)	–		0
A_1	50 % emergence (10 DAP)	30	–59	5
A_2	50 % emergence (10 DAP)	33	–115	8
A_3	50 % emergence (10 DAP)	35	–225	10
A_4	50 % emergence (10 DAP)	37	–407	12
A_5	50 % emergence (10 DAP)	40	–722	15
B_1	tuber initiation (37 DAP)	8	–154	4
B_2	tuber initiation (37 DAP)	11	–754	7
B_3	tuber initiation (37 DAP)	13	–1493	10
B_4	tuber initiation (37 DAP)	16	–2116	11
B_5	tuber initiation (37 DAP)	20	–3030	16

[1] DAP – days after planting – *Tage nach Pflanzung – Jours après plantation;* [2] Values of soil water potential less than about -70 kPa could not be measured in 1982 – *Wasserpotential-Werte unter ca. -70 kPa konnten 1982 nicht gemessen werden – Les valeurs du potentiel capillaire inférieures à 70 kPa n'ont pu être mesurées en 1982.*

Tabelle 1. Zusammenfassung der Behandlungen. (a) Behandlungen aus 1982; (b) Behandlungen aus 1983.
Tableau 1. Récapitulatif des traitements. (a) Traitements imposés en 1982; (b) traitements imposés en 1983.

last named treatments were harvested six hours after relief of water stress in the plants of treatment C_3. The remaining plants were allowed to continue growth under irrigated conditions until they began to show signs of senescence, when the shoots were cut off. Two weeks later the tubers were harvested. For each plant, stem and tuber numbers were recorded, total yield and individual tuber weights were measured and the dry matter concentration of a sample of tubers was determined. All tubers were counted whose longest dimension was ≥ 10 mm.

Experiment 2
In Experiment 2, stem number was closely controlled by planting groups of four

