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The effect of early drought stress on numbers of tubers and stolons of potato in controlled and field conditions

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Summary

Potatoes were grown in plots, pots or containers in a glasshouse or under a rainshelter. Water was withheld from emergence onward or from tuber initiation onward in some treatments. The number of stolons per stem was greatly reduced but the number of tubers + tuber initials per stolon remained unchanged (cv. Radosa) or increased (cv. Bintje) as a result of the earliest drought treatment. The later dry period did not affect numbers of stolons and tubers (+ initials). These findings correspond well with data from field trials which were sampled for 13 consecutive years and which showed a highly significant linear relationship between the number of tubers per stem and total rainfall during the first 40 days after planting, which ranged from 17.5 to 120 mm.

Introduction

Numbers of tubers per plant and total tuber fresh yield determine the average tuber size. The number of tubers per plant is the product of the number of stems per plant and the number of tubers per stem.

The number of stems per plant are mainly determined by the size of the seed tuber (Wurr, 1974) and its condition and by soil and soil moisture at planting, although pathogens (black scurf) and pests may have an effect. Numbers are also influenced by the length and the conditions of the pre-sprouting period (Allen, 1978). Application of growth regulators to the seed tubers may also affect the number of stems per plant. Marinus & Bodlaender (1978) recorded an increase in number of stems using gibberellic acid while Iritani (1987) found a decrease using napthalene acetic acid. Soil conditions between planting and emergence may also influence the number of stems. Morris (1967) reported for controlled, and Haverkort & Rutayisire (1986) for field conditions that soil NPK levels affected stem numbers. Numbers of stems produced per plant are further determined by the ambient temperatures (Haverkort & Harris, 1987).

Relationships between numbers of stolons and tubers (Wurr, 1977) are similar to those between numbers of sprouts and subsequent stems (Allen, 1978). Larger seed tubers tend to yield more stems, and larger stems to yield more stolons. This seems to indicate that one way to increase the number of tubers per plant, besides aiming for a higher number of stems per plant, is through measures which favour initial stem growth resulting in larger stems. There are other factors, however, which may affect the number of tubers per stem such as the application of growth regulators (Kumar & Wareing, 1972; Bodlaender, 1972), the occurence of diseases such as *Rhizoctonia solani*

(Davis & Groskopp, 1981), temperature during growth (Haverkort & Harris, 1987) and stress conditions during early growth. Levy (1985) found an increase in tuber numbers after a short period of heat stress in the field and De Jong (1985) reported a decrease when brackish water was used for irrigation.

Most authors reporting on the influence of soil moisture on yield do so in terms of changes in total tuber production (Harris, 1978; Van Loon, 1981), or of tuber size distribution (MacKerron & Jefferies, 1988), or on its effect on radiation interception and radiation use efficiency (Devaux & Haverkort, 1987; Jefferies & MacKerron, 1987). The influence of drought and the timing of dry periods on the number of tubers have received less attention. Struik & Van Voorst (1986) found in controlled conditions, that drought in the stolon environment enhanced the initiation of stolons and tubers, but at harvest it had led to fewer tubers. A study with potatoes growing in containers subjected to early drought stress showed that when drought occurred before the onset of tuber initiation it effectively reduced the number of tubers (MacKerron & Jefferies, 1986).

The work reported here was designed to investigate the effect of drought at several early stages of growth on the number of stolons, tubers (larger than 5 mm) and tuber initials (smaller than 5 mm) per stem. These experiments, together with long-term field experiments, were designed to explain seasonal variability in number of tubers per plant and tuber size distribution due to shortage of water supply.

Materials and methods

Experiments under controlled conditions. Three experiments were carried out from 1981 to 1984 in or near Wageningen. In 1983 two other experiments were planted, but in one drought occurred too late due to the high buffering capacity of the large containers (800 l) used, and another did not succeed because there was waterlogging in the control plots which retarded growth.

Some of the agronomic and statistical descriptors of the experiments are listed in Table 1. The first dry period (D1) was started by withholding water from the moment that the first plants emerged. At stolon initiation, a second dry period (D2) was started with another set of experimental units. To determine when tuber initiation occurred, plants were checked every other day in additional border units. In both treatments watering started again when visible symptoms of stress appeared such as wilting in the afternoon and growth retardance. At about weekly intervals soil samples were taken at various depths and their moisture content was used to determine the current kPa values with the aid of moisture retention curves of the soil (experiment I) or soil types (experiments II and III) used. For soil sampling, additional plots were used in experiment II which were not used for the final harvest.

