Potato Research 35 (1992) 419–432

Production of potato minitubers by repeated harvesting: Effects of crop husbandry on yield parameters

W. J. M. LOMMEN and P. C. STRUIK

Department of Field Crops and Grassland Science, Wageningen Agricultural University, Haarweg 333, 6709 RZ Wageningen, the Netherlands

Accepted for publication: 23 June 1992

Additional keywords: Solanum tuberosum L., seed production, rapid multiplication, tuber pruning, non-destructive harvest, nutrient supply, plant density, plant arrangement

Summary

Minitubers can be produced in large quantities by repeated harvesting of tubers from in vitro propagated plantlets at 4, 7 and 10 weeks after transplanting to the glasshouse at high plant densities. Yield parameters of minitubers can be manipulated by crop husbandry.

By supplying nutrients or using a square plant arrangement, minituber yield increased. Effects on numbers of tubers were cultivar-dependent.

Changing plant density from 50 to 800 plants per m^2 or the minimal diameter of harvested tubers from 5 to 12 mm did not significantly affect tuber yield per m^2. Higher plant densities resulted in more tubers per m^2 but fewer tubers per plant. Removing smaller tubers greatly increased the number of small tubers, but did not affect yield and number of tubers in larger grades.

Crop husbandry techniques affected minituber yield mainly through their effects on leaf area duration, and the number of minitubers through their effects on growth of tubers to a harvestable size.

Introduction

Minitubers are small seed potato tubers, produced on in vitro propagated plantlets after transplanting to the glasshouse at a high plant density. By using minitubers in a seed potato programme, the number of field multiplications can be reduced.

In a previous paper (Lommen & Struik, 1992b), a production method for minitubers was suggested by which over 1800 minitubers could be produced per m^2 within 10 weeks. This method was suitable for several cultivars and it consisted of growing plants at a high plant density and removing tubers ≥ 0.3 g in three harvests, of which two were non-destructive. The first non-destructive harvest stimulated the initiation of new tubers (Lommen & Struik, 1992a,b), the second non-destructive harvest stimulated the growth of tubers which otherwise would have been resorbed or would have remained too small (Lommen & Struik, 1992b). Compared to plants left undisturbed, the number of minitubers was greatly increased, but the weight of the tubers was reduced, probably because of root damage and the removal of tuber sinks (Lommen & Struik, 1992a).

When producing minitubers, five mutually dependent yield parameters may be manipulated; (1) the number of minitubers per in vitro plantlet, (2) the number of minitubers per unit area, (3) the average weight per minituber, (4) the minituber yield per plantlet, and (5) the minituber yield per unit area. Which parameters are favoured will depend on the costs and availability of facilities and labour and the intended use of the minitubers. Yield parameters may be manipulated by crop husbandry during minituber production.

In undisturbed plants of normal crops, *number of tubers per plant* increases when plants are fertilized before tuber initiation (cf. Gunasena & Harris, 1968). Number of tubers per stem may increase (cf. Wurr, 1974) or remain constant (cf. Bremner & Taha, 1966; Vander Zaag et al., 1990) at lower plant densities. *Number of tubers per unit area* increases at higher plant densities (Ifenkwe & Allen, 1978). *Average weights per tuber* are reported to be higher at lower densities (cf. Vander Zaag et al., 1990; Bremner & Taha, 1966) and in fertilized compared to non-fertilized plants (cf. Simpson, 1962). *Tuber yields per plant* are higher at lower plant densities (cf. Bremner & Taha, 1966). *Tuber yield per unit area* may be increased by fertilization (cf. Ryan, 1961) or higher plant densities (cf. Bremner & Taha, 1966); it may (Svensson, 1972) or may not (Bleasdale & Thompson, 1963) increase by less rectangular plant arrangements. If these cultivation techniques are also effective on in vitro plantlets, they could be used to manipulate minituber production. Therefore, the effects of nutrient supply, plant density and plant arrangement on yield parameters of minitubers were studied. In addition, the effects were studied of changing the diameter of the tubers, removed at the three harvests. Decreasing this diameter may increase the number of minitubers harvested, because many tubers initiated do not grow to the desired size (Lommen & Struik, 1992b).

Materials and methods

Production of in vitro plantlets. In vitro plantlets of *Solanum tuberosum* L. cv. Ostara (early), cv. Bintje (mid-early) and cv. Elkana (late) were produced by subculturing single-node stem cuttings about every 4 weeks. Details are described by Lommen & Struik (1992a,b). The growing periods from the last subculturing until transplanting were 17 days (Expt 1), 8 days (Expt 2), 13 days (Expt 3, cvs Ostara and Bintje) or 9 days (Expt 3, cv. Elkana).