Fig. 1. The progress of measured soil water potential, kPa (log scale) and the timing of relief of stress.
(a) Experiment 1. Continuous line, unstressed treatments. Dotted lines treatments in the series A, B and C as indicated. Note that soil water potentials would have fallen well below -70 kPa in the more severely stressed treatments but the values could not be measured.
(b) Experiment 2. Continuous line, A series of treatments. Dotted line, B series of treatments. Arrows indicate dates of relief of water stress.
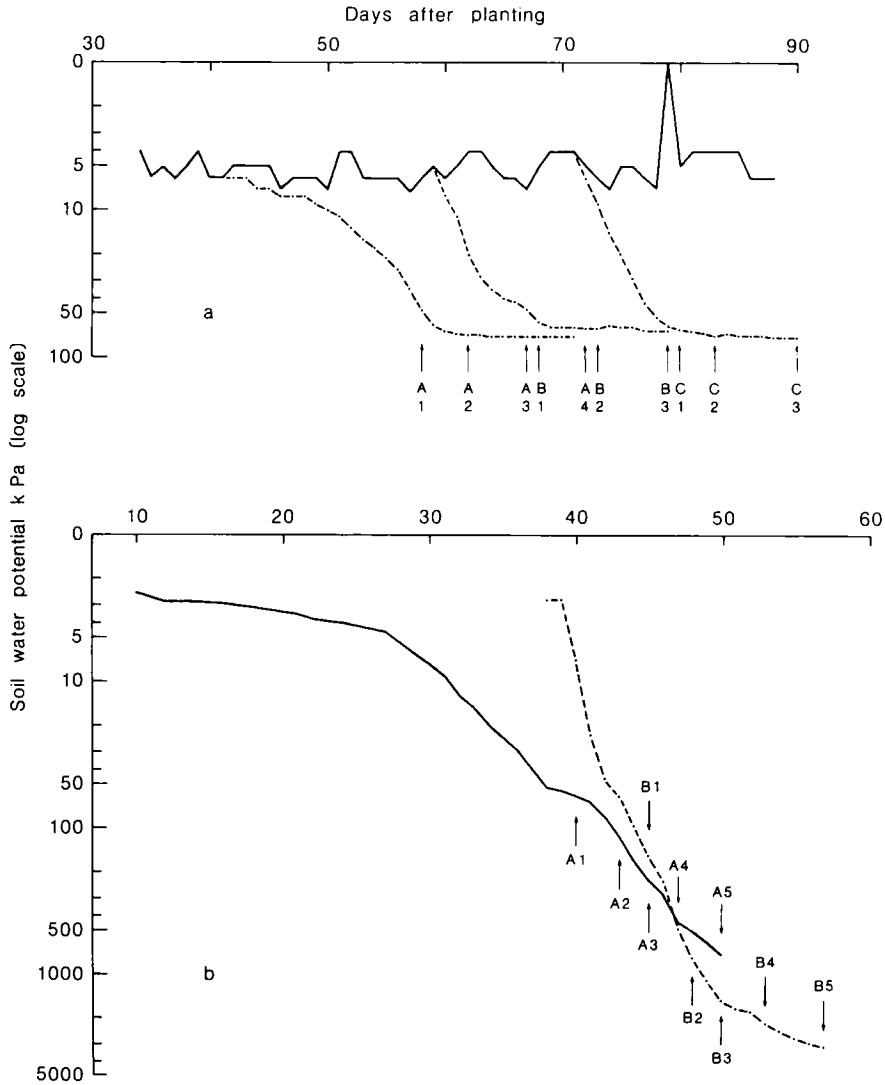
Abb. 1. Verlauf des gemessenen Bodenwasser-Potentials kPa (log-Skala) und der zeitlichen Abstufung der Stressunterbrechung.
(a) Versuch 1. Durchgehende Linie: ungestresste Behandlung. Gepunktete Linie in den Serien A, B und C wie abgebildet. Bemerkung: Bodenwasser-Potential würde in den stärker gestressten Behandlungen erheblich unter −70 kPa gefallen sein, die Werte konnten jedoch nicht gemessen werden.
(b) Versuch 2. Durchgehende Linie: A-Serie der Behandlungen. Gepunktete Linie: B-Serie der Behandlungen. Pfeile zeigen die Daten der Aufhebung des Wasserstress.
Fig. 1. Evolution des mesures du potentiel capillaire, kPa (échelle log) et dates de relachement du déficit hydrique.
(a) Expérimentation 1. Courbe en trait plein: traitement bien pourvu en eau. Courbe en pointillés: traitement des séries A, B et C, selon indication. A noter que les potentiels capillaires seraient descendus en dessous de 70 kPa dans les traitements de déficit les plus importants, mais les valeurs n'ont pu être enregistrées.
(b) Expérimentation 2. Courbe en trait plein: traitements des séries A. Courbe en pointillés: traitements des séries B. Les flèches indiquent les dates de relachement du déficit hydrique.

single-sprouted cores that had been cut from tubers of cv. Maris Piper sprouted in the light. The cores, 12 mm in diameter, had their bases trimmed to leave 10 g tuber tissue. They were kept 48 h at 12 °C in a humid atmosphere to allow the cut surfaces to suberize. They were then tied together in groups of four which were planted on 9 May 1983, in the same way as the single tubers had been planted in Experiment 1, and the containers were spaced to give a plant density of 3.27 m^{-2}.

Plants were assigned to eleven treatments (Table 1b) arranged in ten randomized blocks each of which included a spare plant for monitoring plant development.

Soil water potential was monitored and irrigation was scheduled as in Experiment 1 viz. whenever ψ soil < -10 kPa, except when water was deliberately withheld. In addition to the tensiometers, gypsum soil moisture blocks (SMEC, California) were installed in treatments A_5 and B_5 at 15 cm depth.

There was no early harvest, in Experiment 2 and all plants were allowed to continue growth until the end of August when the shoots were harvested. Stem number, and haulm fresh and dry weights were recorded. Two weeks later the tubers were harvested and measured as in Experiment 1.

In both experiments the date of 50 % emergence was determined by daily examination, a single visible shoot being the criterion for emergence of a plant. Spare plants were harvested at intervals to determine the dates of tuber initiation and of the small tuber stage. Tuber initiation was arbitrarily defined by the time at which the tips of 5 stolons per plant had each swollen to twice their diameter and plants were judged to have reached the small tuber stage when 5 tubers per plant had attained a diameter of 15 mm. The dry weights of shoots were estimated from samples dried for 48 h in a forced air oven at 90 °C, and of tubers by chopping samples into small pieces and drying them for 72 h.