Experiment I was planted in the soil of an unheated glasshouse; experiment II in pots of which 9 made up a 'plot' in a glasshouse; and experiment III was planted in containers with six plants each, placed under wall-less plastic roofing which altered ambient conditions very little, except for rainfall. At harvest, about 60 days after emergence, the number of mainstems, stolons, tubers (larger than 5 mm) and tuber initials (smaller than 5 mm diameter) per plant were recorded.

Field experiments. The data presented in this paper, spanning 13 years from 1976 to 1988, were taken from the so called 'growth curve trials' at the 'Feddemaheerd' ex-

Table 1. Characteristics of three drought stress experiments conducted under controlled conditions.

Descriptors	Experiment number		
	I	II	III
Year	1981	1983	1984
Planting date	April 1	Feb. 15	April 11
100 % emergence date	April 29	March 4	May 5
Cultivar	Radosa	Bintje	Radosa
Site	Glasshouse	Glasshouse	Plastic roof *
Soil type	Clay	Sand	Loam
Experimental unit	1 plot	9 plots	container
Unit size (m^2)	24	9×0.04	0.63
Unit volume (litres)	-	9×8	252
Plants per unit	120	9×1	6
Number of replicates	4	2	3
Harvest (days after emergence)	52	64	53

* This consisted of wall-less plastic roofing which changes ambient conditions but little, except for rainfall.

perimental farm situated in the most northern part of the Netherlands (Proefveldverslagen, 1975–1988). In most years these trials were planted with pre-sprouted and unsprouted seed, cv. Bintje, class E, grade 40–45 mm at about 60000 plants per hectare. Starting in early July, samples were taken at weekly intervals and graded into the following classes: <25, 25–28, 28–35, 35–45, 45–55 and >55 mm. In each year, the data for the present study were taken at the harvest and for the treatment whose total yield was nearest 35 t/ha. From 1986 to 1988 the number of tubers were also recorded and mean tuber weights per class calculated and used to estimate the number of tubers in the years prior to 1986. No irrigation was applied and rainfall was recorded.

Results

Experiments under controlled conditions. Figure 1 shows the pF values of soil in the three experiments from emergence until harvest. The early drought treatment (D1) exceeded the value of 32 kPa before or at 10 days after emergence (DAE). Figure 1 also shows kPa values of the second dry period (D2) that occasionally showed an overlap with the first. For each of the drought treatments plants were watered to field capacity after soil moisture reached values exceeding 100 kPa. The unstressed treatment (M) was watered regularly to maintain soil moisture continuously near field capacity.

Table 2 shows the results of the counts of the various plant parts and total tuber fresh weight at harvest. Number of stems per plant did not differ; this was to be expected because the treatments started after the emergence of the stems. Fresh tuber yield was strongly affected by the early drought period but less strongly by the second drought stress. The following tendencies apply to number of stolons, tubers and tuber initials:

- an early dry period, starting at emergence, led to a significant reduction in the num-

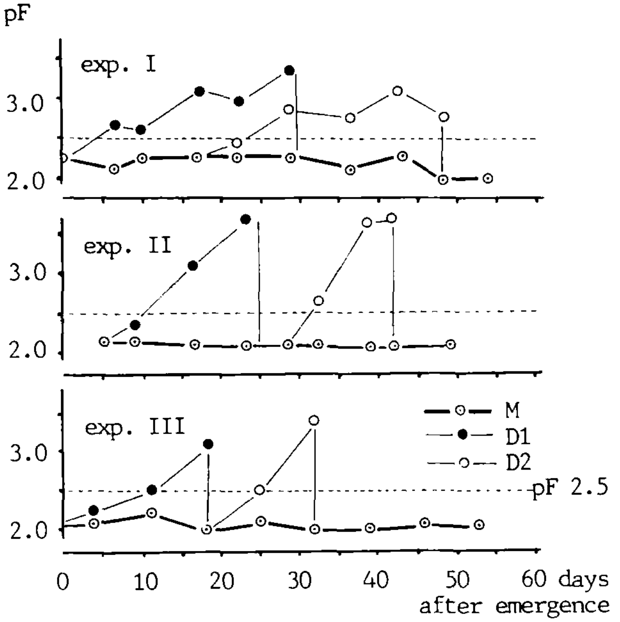

Fig. 1. kPa values at 20 to 30 cm soil depth between planting and harvest for each of three experiments conducted under controlled conditions with treatments: M = control, D1 = drought at stolon initiation (from emergence), D2 = drought at tuber initiation (from stolon initiation).