Culture in the glasshouse. All experiments were conducted in Wageningen, the Netherlands. In vitro plantlets were transplanted to a controlled-environment glasshouse into a mixture of perlite and potting soil (50/50% v/v, containing 131.4 mg N l^{-1}). Photoperiod was fixed at 12 hours. Natural light was supplemented to at least 80 W m^{-2} (total radiation) by high-pressure sodium lamps (Philips SON-T). Day temperature was set at 18 °C, night temperature at 12 °C. For fertilization, a low concentration nutrient solution was used ($Ca(NO_3)_2.4H_2O$ 0.890 g l^{-1}, KNO_3 0.446 g l^{-1}, KH_2PO_4 0.135 g l^{-1}, K_2SO_4 0.140 g l^{-1}, $MgSO_4.7H_2O$ 0.472 g l^{-1}, H_2SO_4 0.034 g l^{-1}, FeEDTA 0.035 g l^{-1}, $MnSO_4.H_2O$ 2.0 mg l^{-1}, H_3BO_3 3.0 mg l^{-1}, $ZnSO_4.7H_2O$ 0.5 mg l^{-1}, $Na_2MoO_4.2H_2O$ 0.1 mg l^{-1} and $CuSO_4.5H_2O$ 0.1 mg l^{-1}, pH 6.0).

Tubers were removed in three harvests at 4, 7 and 10 weeks after transplanting. The minimum diameter of the tubers removed differed between experiments. A non-destructive harvesting procedure was used at the first two harvests (Lommen & Struik, 1992a). At these harvests, root damage could not be avoided, but care was taken not to damage stems and stolons. After a non-destructive harvest, plants were replanted deeper than initially.

Experiment 1. Influence of start of nutrient supply. Cvs Ostara and Bintje were fertilized with the low concentration nutrient solution, starting at different times:
(1) 11 days after transplanting, just before tuber initiation;
(2) 28 days after transplanting, right after the first non-destructive harvest;
(3) 47 days after transplanting, right after the second non-destructive harvest.
In a fourth treatment no nutrient solution was applied.

The experimental unit was a square pot (13 × 13 cm) containing 1.75 l of soil mixture. Pots were arranged contiguously in a block design with three blocks. At least one row of guard pots surrounded the experiment. Plants were grown at a density of 350 plants per m^2, by planting six plants in a row in the middle of each pot. Pots received nutrient solution in doses of 100 ml, if possible twice a week, but only if the plants needed water. Total volumes of nutrient solution supplied were 1500, 1000 and 600 ml per pot for treatments starting 11, 28 and 47 days after transplanting, respectively. Unfertilized pots and pots in which the fertilization had not yet started, received the same quantities of tap water. At the three harvests, tubers ≥0.3 g were removed. The weight of these tubers in the non-destructive harvests was estimated, using a diameter of 8 mm as a criterion. Experiment 1 was carried out from January 8 to March 18.

Experiment 2. Influence of plant density and plant arrangement. Cvs Ostara and Bintje were planted at densities of 50, 200, 400 and 800 plants per m^2, using a distance of 10 cm between rows, and at two additional plant arrangements of 400 plants per m^2: 5 cm × 5 cm and 1.25 cm × 20 cm. All plants were single-stemmed and were grown on glasshouse benches covered with a sheet of plastic film without perforation, in 18 cm deep soil mixture. They were fertilized twice a week from the first harvest onwards, with 100 ml of nutrient solution per six plants. Additional watering was necessary. In all three harvests, only tubers ≥0.3 g (i.e. Ø ≥8 mm) were removed. Experiment 2 was carried out from May 10 to July 19. Treatments were replicated in four blocks, which were harvested by different persons. Within each block, plots with increasing plant densities were contiguous. Cultivars were assigned at random to one or the other half of a block. Each net plot consisted of one row of six plants. A group of three net plots, used for determination of leaf area at the three harvest dates, was surrounded by guard plants. The number of guard plants increased at increasing densities, to ensure a uniform plant size in the net plots. At each harvest date all plants (including guard plants) were harvested, but the tuber data presented were collected from the plants from which leaf area was determined at the final harvest. Below ground between guard plants and net plants, a 5 cm wide strip of plastic prevented entanglement of stolons and roots. After a harvest, the guard plants were replanted at different positions to guard the remaining plots. Thus, plant densities and plant arrangements were maintained throughout the experiment.

Experiment 3. Influence of the diameter of the removed tubers. Tubers with diameters ≥5 mm, ≥8 mm and ≥12 mm were removed at each of three harvests from cvs Ostara, Bintje and Elkana. Plant density was 350 plants per m^2, achieved by planting six plants in a row in the middle of a pot measuring 13 × 13 × 13 cm and joining all pots. Each pot contained 1.75 l of soil medium. Nutrient supply started after the first harvest, using 100 ml of nutrient solution per pot, twice a week. Additional watering was necessary. Experiment 3 was carried out from March 30 to June 8. The

Table 1. Influence of the start of nutrient supply on yield, number and size of tubers ≥8 mm of two cultivars, expressed per plant. Plant density: 350 plants per m^2; distance between rows: 13 cm (Expt 1). Treatments in braces were similar until that harvest.