Results

Shoots on pre-sprouted cores in 1983 emerged more quickly than did those from tubers in 1982 but thereafter their rates of development were similar. In both years low soil water potentials developed most slowly in the A series of treatments (Fig. 1a,

b) because the plants were then small. Plants in the more severely stressed treatments, B and C, reached permanent wilting point, recovering only when the water stress was relieved by watering.

In Experiment 1, the minimum soil water potential that developed is unknown because the tensiometers reached their maximum readings of c. -70 kPa at those times when water stress was relieved in treatments A_2, B_2 and C_1. Water loss continued

Fig. 2. Soil moisture release curve of the peat-sand compost. Water potential is on a logarithmic scale. Bulk density = 0.708 ± 0.019 g cm^{-3}. Porosity 0.698. Horizontal bars indicate standard errors of the mean.
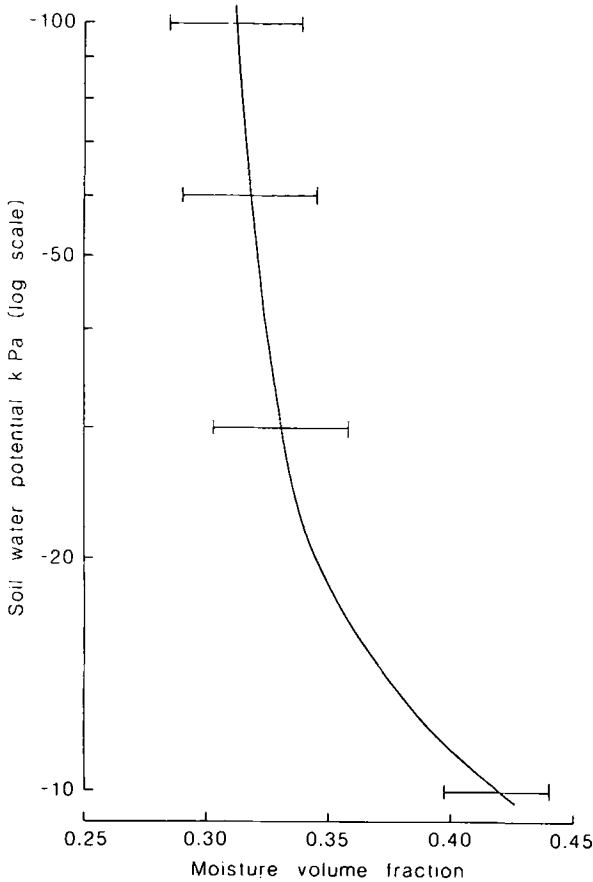

Abb. 2. Bodenfeuchtigkeits-Abgabekurve im Torf-Sand-Kompost. Wasserpotential auf einer logarithmischen Skala. Kompost-Dichte = 0,708 ± 0,019 g cm^{-3}. Porosität 0,698. Die horizontalen Balken zeigen die Standardfehler des Mittelwertes.
Fig. 2. Profil hydrique du mélange tourbe-sable. Echelle logarithmique du potentiel capillaire. Densité réelle = 0,708 ± 0,019 g cm^{-3}. Porosité 0,698. Les barres horizontales indiquent les erreurs standard de la moyenne.

but was not measured for 9, 6 and 10 days (treatments A_4, B_3, C_3 respectively) but it may be inferred from Experiment 2 that the final soil water potentials were much lower.

The declining rate of transpiration from the stressed plants is indicated by the changes in soil water potential (Fig. 1a, b) and by the soil moisture release curve for the compost (Fig. 2) determined in a pressure membrane apparatus.

The minimum soil water potentials developed in Experiment 2 were −0.72 MPa after 40 days in treatment A_5 and −3.03 MPa after 20 days in treatment B_5.