Table 2. Results of three drought stress experiments conducted under controlled conditions. M = moist soil, D1 = drought from emergence, D2 = drought from stolon initiation (pl = plant, sn = stolon, st = stem, ti = tuber initial, tu = tuber).

Experiment	Treatment	st/pl	sn/st	tu/st	ti/st	tu+ti/st	tu/sn	ti/sn	tu+ti/sn	Yield (g/st)
I	M	4.11	7.75	1.85	3.43	5.28	0.239	0.443	0.681	41.7
	D1	4.05	7.15	1.25	3.58	4.83	0.175	0.501	0.675	20.6
	D2	4.12	7.32	2.00	2.92	4.92	0.273	0.399	0.672	46.3
	LSD 0.05	NS	0.41	0.28	NS	NS	0.041	0.038	NS	2.8
II	M	3.05	7.19	4.03	1.77	5.80	0.561	0.246	0.807	111.2
	D1	3.10	4.46	3.16	1.62	4.78	0.709	0.363	1.07	55.5
	D2	3.13	6.77	4.66	2.31	6.97	0.688	0.341	1.03	58.9
	LSD 0.05	NS	0.82	1.22	0.39	1.58	0.092	0.029	0.122	6.5
III	M	3.01	5.37	2.79	1.64	4.43	0.520	0.305	0.825	32.0
	D1	3.05	4.88	2.46	1.45	3.91	0.504	0.297	0.801	25.2
	D2	2.99	5.16	2.45	1.64	4.09	0.475	0.318	0.793	28.2
	LSD 0.05	NS	0.42	0.18	0.20	0.43	NS	NS	NS	4.2

ber of stolons per stem, an 8 to 9 % reduction with cv. Radosa and with cv. Bintje almost 40 % (in this particular trial);
- the number of tubers per stem and numbers of tubers + tuber initials per stem showed similar responses;
- with the cv. Bintje, this was associated with an increase in the number of tubers + initials per stolon;
- with cv. Radosa, the second dry period did not affect any plant characteristic, while with Bintje, it induced a higher number of tubers and tuber initials and tuber yield was reduced to 53% compared with the unstressed treatment.

Field experiments. Figure 2 shows the relationship between precipitation during the first 40 days after planting and the number of tubers per plant which varied from 9.15 to 20.78 in the 13 years that the trials were sampled. From Figure 2 it can be inferred that rainfall over about 60 mm did not lead to a further increase of the number of tubers per plant. The factor 'stems per plant' did contribute to variation and was eliminated. A significant linear relationship was found between the number of tubers per stem (tu/st) and the whole range of observed rainfall (mm), for the first 40 days after planting, of between 17.5 and 120 mm;

$$tu/st = 0.0196 \text{ mm} + 1.44 \ (r=0.927)$$

The two observations in 1979 were discarded because larger seed pieces were planted (45–50 mm) which led to a high number of stems; moreover, in that year, of the rainfall recorded during the first 40 days after planting, over 60 mm fell during the last 5 days, after a dry spell, which may have reduced the number of tubers per stem.

Discussion

The mechanism by which tuber numbers are reduced is interesting; it occurs through the reduction of the number of stolons per stem and not through a reduction of the number of tubers per stolon. Once stolons are initiated, they yield tubers regardless of a subsequent drought period (D2). A greatly reduced number of stolons for Dl as with Bintje in experiment II (4.46 stolons per stem instead of 7.19) led to a subsequent increase form 0.807 to 1.07 in the number of tuber + initials per stolon. The results indicate that the two processes, stolon initiation and growth, and tuber initiation and growth, are controlled by different mechanisms. It may well be that the reduced size of the stem due to early drought leads to fewer stolons. Wurr (1977) also found a relationship between stem size and number of stolons. Subsequent initiation seemed less vulnerable to either stem size or external factors such as drought, which also caused internal changes such as decreases in leaf water potential during the second drought period (D2) which was also observed in experiment II. From these experiments we cannot conclude whether resorption played a role in the effects of the drought treatment D2. Krug & Wiese (1972) recorded a marked decrease in the number of tubers with cv. Barima when water was withheld for about 15 days after emergence, compared with plants that were watered continuously. For resorption to occur, the dry spell should have been longer and the harvest date postponed. With 'Bintje', the late drought was associated with an increase of the number of tubers and initials per stolon, possibly caused by second growth.