Start of nutrient supply	Tuber yield (g fresh per plant)				Number of tubers (number per plant)				Tuber size (g fresh per tuber)			
	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined
Cultivar Ostara												
Tuber initiation	1.0	5.6	2.9	9.4	1.1	2.2	1.1	4.3	1.0	2.6	2.6	2.2
1st harvest	0.6	7.0	3.8	11.4	0.6	2.6	1.8	4.9	0.9	2.8	2.2	2.3
2nd harvest	1.2	5.5	2.5	9.2	1.1	2.6	1.1	4.8	1.1	2.2	2.3	2.0
No fertilization	1.0	5.1	2.2	8.4	0.8	2.3	1.7	4.8	1.3	2.2	1.4	1.8
Cultivar Bintje												
Tuber initiation	1.4	6.4	3.4	11.2	1.3	5.8	3.0	10.1	1.1	1.1	1.1	1.1
1st harvest	0.9	5.7	2.8	9.5	0.9	4.5	2.4	7.8	1.0	1.3	1.1	1.2
2nd harvest	0.4	5.3	3.2	8.9	0.6	3.7	2.6	6.9	0.8	1.6	1.4	1.3
No fertilization	0.9	4.6	1.7	7.2	0.8	3.7	2.1	6.6	0.9	1.3	0.8	1.1
Statistical analysis[a]												
Nutrient supply (NS)	ns	*	ns	***/ns	ns	ns	ns	*/ns	ns	ns	**	ns
Cultivar (CV)	ns	ns	ns	ns	ns	***/*	**	***/*	ns	***	***	***
Interaction (NS × CV)	*	ns	ns	*	ns	*	ns	**	ns	ns	ns	ns
CV%	42.9	13.6	40.7	9.1	36.3	17.7	41.9	14.5	30.7	22.0	22.8	13.5
SE	0.4	0.8	1.1	0.9	0.3	0.6	0.8	0.9	0.3	0.4	0.4	0.2

[a] The first indications of statistical significance presented and the CV% and SE are the results of a standard analysis of variance. Only if both main effects and interaction were significant, an F-test was performed on mean squares of main effects and interactions, to determine the relative importance of the main effect. The results of this test are presented as the second indications of statistical significance. *** $P<0.001$, ** $0.001 \leq P<0.01$, * $0.01 \leq P<0.05$, ns not significant: $P \geq 0.05$.

experimental unit was a pot with six plants. Pots were arranged in a completely randomized design with four replications. One row of guard pots surrounded the experiment.

Results

Start of nutrient supply (Expt 1). Fertilization increased minituber yields in both cultivars (Table 1). However, the optimal moment for starting nutrient supply differed. In cv. Ostara tuber yield was highest when fertilization started after the first harvest. In cv. Bintje, the sooner the fertilization started, the higher the tuber yield. Late applications only had small effects.

Cv. Bintje produced more tubers than cv. Ostara (Table 1). In cv. Ostara the number of minitubers ≥ 8 mm was not influenced by the fertilization treatments. In cv. Bintje, more minitubers were produced after the first harvest when nutrient supply started earlier.

Average tuber weight in cv. Ostara was higher than in cv. Bintje (Table 1). Only in the third harvest was the average weight of the minitubers significantly higher in the fertilized treatments (Table 1). Fertilization did not affect the average tuber weight significantly if results of all harvests were combined (Table 1).

At the end of the experiment the haulm of unfertilized plants had deteriorated more than the haulm of fertilized plants.

Plant density (Expt 2). By increasing plant density from 50 to 800 plants per m^2, minituber yield per plant and number of minitubers per plant decreased in both cultivars (Table 2; data and analysis of treatments with standard row distance only). These effects were clear from the second harvest onwards. Differences between 400 and 800 plants per m^2 were small. The average weight per minituber decreased at increasing plant densities in all harvests of both cultivars (Table 2).

Tuber yield per m^2 was not significantly influenced by plant densities from 50 to 800 plants per m^2 (Table 3; data and analysis of treatments with standard row distance only), except in the first harvest. More tubers were produced per m^2 at higher plant densities, in all harvests and both cultivars (Table 3). This effect was clear between 50 and 200 plants per m^2, but not significant between 200 and 400 plants per m^2. At still higher densities, numbers of tubers per m^2 again clearly increased. Coefficients of variation, however, were high (Table 3), because data per plant were converted to data per m^2. These high coefficients of variation could be reduced by $\ln(1+x)$ or square root transformations (not shown), but differences in tuber yield per m^2 and differences in number of minitubers per m^2 at 200 and 400 plants per m^2 remained statistically non-significant from the second harvest onwards.

In the first two harvests and both cultivars, Leaf Area Index (LAI) was higher at higher plant densities (Table 3). In the final harvest, LAI tended to be higher at lower densities. At all but the lowest plant density, LAI was maximal by the first harvest. Thereafter, leaf area declined at variable rates, leading to large differences between replicates and high coefficients of variation (Table 3). In some plots, especially at 400 plants per m^2, haulm had senesced completely by the third harvest.