Stem numbers per plant ranged from 4.3 to 7.7 in Experiment 1 (Table 2) but were unaffected by treatment. Maris Piper, the cultivar used, is known sometimes to be prolific in its production of stems. Because stem number is a major factor determining tuber number per plant (Svensson, 1962; Moorby, 1967) the range was an unwelcome source of variation and required that any effect of treatment on tuber numbers had to be expressed by stems and not by plants. The control of stem number in Experiment 2, by planting bundles of single-sprouted cores, gave plants which were more uniform. Stem number per plant varied between 3.9 and 4.3. Again, there was no effect of treatment on stem number.

Table 2. Harvest data from Experiment 1.

Treatment	Stem number per plant	Tuber number per stem	Tuber yield per plant (g)	Total dry matter per plant (g)
(a) Early harvest				
unstressed	5.0	11.1	1280	379
A_4	4.7	4.1 **	591 **	183 **
B_3	4.3	9.5	814 **	248 *
C_3	5.3	7.0	509 ***	222 *
(b) Final harvest				
unstressed	5.0	7.6	2359	–
A_1	6.0	6.8	2508	–
A_2	5.0	6.8	2145	–
A_3	5.0	5.7	2829	–
A_4	6.0	4.6 *	2229	–
B_1	5.3	7.4	2768	–
B_2	5.7	8.0	2903	–
B_3	5.7	7.3	2804	–
C_1	5.3	6.0	1984	–
C_2	7.7	5.1	3010	–
C_3	5.7	7.4	2107	–

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ − Asterisks indicate values which are statistically significantly different from the value for the unstressed treatment − *Sternchen bezeichnen Werte, welche sich statistisch signifikant vom Wert der ungestressten Behandlung unterscheiden* − *Les astérisques indiquent les valeurs différentes de façon significative au témoin bien pourvu en eau.*

Tabelle 2. Erntedaten von Versuch 1.
Tableau 2. Résultats de l'expérimentation 1 à la récolte.

Tuber number

Tuber number per stem was analysed after logarithmically transforming the data. At the final harvest of Experiment 1 only treatment A4 affected tuber number per stem (Table 2) and thus differed from the unstressed treatment, although there was a similar trend in the other treatments in which water was withheld from the time of emergence. The results from the early harvest in Experiment 1 (Table 2) show that the difference in final tuber number per stem had already been established just after the period of tuber initiation. The difference in tuber number per stem in the unstressed treatment between harvests was not statistically significant.

In Experiment 2 tuber number per stem was reduced in the three most severely stressed of those treatments that started at emergence (A series, Table 3) but the numbers were not affected even by quite severe stress if it was not applied until after the period of tuber initiation (B series).

Treating water stress as a factor does not suffice to quantify its effect on tuber number per stem; it must be considered as a variable. Initially water stress was measured by the time-integral of the course of soil water potential but this was found to be unnecessarily complicated and a simple count of days spent beyond a threshold of -25 kPa sufficed. Tuber number per stem (N) at final harvest in the two experiments was regressed on number of days (D) with soil water potential < -25 kPa. The relationship:

$$N = 7.20 - 0.16 \, D$$
$$(\pm 0.21) \quad (\pm 0.02)$$

was statistically significant ($P < 0.001$) for plants stressed before and during tuber initiation and accounted for 85 % of the variance (values in brackets are standard errors of the coefficients). Tuber number per stem was also expressed as a proportion (Q) of the value from the unstressed treatment to make the data from the two experiments more homogeneous. The relationship:

Table 3. Harvest data from Experiment 2.

Treatment	Stem number per plant	Tuber number per stem	Tuber yield per plant (g)	Total dry matter per plant (g)
unstressed	4.1	6.5	1773	499
A$_1$	3.9	6.3	1741	506
A$_2$	4.4	6.2	1752	508
A$_3$	4.3	5.2*	1616	456
A$_4$	4.2	5.5*	1553*	450
A$_5$	4.3	4.6**	1309**	401**
B$_1$	4.4	7.0	1490*	433*
B$_2$	4.2	6.5	1536*	427*
B$_3$	3.9	6.2	1425**	389**
B$_4$	4.1	6.4	1474*	410*
B$_5$	4.3	5.6	1267***	371**

*, **, *** See footnote to Table 2 — *Siehe Fussnote Tabelle 2* — *Voir indications tableau 2.*

Tabelle 3. Erntedaten von Versuch 2.
Tableau 3. Résultats de l'expérimentation 2 à la récolte.

$$Q = 1.011 - 0.020\ D$$
$$(\pm 0.035) \qquad (\pm 0.004)$$

was also statistically significant ($P < 0.001$) in plants stressed before and during tuber initiation and accounted for 76 % of the variance. Water stress imposed after the period of tuber initiation had no effect on tuber number per stem.