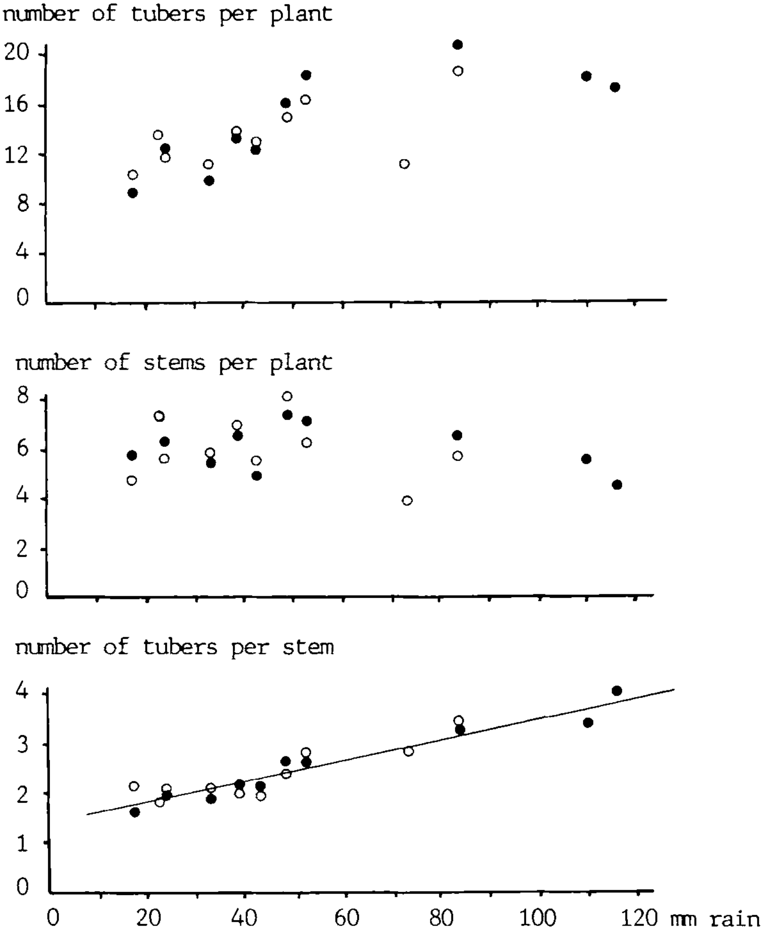

Fig. 2. Relation between total precipitation during the first 40 days after planting and numbers of tubers and stems, $y = 0.0196x + 1.44$, $r = 0.927$ cv. Bintje, 1975–1988 data from the experimental farm Feddemaheerd. Closed symbols represent data from pre-sprouted seed, open symbols from unsprouted seed.

Our data are not sufficiently extensive to validate MacKerron & Jefferies (1986) negative correlation between number of tubers per stem and the number of days with soil moisture potential < -25 kPa. The treatments D1 and D2, however, are analogous to one member each of the A and B series respectively in these authors' research, and the results are broadly consistent. We did, moreover, establish the relationship, which may provide in practice, that the number of tubers per stem is dependent on the amount of rainfall during the beginning of the season (up to about 2 to 3 weeks after emergence). This relationship was linear over the whole range of observations from very dry springs, with less than 20 mm, to very wet ones, with over 120 mm, of rain falling within the first 40 days after planting.

It should be noted that this relationship was established only for the cv. Bintje growing on a loamy soil of the North of the Netherlands and it may not hold for other cultivars and other conditions. The number of stems per plant, contrary to what might have been expected, did not increase with rainfall between planting and early crop growth. The main factor controlling the number of stems per seed piece are temperature differences during growth, storage, and pre-sprouting of the seed. These apparently had a much greater influence on the number of stems per plant than precipitation early in the season.