Table 2. Influence of plant density on yield, number and size of tubers ≥ 8 mm of two cultivars, expressed per plant. Distance between rows: 10 cm; start of fertilization: after first harvest (Expt 2).

Plant density (plants per m²)	Tuber yield (g fresh per plant)				Number of tubers (number per plant)				Tuber size (g fresh per tuber)			
	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined
Cultivar Ostara												
50	2.2	24.8	30.2	57.2	0.7	7.0	6.7	14.4	3.4	3.7	4.5	4.0
200	1.1	12.4	9.5	23.0	0.6	4.4	3.0	8.0	1.9	2.9	3.1	2.9
400	1.3	5.5	2.4	9.2	0.8	2.1	1.3	4.2	1.6	2.5	1.7	2.1
800	0.6	3.3	2.2	6.1	0.6	1.7	1.1	3.4	1.0	1.6	1.7	1.6
Cultivar Bintje												
50	0.8	34.9	35.7	71.4	0.3	10.6	9.8	20.7	2.0	3.3	3.7	3.5
200	0.8	9.8	6.3	16.9	0.5	4.8	3.5	8.8	1.6	2.1	1.7	1.9
400	0.6	4.0	2.0	6.6	0.4	2.3	1.0	3.7	1.4	1.6	2.0	1.7
800	0.5	4.4	1.1	6.0	0.3	2.9	1.0	4.3	1.4	1.5	1.2	1.4
Statistical analysis[a]												
Plant density (PD)	ns	***/*	***	***/**	ns	***/*	***/*	***/*	**	***	***	***
Cultivar (CV)	*	ns	ns	ns	*	**/ns	**/ns	**/ns	ns	ns	ns	*
Interation (PD × CV)	ns	**	ns	*	ns	*	***	***	ns	ns	ns	ns
CV%	66.8	27.2	27.7	21.6	54.4	23.3	22.4	17.3	43.9	35.3	34.8	24.4
SE	0.7	3.4	3.1	5.3	0.3	1.0	0.8	1.5	0.8	0.8	0.9	0.6

[a] The first indications of statistical significance presented and the CV% and SE are the results of a standard analysis of variance. Only if both main effects and interaction were significant, an F-test was performed on mean squares of main effects and interactions, to determine the relative importance of the main effect. The results of this test are presented as the second indications of statistical significance. *** $P<0.001$, ** $0.001 \leq P<0.01$, * $0.01 \leq P<0.05$, ns not significant: $P \geq 0.05$. The analysis was conducted only on the set of plots planted at 10 cm spacing.

Table 3. Influence of plant density on yield and number of tubers ≥8 mm per m^2 and LAI of two cultivars. Distance between rows: 10 cm; start of fertilization: after first harvest (Expt 2).

Plant density (plants per m^2)	Tuber yield (g fresh per m^2)				Number of tubers (number per m^2)				Leaf Area Index		
	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest
Cultivar Ostara											
50	109	1239	1509	2858	33	352	335	721	2.0	3.7	2.0
200	215	2478	1904	4597	117	883	600	1600	5.1	4.9	2.3
400	522	2178	969	3669	300	850	533	1683	8.4	4.0	0.7
800	480	2613	1767	4860	467	1333	900	2700	7.5	7.5	2.1
Cultivar Bintje											
50	42	1744	1784	3570	17	529	490	1035	2.5	3.8	2.7
200	164	1967	1257	3387	108	950	708	1767	6.6	5.2	1.8
400	242	1593	815	2655	167	917	383	1467	8.0	6.0	0.8
800	411	3534	853	4799	267	2333	833	3433	11.0	10.6	0.4
Statistical analysis[a]											
Plant density (PD)	**	ns	ns	ns	***	***	*	***	***/*	*	*
Cultivar (CV)	ns	ns	ns	ns	ns	ns	ns	ns	***/ns	ns	ns
Interaction (PD × CV)	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns
CV%	71.1	61.5	53.4	51.3	68.4	46.3	45.1	39.3	14.7	58.9	70.7
SE	194.7	1332.7	724.4	1948.0	126.2	471.2	269.1	708.2	0.9	3.4	1.1

[a] The first indications of statistical significance presented and the CV% and SE are the results of a standard analysis of variance. Only if both main effects and interaction were significant, an F-test was performed on mean squares of main effects and interactions, to determine the relative importance of the main effect. The results of this test are presented as the second indications of statistical significance. *** $P<0.001$, ** $0.001 \leq P<0.01$, * $0.01 \leq P<0.05$, ns not significant: $P \geq 0.05$. The analysis was conducted only on the set of plots planted at 400 plants per m^2.

Table 4. Influence of plant arrangement on yield, number and size of tubers ≥ 8 mm of two cultivars, expressed per plant. Plant density: 400 plants per m^2; start of fertilization: after first harvest (Expt 2).