Tuber yield and dry matter production

In Experiment 2, the periods of water stress reduced tuber yield (Table 3) and in both the A and B series of treatments yield was negatively correlated with the duration of stress (days of soil water potential < -25 kPa). Although the depression in yield

Fig. 3. Cumulative frequency distributions of tuber size (g) from experiment 2. Unstressed treatment (●). Treatment A_5 (○). Treatment B_5 (□).
Vertical bar represents the Kolmogorov-Smirnov quartile for the comparison between the treatments B_5 and unstressed. The distributions are significantly different ($P \leq 0.05$) where their curves are separated by this distance.
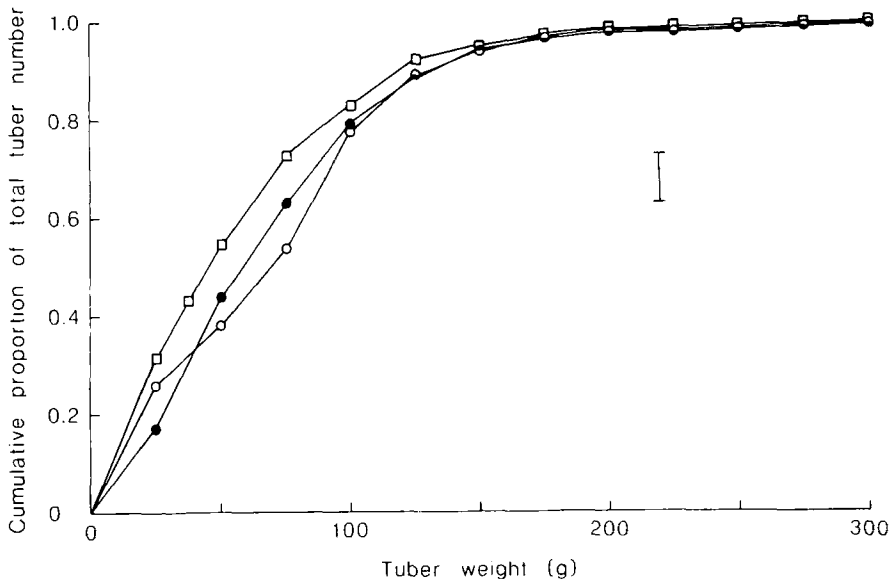

Abb. 3. Kumulative Frequenzverteilungen der Knollengrösse (g) von Versuch 2. Ungestresste Behandlung (●). Behandlung A_5 (○). Behandlung B_5 (□).
Vertikale Linie zeigt die Kolmogorov-Smirnov-Quartile für den Vergleich zwischen den Behandlungen B_5 und ungestresst. Die Verteilungen sind signifikant unterschiedlich ($P \leq 0,05$), wo ihre Kurven durch diese Distanz getrennt sind.
Fig. 3. Distributions de la fréquence cumulée du poids des tubercules (g) pour l'expérience 2. Traitement bien pourvu en eau (●). Traitement A_5 (○). Traitement B_5 (□).
La barre verticale représente l'écart de Kolmogorov-Smirnov pour la comparaison entre le traitement B_5 et le témoin. Les distributions sont différentes de façon significative ($P \leq 0,05$) lorsque les courbes s'écartent au delà de cette distance.

was greater in the B series in which the plants were larger at the time of the water stress, a single regression accounted for 59 % of the variance across all treatments (correlation coefficient 0.770, $P < 0.01$).

The yields at final harvest in all treatments were higher and the differences between treatments were greater in Experiment 1 than in Experiment 2. The absence of a measurable effect of stress on yield at final harvest in the first experiment (Table 2) is attributed to the variability of the plants. Those taken at the first harvest in Experiment 1 were more comparable to those grown in Experiment 2 (compare stem numbers, Tables 2, 3) and at that harvest an effect of stress on yield was apparent and the size of the depression was consistent with that recorded in Experiment 2.