There is a practical use for these findings in seed production where the aim is for a high number of tubers per stem. Our results suggest that if conditions between planting and emergence are drier than usual, then irrigating the crop at around emergence will increase the number of tubers per plant.

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References

Allen, E. J., 1978. Plant density. In: P. M. Harris (Ed.), The potato crop, the scientific basis for improvement. Chapman & Hall, London: p. 278–326.

Boadlaender, K. B. A., 1972. De invloed van groeiregulerende stoffen op aardappelen. *Bedrijfsontwikkeling* 3: 595–601.

Davis, J. R. & M. D. Groskopp, 1981. Yields and quality of Russet Burbank potato as influenced by interactions of Rhizoctonia, maleic Hydrizide and PCNB. *American Potato Journal* 58: 227–237.

Devaux, A. & A. J. Haverkort, 1987. The effect of shifting planting dates and mulching on late blight (*Phytophthora infestans*) and drought stress of potato crops grown under tropical highland conditions. *Experimental Agriculture* 23: 325–333.

Harris, P. M., 1978. Water. In: P. M. Harris (Ed.), The potato crop, the scientific basis for improvement. Chapman & Hall, London: p. 244–277.

Haverkort, A. J. & P. M. Harris, 1987. A model for potato growth and yield under tropical highland conditions. *Agricultural and Forest Meteorology* 39: 271–282.

Haverkort, A. J. & C. Rutayisire, 1986. Utilisation des engrais chimiques sous conditions tropicales. I. Effect de l'application d'azote, phosphore et potasse sur les rendements de la pomme de terre en Afrique centrale. *Potato Research* 29: 347–355.

Iritani, W. M., 1987. Manipulation of seed tuber behaviour with storage. Abstract 10th Triennial Conference EAPR (Aalborg), p. 348–349.

Jefferies, R. A. & D. K. L. MacKerron, 1987. Aspects of the physiological basis of cultivar differences in yield of potato under droughted and irrigated conditions. *Potato Research* 30: 201–217.

Jong, J. A. de, 1985. De teelt van aardappelen. Krips Repro Meppel, 319 pp.

Krug, H. & H. Wiese, 1972. Einfluss der Bodenfeuchte auf Entwicklung und Wachstum der Kartoffelpflanze (*Solanum tuberosum* L.). *Potato Research* 15: 354–364.

Kumar, D. & P. F. Wareing, 1972. Factors controlling stolon development in the potato plant. *New Phytologist* 71: 639–648.

Levy, D., 1985. The response of potatoes to a single transient heat or drought stress imposed at different stages of tuber growth. *Potato Research* 28: 415–424.

Loon, C. D. van, 1981. The effect of water stress on potato growth, development and yield. *American Potato Journal* 58: 51–69.

MacKerron, D. K. L. & R. A. Jefferies, 1986. The influence of early soil moisture stress on tuber numbers in potato. *Potato Research* 29: 299–312.

MacKerron, D. K. L. & R. A. Jefferies, 1988. The distribution of tuber sizes in droughted and irrigated crops of potatoes. I. Observations on the effect of water stress on graded yields from differing cultivars. *Potato Research* 31: 269–278.

Marinus, J. & K. B. A. Bodlaender, 1978. Growth and yield of seed potatoes after application of gibberellic acid to the tubers before planting. *Netherlands Journal of Agricultural Science* 26: 354–365.

Morris, D. A., 1967. Intersprout competition in the potato. II Competition for nutrients during pre-emergence growth after planting. *European Potato Journal* 10: 296–311.

Proefveldverslag, 1975–1988. Stichting Proefboerderijen Noordelijke Akkerbouw. Series of annual reports on the 'Feddemaheerd Experimental Farm'.

Struik, P. C. & G. van Voorst, 1986. Effects of drought on the initiation, yield and size distribution of tubers of *Solanum tuberosum* L. cv. Bintje. *Potato Research* 29: 487–500.

Wurr, D. C. E., 1974. Some effects of seed size and spacing on the yield and grading of two main crop potato varieties. I. Final yield and its relation to plant population. *Journal of Agricultural Science, Cambridge* 82: 37–45.

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