Plant arrangement	Tuber yield (g fresh per plant)				Number of tubers (number per plant)				Tuber size (g fresh per tuber)			
	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined
Cultivar Ostara												
5.00 × 5.00 cm	0.7	4.6	5.0	10.3	0.5	1.5	1.8	3.8	1.8	3.7	2.9	2.8
10.00 × 2.50 cm[a]	1.3	5.5	2.4	9.2	0.8	2.1	1.3	4.2	1.6	2.5	1.7	2.1
20.00 × 1.25 cm	0.7	5.8	2.2	8.7	0.5	2.3	0.9	3.7	1.3	2.7	2.1	2.2
Cultivar Bintje												
5.00 × 5.00 cm	0.6	10.5	7.7	18.8	0.3	5.0	3.0	8.4	1.8	2.2	2.5	2.2
10.00 × 2.50 cm[a]	0.6	4.0	2.0	6.6	0.4	2.3	1.0	3.7	1.4	1.6	2.0	1.7
20.00 × 1.25 cm	0.7	5.8	2.1	8.6	0.5	3.2	1.6	5.3	1.2	1.8	1.3	1.6
Statistical analysis[b]												
Plant spacing (PS)	ns	ns	***	*	ns	ns	***/ns	*/ns	ns	ns	ns	ns
Cultivar (CV)	ns	ns	ns	ns	ns	*/ns	*/ns	*/ns	ns	ns	ns	ns
Interaction (PS × CV)	ns	ns	ns	ns	ns	*	*	*	ns	ns	ns	ns
CV%	65.3	49.8	63.5	50.7	45.2	39.3	34.2	32.4	57.0	55.5	56.6	37.5
SE	0.5	3.0	2.3	5.3	0.2	1.1	0.5	1.6	0.9	1.4	1.2	0.8

[a] Same values as shown in Table 2.

[b] The first indications of statistical significance presented and the CV% and SE are the results of a standard analysis of variance. Only if both main effects and interaction were significant, an F-test was performed on mean squares of main effects and interactions, to determine the relative importance of the main effect. The results of this test are presented as the second indications of statistical significance. ***$P<0.001$, **$0.001 \leq P<0.01$, *$0.01 \leq P<0.05$, ns not significant: $P \geq 0.05$.

Plant arrangement (Expt 2). Differences between plant arrangements were significant in the third harvest and when yields from all harvests were combined. In both cultivars, tuber yield was highest at a square plant arrangement (Table 4).

The effect of the different plant arrangements at 400 plants per m^2 on number of minitubers per plant again depended on the cultivar (Table 4). Number of tubers in cv. Ostara was hardly affected by the different plant arrangements. Only in the third harvest did the number of tubers slightly increase when the within-row spacing increased, but when results of all harvests were combined, no effect of plant arrangement on number of minitubers was observed in cv. Ostara. In contrast, cv. Bintje clearly produced most tubers in a square arrangement; this showed from the second harvest onwards.

Average tuber weight tended to be higher at a square spacing (Table 4), but this effect was not significant at the 5 % level.

Diameter of tubers removed (Expt 3). The size of the tubers removed did not affect tuber yield (Table 5), except in the first harvest when many tubers had not yet grown to a size of 12 mm. Regardless of the diameter of the tubers removed, the yield of tubers ≥ 12 mm was similar (results not shown). In addition, yield of tubers ≥ 8 mm was similar in the treatments in which tubers from 5 or 8 mm upwards were removed (not shown).

The smaller the diameter of the tubers removed, the more tubers were harvested in all cultivars (Table 5). Regardless of the diameter of the tubers removed, similar numbers of tubers ≥ 12 mm were produced (results not shown) and similar numbers of tubers ≥ 8 mm were produced by the treatments in which tubers from 5 and 8 mm upwards were removed (not shown).

From the second harvest onwards, the average tuber weight was higher when the diameter of the tubers removed was larger (Table 5). Even if tubers ≥ 5 mm were removed, the average weight of the tubers was still over 1 g in all cultivars.

Discussion

Effects of crop husbandry on tuber yield. Effects of the different treatments on minituber yield will have been exerted through their effects on the canopy. Under field conditions in normal crops, Leaf Area Duration or Intercepted Radiation correlate well with tuber yield when fertilizer application (Gunasena & Harris, 1969) or plant density (Vander Zaag et al., 1990) are varied. In our experiments with in vitro plantlets, effects of plant density on LAI showed trends similar to those of density effects on yield per m^2, if treatments were compared within a single harvest date (Table 3). A higher maximum LAI (cf. Gunasena & Harris, 1971) may have contributed to the higher minituber yields per plant after fertilization (Table 1). Because a complete nutrient solution was supplied, the availability of all essential minerals increased. However, when the supply of nutrients in cv. Ostara was begun at tuber initiation, the increase in tuber yield was less than when it was begun after the first harvest (Table 1). Although the nutrient solution was low in concentration, the total dose of N added at this early stage may have reduced the partitioning of assimilate to the tubers (cf. Simpson, 1962; Gunasena & Harris, 1968).