The mean values for tuber dry matter content at final harvest were 21.2 ± 1.5 and 23.1 ± 0.7 % in Experiments 1 and 2 respectively and were unaffected by treatment.

Total dry matter production was not measured at the end of Experiment 1 but in Experiment 2 (Table 3) it showed the same trends with duration of water stress as did tuber yield. A single regression accounted for 48 % of the variance (correlation coefficient 0.696, $P < 0.025$).

Frequency distribution of tuber size
The cumulative frequency distributions of individual tuber sizes (weights) were compared by using the Kolmogorov-Smirnov test (Daniel, 1978). In Experiment 1 the distributions did not differ significantly between the unstressed and stressed treatments. However, in Experiment 2 the contrasting effects of water stress in the A and B series of treatments on yield and tuber numbers produced differences in the distributions of tuber sizes (Fig. 3). One-tailed tests of significance were used because it had been anticipated that the A series of treatments would result in fewer and larger tubers than the control and that the B series would give smaller tubers. The results show that expectation was wrong for plants stressed during tuber initiation (treatment A_5) but right for plants stressed after tuber initiation (treatment B_5). The reduction in tuber number in treatment A_5 was offset by the reduction in yield so that mean tuber size and the frequency distribution of sizes were not significantly different from those for the unstressed treatment. In treatment B_5 mean tuber size was lower than in the unstressed treatment and the frequency distribution (Fig. 3) showed a significantly ($P < 0.05$) higher proportion of small tubers.

Discussion

Rieman et al. (1953) reported that stem number per plant influences tuber number per stem but their results were obtained from an unstructured sample of plants grown from seed tubers and seed pieces which ranged in size from 30−280 g. In more critical experiments Svensson (1962) showed that tuber number per stem was increased by increasing both the size of the seed piece and the space between plants, and that it was decreased by increasing the number of stems per plant although the net effect of the last factor was to increase tuber number per plant. Using widely spaced plants Moorby (1967) showed that if the size of the seed piece was kept constant then the number of tubers per stem was independent of the number of stems per plant.

In our experiments the canopies of the plants were still separate and within the areas of the rectangular containers at the time of tuber initiation so that it is, therefore, unlikely that there was competition between plants for light. The results of our

first experiment (1982, Control, B and C series) were consistent with Moorby's findings but we were concerned to find that despite using closely graded seed tubers, stem number and plant size were not controlled. We therefore planted bundles of single-sprouted cores in the second, 1983, experiment with satisfactory results in that where tuber number per stem was unaffected so was tuber number per plant.

The results confirmed earlier reports that tuber number per stem was reduced by soil moisture stress early in the season and, further, showed that tuber number is sensitive to this stress only during the short period of tuber initiation (2 or perhaps 3 weeks). Evidently, a period of drought must begin before tuber initiation if the plants are to be stressed at an appropriate time.

In practice, if a crop is required to produce the maximum number of tubers (e.g. many small tubers for canning or for seed) then irrigation may be necessary at a very early stage when the stolon tips are just swelling. This is consistent with the findings of Steineck (1958) that water supply must be adequate as early as 3 weeks from emergence, although he concluded this to be a requirement for stolon formation.

The development of soil moisture stress after tuber initiation had no effect on tuber number per stem.

The differences in tuber numbers per stem reported here must be considered to result from a reduction due to stress, not from an increase due to irrigation (as has sometimes been reported), because the number of stolon tips, the potential sites for tuber formation, is always greater than the number of tubers that eventually form.

The investigation raises the question of how the *duration* of water stress may influence tuber number. We offer two simple hypotheses. First, on each stem at tuber initiation there are already ample sites for tuber formation and these fit into a hierarchy of sink strengths and that assimilate supply sets an upper limit on numbers and then other environmental constraints, such as water stress, progressively reduce that number. Second, the many potential sites become eligible for tuberization sequentially, either individually or in groups, and stress at any one time eliminates the sites that would then have been eligible. Given a short period of water stress during tuber initiation these two models would result in different distributions of tubers on each stem. A detailed examination of patterns of tuber bearing on stems after controlled periods of stress should show which hypothesis is correct.