In addition, minituber yield was higher because haulm senescence was reduced or delayed in fertilized plants, at a square plant arrangement, and at lower densities

Table 5. Influence of diameter of removed tubers on yield, number and size of tubers of three cultivars, expressed per plant. Plant density: 350 plants per m^2; start of fertilization: after first harvest (Expt 3).

Diameter of removed tubers	Tuber yield (g fresh per plant)				Number of tubers (number per plant)				Tuber size (g fresh per tuber)			
	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined	1st harvest	2nd harvest	3rd harvest	all harvests combined
Cultivar Ostara												
≥ 5 mm	3.1	7.1	4.0	14.2	1.6	3.5	3.5	8.6	1.9	2.0	1.1	1.6
≥ 8 mm	4.3	6.6	4.3	15.2	1.3	2.1	2.1	5.5	3.7	3.1	2.0	2.8
≥ 12 mm	2.0	8.1	5.2	15.3	0.8	2.2	1.4	4.4	2.4	3.8	3.7	3.5
Cultivar Bintje												
≥ 5 mm	3.5	7.3	3.6	14.5	1.5	7.3	3.5	12.3	2.4	1.0	1.0	1.2
≥ 8 mm	3.0	8.1	3.1	14.2	1.3	5.2	3.2	9.7	2.4	1.5	1.0	1.5
≥ 12 mm	2.8	5.1	2.3	10.2	1.1	2.0	1.2	4.3	2.7	2.6	1.9	2.4
Cultivar Elkana												
≥ 5 mm	1.4	8.5	3.6	13.5	1.0	4.7	3.5	9.2	1.1	1.9	1.0	1.5
≥ 8 mm	1.6	7.1	4.2	12.9	0.9	2.8	2.6	6.3	1.8	2.6	1.7	2.1
≥ 12 mm	0.6	7.6	4.4	12.7	0.3	1.9	1.5	3.7	2.5	4.0	2.9	3.4
Statistical analysis[a]												
Tuber diameter (TD)	*	ns	ns	ns	***	***/ns	***	***/**	ns	***	***/*	***
Cultivar (CV)	***	ns	*	ns	***	***/ns	ns	***/ns	ns	***	***/ns	***
Interaction (TD × CV)	ns	*	ns	ns	ns	***	ns	***	ns	ns	*	ns
CV%	38.2	19.9	29.6	15.7	29.8	17.8	19.2	10.8	40.1	20.6	26.2	16.0
SE	1.0	1.5	1.1	2.1	0.3	0.6	0.5	0.8	0.9	0.5	0.5	0.4

[a] The first indications of statistical significance presented and the CV% and SE are the results of a standard analysis of variance. Only if both main effects and interaction were significant, an F-test was performed on mean squares of main effects and interactions, to determine the relative importance of the main effect. The results of this test are presented as the second indications of statistical significance. ***$P<0.001$, **$0.001 \leq P<0.01$, *$0.01 \leq P<0.05$, ns not significant: $P \geq 0.05$.

(Table 3). This reduced senescence is often observed in the field after fertilization (Simpson, 1962; Van Burg, 1967) but is in contrast with the general view expressed by Proctor (1969) that higher yields at more uniform plant arrangements are caused by a delay in competition for light, and thus a higher production early in the growing season. In our experiment, tuber yields were higher at the square spacing because plants suffered less from the second non-destructive harvest as they had shorter stems (cf. Proctor, 1969) and were more compact. Stem damage also contributed to the haulm senescence of the more etiolated plants at high densities. A higher rate of senescence at higher densities may also be observed under field conditions (Van Burg, 1967; Bodlaender & Reestman, 1968), but then the availability of nutrients (Bremner & El Saeed, 1963; Van Burg, 1967) or water is often thought to limit yield at high plant or stem densities. In our experiment each plant received the same volume of nutrient solution, thus fertilizer application per m^2 was higher at high plant densities.

Yield of minitubers may also be affected by the photosynthetic efficiency of the canopy: Lommen & Struik (1992b) showed that tuber growth rates after a non-destructive harvest were lower than those of plants left undisturbed, but non-tuber growth rates were similar. After a non-destructive harvest, photosynthesis may be reduced by a temporary drought stress or the removal of tuber sinks. The reduction caused by removal of tuber sinks may be less severe in better fertilized plants, as observed by Nösberger & Humphries (1965), though not by Burt (1964). Under the well fertilized conditions of Expt 3, where tubers with different diameters were removed and as a consequence a varying number and size of tuber sinks remained on the plants, no effect on minituber yield in the second harvest was observed (Table 5).

Effects of crop husbandry on number of tubers. Lommen & Struik (1992b) showed that the number of minitubers ≥8 mm after non-destructive harvests was not limited by the total number of tubers and tuber initials present, but by the growth of these tubers to a harvestable size. Thus, if crop husbandry techniques increase the number of minitubers harvested per plant, it may be through their effects on tuber growth. Our research shows that these effects on number of minitubers harvested per plant strongly depended on the cultivar.