Epstein and Grant (1973) suggested that the potato plant becomes stressed when the soil water potential drops below −25 kPa. The choice of this value was arbitrary, falling as it did on one point in a continuum within their data. The value was approximately the soil water potential which was maintained in their irrigated treatment, but to chose any value of soil water potential is to ignore the fact that the water stress experienced by the plant will depend not only upon the soil water potential but upon the balance between the rates of water loss by evaporation and of water supply from the soil. Thus Fuehring et al. (1966) showed that under evaporation rates of roughly 10 mm day^{-1} stomatal closure occurred in potatoes two days after irrigation when most of the 'available' soil moisture was still present. Our investigation can be criticised in the same way as that of Epstein & Grant (1973); plant water stress was not measured directly. Future work might be designed to examine which measure of plant water stress is the most appropriate to use in this kind of study. In the meantime the use of soil water potential may in part be justified because, a) it is readily measured and, b) it gives some indication of the water status of the plant at night between periods of evaporation that is independent of soil type. Since the duration

of the period of stress has been identified as an independent variable which modifies tuber number per stem, the threshold value taken to indicate the onset of that stress is less important than if time-integrals were used.

A change in the value from 25 kPa to either 20 or 30 kPa would result in no more than the addition of 1 day or the subtraction of 2 days from all values in the A series of treatments in 1982 and similar changes of 1 day in the other treatments of 1982 and in 1983.

One of the initial aims of this investigation was to quantify the effect of water stress on tuber number and this has been achieved in so far as the reduction in numbers has been quantified. Among the remaining uncertainties is the upper number from which these reductions occur. Apart from the effects of seed size and stem number (Svensson, 1962) the weather at the time of tuber initiation may influence tuber number (Gray & Holmes, 1970). These and the effects of spacing between plants and of the period between emergence and tuber initiation may all exert their influence on tuber number through their effects on assimilate supply. Until these effects can be quantified the reduction in numbers due to other constraints such as water supply can be expressed only in proportional terms and their consequences for tuber grade distribution can be given only qualitatively.

Zusammenfassung

Einfluss eines frühen Mangels an Bodenwasser auf die Knollenzahl bei Kartoffeln

Das Verhältnis zwischen Wassermangel im frühen Teil der Wachstumsperiode und der Knollenbildung bei der Sorte Maris Piper wurde in zweijährigen Gewächshausversuchen, bei unterschiedlichen Phasen und unterschiedlicher Schwere des Wassermangels, untersucht.

Die Pflanzen wuchsen in einem Torf-/Sand-Gemisch in Behältern. Das Wasser wurde von der Zeit des Aufgangs, der Knollen-Initiierung oder des 'kleine-Knollen-Stadiums' zurückgehalten (Serien A, B und C der Behandlungen; Tabelle 1) und daran anschliessend verabreicht (Tabelle 1, Abb. 1a, b). Die Kontrollbehandlung wurde während der gesamten Wachstumszeit gut gewässert. Sinkende Raten bei der Transpiration während des Wassermangels könnten durch den Wechsel des Bodenwasser-Potentials (Abb. 1a, b) und der Bodenfeuchtigkeits-Abgabekurve des Kompostes (Abb. 2) verursacht worden sein.

In beiden Versuchen wurde die Knollenzahl pro Stengel in denjenigen Behandlungen reduziert, welche beim Auflaufen (A-Serien) begonnen worden waren. Die Knollenzahl war dagegen sogar bei ganz schwerem Stress nicht beeinträchtigt, wenn die Behandlung nach der Periode der Knollen-Initiierung begonnen worden war (B- und C-Serien; Tabellen 2 und 3). Bei Verwendung der Daten der Kontrolle und der A-Serie der Behandlungen in beiden Versuchen zeigte die Knollenzahl pro Stengel *(N)* zum letzten Erntetermin hin zwischen der Zahl der Tage *(D)* und dem Bodenwasser-Potential eine Regression < −25 kPa. Die Knollenzahl als Ausdruck einer Proportion *(Q)* des Wertes der Kontrollbehandlung ergab zu *D* ebenfalls eine Regression. Beide Verhältnisse: $N = 7,20 - 0,16 D$ und $N = 1,001 - 0,020 D$ waren statistisch signifikant $(P < 0,001)$ bei 85 bzw. 76 % der Varianz.