Combined over all harvests, in cv. Ostara, fertilization and a square plant arrangement did not affect number of minitubers, although they increased minituber yield. Only when plant density was lowered and tuber yield per plant increased substantially, did the number of tubers per plant growing to ≥8 mm increase (Table 2). Similar effects of density on tuber number per stem are generally observed in the field (cf. Wurr, 1974) or in beds (Wiersema, 1986), although not always (Vander Zaag et al., 1990).

Combined over all harvests, in cv. Bintje all crop husbandry techniques that increased minituber yield per plant (fertilization, lowering plant density and a square plant arrangement) also increased number of minitubers per plant (Tables 1, 2, 4). Also, under field conditions numbers of tubers are higher where plants are fertilized with N before tuber initiation (Gunasena & Harris, 1971).

At very high densities (400 to 800 plants per m^2) and in both cultivars, the number of minitubers per plant appeared to level off at a minimal number when density increased (Table 2). This led to a discontinuous increase in the number of tubers per

m^2 with an increase in density. Because of the relatively low number of tubers produced by cv. Bintje at 400 plants per m^2 in this experiment, the discontinuity occurring in this experiment was extremely strong. However, a discontinuous increase was also observed in a preliminary experiment (W. J. M. Lommen, unpublished), and similar discontinuous effects of plant density are reported in other crops, for instance on ear number in winter wheat (Darwinkel, 1978).

In Expts 1, 2 and 3, 1731, 1683 and 1925 tubers per m^2, respectively, were produced by cv. Ostara and 2722, 1467 and 3383 by cv. Bintje in those treatments with 350, 400 (10-cm rows) and 350 plants per m^2, in which tubers ≥ 8 mm were removed and plants were fertilized from the first harvest onwards. Numbers of tubers per m^2 in Expt 2 were lower than in Expts 1 and 3 due to the low number produced by cv. Bintje. In cv. Ostara, differences between experiments were statistically not significant, while in cv. Bintje differences between Expts 1 and 3 were not significant. Part of the differences between experiments may have been caused by the smaller plantlets used for transplanting in Expt 2 (9 days old, compared to 17 and 13 days in Expts 1 and 3) and brighter weather during Expt 3. In addition, slightly more damage may have occurred in Expt 2 during harvesting, because of the smaller distance between rows (10 cm) and the difficulties of harvesting and replanting plants on fixed positions in large plots, while in Expts 1 and 3 pots could be harvested one by one.

Possibilities of manipulating yield parameters by crop husbandry and the practical implications. Adjusting plant density (Tables 2 and 3) and the diameter of the tubers removed (Table 5) proved to be perfect tools in all cultivars for manipulating minituber number and size. These practices had no significant effect on tuber yield per m^2; thus increases in number of tubers per m^2 were directly reflected in decreases in average tuber weight.

Number and size of minitubers could not be manipulated in all cultivars by adjusting the time at which the supply of nutrient solution started (Table 1) or the plant arrangement (Table 4). When results of all harvests were combined, numbers of tubers in cv. Ostara were not affected. Supplying nutrients and using a square plant arrangement, however, increased minituber yield in both cultivars and did not reduce average tuber weight. No significant interactions between cultivars and treatments in average tuber weight were observed, although the cultivars responded similarly in tuber yield and differently in tuber number.

For practical production of minitubers, a continuous supply of a low-dose nutrient solution starting at the first harvest may be adopted as a means of increasing tuber yield. Square plant arrangements, however, were less convenient than row arrangements for carrying out the non-destructive harvests.

When controlled glasshouse space is limited and high numbers of tubers per unit area are desirable, plant density may be increased. At 800 plants per m^2, 2700 and 3400 minitubers per m^2 were produced by cvs Ostara and Bintje respectively (Table 3). The average weights were 1.4 and 1.6 g and all tubers were ≥ 8 mm. Smaller tubers may also be removed. When tubers ≥ 5 mm were removed at 350 plants per m^2 in Expt 3, 3000, 4300 and 3200 minitubers per m^2 were produced by cvs Ostara, Bintje and Elkana (calculated from Table 5), still with average weights between 1.2 and 1.6 g.

When in vitro plantlets are expensive and a high number of minitubers per plantlet is preferred over a high number of minitubers per m^2, plant density can be lowered. Lowering plant density was the only treatment investigated which increased the number of minitubers ≥ 8 mm per plantlet in all cultivars, except at very high plant densities. Simultaneously, the average tuber weight increased. For further studies, we adopted a plant density of 175 plants per m^2, preferring high numbers of tubers per plantlet to high numbers of tubers per m^2. To increase the number of tubers per plantlet even further, the diameter of the tubers removed may be lowered from 8 to 5 mm. From a practical point of view, this seems logical: it increases number of tubers considerably, does not affect the number and weight of tubers in the larger (≥ 8 or ≥ 12 mm) grades, and will hardly affect the time necessary to carry out the harvest. Tubers between 5 and 8 mm, however, may prove less suitable for direct field planting (cf. Struik & Lommen, 1990).