Der Knollenertrag in Versuch 2 (Tabelle 3) war negativ korreliert mit der Dauer des Wasserstress *(D)* und die Gesamttrockenmasse zeigte den gleichen Trend. Der Trockenmassegehalt der Knollen zum letzten Erntetermin wurde durch die Behandlung nicht beeinflusst $(21,2 \pm 1,5 \%$ und $23,0 \pm 0,7 \%$ in Versuch 1 bzw. 2).

Im Versuch 2 verursachten der kontrastierende Effekt bei Wassermangel in den A- und B-Serien der Behandlungen auf Ertrag und

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Knollenzahlen Unterschiede in der Verteilung der Knollengrösse (Abb. 3). In Behandlung A_5 wurde die Reduktion der Knollenzahl durch die Ertragsreduzierung ausgeglichen, so dass sich die Knollengrössen von denen in der ungestressten Kontrolle nicht unterschieden. In Behandlung B_5 dagegen war die mittlere Knollengrösse niedriger; ausserdem ergab sich hier eine signifikant höhere Proportion kleiner Knollen (Abb. 3).

Résumé

Influence d'un déficit hydrique précoce sur le nombre de tubercules de pommes de terre

La relation entre un manque d'eau en début de végétation et l'initiation des tubercules est examinée sur deux années avec la variété Maris Piper. Les expériences ont lieu sous serre, à différents stades et différents degrés d'importance du déficit hydrique.

Les plantes sont cultivées en containers dans un mélange tourbe-sable. L'eau est apportée au moment de la levée, de l'initiation des tubercules ou à la formation des petits tubercules (séries A, B et C des traitements) (tableau 1) et est approvisionnée par la suite (tableau 1, fig. 1a, b). Le témoin est bien pourvu en eau pendant toute la période. Les baisses du taux de transpiration pendant le déficit hydrique peuvent être déduites à partir des changements du potentiel capillaire (fig. 1a, b) et à partir du profil hydrique du compost (fig. 2).

Dans les deux expériences, le nombre de tubercules par tige est réduit pour les traitements en début de levée (séries A) mais n'est pas modifié, même en cas assez grave de déficit hydrique, lorsque les traitements ont lieu après la période d'initiation des tubercules (séries B et C) (tableau 2, 3). A partir des valeurs du témoin et des séries A des deux expérimentations, il apparaît que le nombre de tubercules par tige *(N)* à la récolte finale diminue avec le nombre de jours *(D)* pour lesquels le potentiel capillaire est inférieur à 25 kPa.

Le nombre de tubercules par tige exprimé par le rapport *(Q)* des valeurs du traitement sur celles du témoin, diminue également avec *D*. Les deux relations $N = 7.20 - 0.16\,D$ et $N = 1.001 - 0.020\,D$ sont hautement significatives ($P < 0.001$) et expliquent respectivement 85 et 76 % de la variance.

Dans la deuxième expérimentation (tableau 3) le rendement en tubercules est négativement corrélé à la durée du déficit hydrique *(D)* et la production totale de matière sèche va dans le même sens. La teneur en matière sèche des tubercules à la récolte finale ne varie pas avec le traitement (21.2 ± 1.5 % et 23.1 ± 0.7 % respectivement pour les expérimentations 1 et 2).

Dans l'expérience 2, les effets opposés du déficit hydrique, pour les traitements des séries A et B, sur le rendement et le nombre de tubercules, entraînent des différences de répartition dans les calibres (fig. 3). Dans le traitement A_5, la réduction du nombre de tubercules est reportée sur le rendement, ce qui ne modifie pas la répartition des calibres par rapport au témoin. Cependant, dans le traitement B_5, le calibre moyen des tubercules est plus faible et la proportion de petits tubercules significativement plus élevée (fig. 3).

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