The effects of climatic factors on yield parameters of minitubers and the behaviour and performance of minitubers of different sizes during storage and in the field will be reported in forthcoming papers.

Acknowledgements

We gratefully acknowledge the role of R. van Putten, B.C.A. Glas, E. van Heusden (Wageningen Agricultural University, the Netherlands) and J.W. Płodowska (Warsaw Agricultural University, Poland) in this research. We thank 'Stichting Begeleiding Snelle Vermeerdering van Aardappelen' (Slootdorp, The Netherlands) for supplying the in vitro plantlets. This research was partly financed by the Dutch Commodity Board for Potatoes.

References

Bleasdale, J.K.A. & R. Thompson, 1963. Competition studies. Potatoes. *Annual Report of the National Vegetable Research Station for 1962*: 37–38.

Bodlaender, K.B.A. & A.J. Reestman, 1968. The interaction of nitrogen supply and plant density in potatoes. *Netherlands Journal of Agricultural Science* 16: 165–176.

Bremner, P.M. & A.K. El Saeed, 1963. The significance of seed size and spacing. In: J.D. Ivins & F. Milthorpe (Eds), The growth of the potato. London, Butterworths, pp. 267–280.

Bremner, P.M. & M.A. Taha, 1966. Studies in potato agronomy I. The effects of variety, seed size and spacing on growth, development and yield. *Journal of Agricultural Science, Cambridge* 66: 241–252.

Burt, R.L., 1964. Carbohydrate utilization as a factor in plant growth. *Australian Journal of Biological Sciences* 17: 868–877.

Darwinkel, A., 1978. Patterns of tillering and grain production of winter wheat at a wide range of plant densities. *Netherlands Journal of Agricultural Science* 26: 383–398.

Gunasena, H.P.M. & P.M. Harris, 1968. The effect of the time of application of nitrogen and potassium on the growth of the second early potato, variety Craig's Royal. *Journal of Agricultural Science, Cambridge* 71: 283–296.

Gunasena, H.P.M. & P.M. Harris, 1969. The effect of CCC and nitrogen on the growth and yield of the second early potato variety Craig's Royal. *Journal of Agricultural Science, Cambridge* 73: 245–259.

Gunasena, H.P.M. & P.M. Harris, 1971. The effect of CCC, nitrogen and potassium on the growth and yield of two varieties of potatoes. *Journal of Agricultural Science, Cambridge* 76: 33–52.

Ifenkwe, O. P. & E. J. Allen, 1978. Effects of row width and planting density on growth and yield of two maincrop potato varieties 2. Number of tubers, total and graded yields and their relationships with above-ground stem densities. *Journal of Agricultural Science, Cambridge* 91: 279 – 289.

Lommen, W. J. M. & P. C. Struik, 1992a. Influence of a single non-destructive harvest on potato plantlets grown for minituber production. *Netherlands Journal of Agricultural Science* 40: 21 – 41.

Lommen, W. J. M. & P. C. Struik, 1992b. Production of potato minitubers by repeated harvesting: Plant productivity and initiation, growth and resorption of tubers. *Netherlands Journal of Agricultural Science* 40 (in press).

Nösberger, J. & E. C. Humphries, 1965. The influence of removing tubers on dry-matter production and net assimilation rate of potato plants. *Annals of Botany* 29: 579 – 588.

Proctor, J. M., 1969. Patterns of spatial arrangements of early potatoes. *European Potato Journal* 12: 238 – 250.

Ryan, P. F., 1961. Recent studies on potato manuring in Ireland. *European Potato Journal* 4: 165 – 173.

Simpson, K., 1962. Effects of soil-moisture tension and fertilizers on the yield, growth and phosphorus uptake of potatoes. *Journal of the Science of Food and Agriculture* 13: 236 – 248.

Struik, P. C. & W. J. M. Lommen, 1990. Production, storage and use of micro- and minitubers. In: D. K. L. MacKerron et al. (Eds), Proceedings of the 11th Triennial Conference of the European Association for Potato Research, Edinburgh, UK, 8 – 13th July 1990, pp. 122 – 133.

Svensson, B., 1972. Influence of the place of a stem in the hill on the weight and dry matter content of its tubers. *Potato Research* 15: 346 – 353.

Van Burg, P. F. J., 1967. Relation of rate of nitrogen fertilization, seed spacing and seed size to yield of potatoes. *Netherlands Nitrogen Technical Bulletin* 4: 1 – 30.

Vander Zaag, P., A. L. Demagante & E. E. Ewing, 1990. Influence of plant spacing on potato (*Solanum tuberosum* L.) morphology, growth and yield under two contrasting environments. *Potato Research* 33: 313 – 323.

Wiersema, S. G., 1986. The effect of density on tuber yield in plants grown from true potato seed in seed beds during two contrasting seasons. *American Potato Journal* 63: 465 – 472.

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