Netherlands Journal of Agricultural Science 40 (1992) 159-172

Relation between stolon and tuber characteristics and the duration of tuber dormancy in potato

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Received 15 January 1992; accepted 18 March 1992

Abstract

The variation in duration of tuber dormancy within potato plants of cv. Diamant was investigated in two observational experiments with plants grown in an experimental set-up which allowed frequent, non-destructive observations on stolon and tuber development. During plant growth, several characteristics were recorded: date of stolon initiation, stolon length, position of the stolon on the stem, date of tuber initiation, position of the tuber on the stolon, tuber shape and tuber weight. After harvest, tubers were stored at 18 °C to assess the duration of dormancy. By means of regression analyses, sets of variables were selected that explained the variation in duration of dormancy best. Tuber weight explained by far the highest proportion of the variation in dormancy. The duration of dormancy was also significantly related to the date of tuber initiation and to the position of the tuber on the plant during its growth.

Keywords : Solanum tuberosum L., potato, dormancy, seed tuber, cultivar, tuber weight, tuber initiation, stolon

Introduction

Dormancy of potato tubers is a varietal characteristic, which can be influenced by factors during growth and storage of the tubers. However, a seed tuber lot consisting of tubers of one genotype and origin and stored in a controlled environment also shows a considerable variation in duration of dormancy (van Ittersum, 1992). Most of this variation is caused by variation of dormancy within plants.

For the cv. Diamant, showing a large variation in duration of dormancy within a seed lot, this variation was related to tuber weight (van Ittersum, 1992). For this cultivar the observed relation between the duration of dormancy and tuber weight confirms earlier research (e.g. Krijthe, 1962). Tubers of one plant may, however, differ in other characteristics as well: they may be initiated at different dates, grown at different positions on the plant, or differ in shape. Burton (1963) suggested that dormancy starts at tuber initiation and if so, it seems logical that the duration of dormancy of single tubers also correlates with their dates of initiation. Moreover, the relation between dormancy and tuber size may be indirect, since tuber size seems to be related to stolon characteristics and the position of the tuber on the stolon (Struik et al., 1991).

In observational experiments carried out in greenhouses, we investigated whether, besides tuber weight, other variables were related to the duration of dormancy and whether the 'effect' of tuber weight on dormancy is (partly) mediated by other variables. Data were analysed by means of (multiple) regression analyses.

Materials and methods

Plant material and experimental set-up

Two greenhouse experiments (Expts 1 and 2) were carried out during April-July in 1989 and 1990, at a temperature of 15 °C day and night and a daylength of 14 h.

Presprouted tubers (cv. Diamant) of 15 ± 2 g (Expt 1) or tuber parts of 12 ± 0.5 g (Expt 2) were desprouted to leave one sprout, before being placed in moist quartz sand to initiate rooting. The tubers were at the optimal physiological age (curing period at 15-20 °C for 1 month, storage at 4 °C for 6 months and pre-sprouting period at 15 °C for 1½ month). After the roots had reached a length of ca 5 cm, the tubers were transferred to an experimental set-up with stolon chambers on aerated containers holding 5 litre nutrient solution (Struik & van Voorst, 1986). The roots were pulled through the gauze at the center of the stolon chamber and put into the nutrient solution.

The stolon chambers were filled with a mixture of equal volumes of quartz sand and agra-perlite that was moistened (moisture content ca 4 % w/w) during emergence and initial growth to allow normal growth of the sprout, roots, stolons and tuber initials. The medium could be removed easily by a vacuum cleaner to allow observations on stolon and tuber initiation and tubers. It was renewed regularly. The stolon chambers and the containers were wrapped in aluminium to prevent local temperature increases inside the chamber because of incoming radiation. For the same reason the top of the stolon chamber was also covered until tuber initiation. Thereafter, leaves were large enough to prevent heating of the stolon chamber.

Plants of Expt 1 grew too luxuriantly and tuber initiation continued. For many plants, the numbers of tubers initiated per plant became extremely high (>30); this made observations almost impossible and would reduce the variability in size. Therefore, some tubers from plants with too many tubers were removed at random 48 days after planting (DAP), so that the total number of tubers per plant did not exceed ca 20. The relations between the duration of dormancy and the stolon and tuber characteristics were essentially similar for the batches with tubers from plants with relatively few and many tubers removed (see Appendix).

To slow down vegetative growth in Expt 1, the nutrient concentrations of the solution were gradually lowered. In Expt 2, low concentrations of nutrients were used from the start. In Expt 1, the initial nutrient solution contained, per litre, 168 mg N, 31 mg P, 274 mg K, 151 mg Ca, 46 mg Mg, 98 mg S, 4.6 mg Fe and all microelements required (for details on the nutrient solution see Lommen & Struik, 1992). The containers were filled up with nutrient solution regularly. From 33 DAP, the solution was renewed weekly, first with 100 % of the above described solution, later gradually lowered to 25 % of this solution. In Expt 2, the nutrient solution contained, per litre, 84 mg N, 15 mg P, 137 mg K, 75 mg Ca, 23 mg Mg, 49 mg S, 4.6 mg Fe and all microelements required. From 21 DAP on, the solution was renewed once per two weeks, later weekly. The containers were filled up with water regularly. The pH of the solution varied between 5 and 6 and was re-adjusted when necessary.

The experiments started with 50 plants; 30 uniform plants were selected for further observations. In Expt 1, observations on tuber initiation started 28 DAP and in Expt 2, observations on stolon and tuber initiation started 21 DAP. Some plants were discarded because of root decay or severe damage by handling the plants. Eighty-two DAP (Expt 1) or 78 DAP (Expt 2), plant growth was stopped by cutting the haulm and the roots. In Expt 1, the tubers were harvested immediately after haulm cutting whereas in Expt 2 they hardened for two weeks before harvest. Temperature during the hardening period was 18 °C.

Observations

Tuber (Expt 1) or stolon and tuber (Expt 2) initiation were recorded ca twice a week (Expt 1) or once a week (Expt 2). All swollen stolon tips more than twice the diameter of the stolon were defined as tubers. The date of stolon/tuber initiation was defined as the date on which the stolon/tuber was observed for the first time. Tubers and stolons were tagged with labels.

Twenty-one (Expt 1) or 25 (Expt 2) plants were harvested. At harvest the position of each tuber on the plant was recorded as follows:
- the length of the main (first order) stolon at which the tuber grew (stolon length = SL);
- the distance along the stem between the main stolon at which the tuber grew and the mother tuber (stolon position = SP);
- the position of the tuber on the stolon (tuber position = TP): at the tip of main stolons (apical tuber; TP = 0) or at the tip of stolon branches (lateral tuber; TP = 1).

The length and diameter of the tubers were determined and the tubers were weighed. The shape of a tuber was defined as the ratio between the length and the maximum diameter. All tubers were stored at 18 °C and 80 % r.h. in darkness, to assess the duration of dormancy. The duration of dormancy of a tuber was defined as the period after haulm cutting until the tuber had formed at least one sprout of 2 mm long.

At haulm cutting, haulm dry weights of the plants were determined.

Statistical analysis

Tubers of which some information was lacking were omitted in the statistical analysis. Data of 260 (Expt 1) or 355 (Expt 2) tubers were used for the analysis. Histograms were made of each variable and a correlation matrix for all variables was determined for each experiment. Subsequently, multiple regression analyses were carried out to find the simpliest subsets of variables that described the highest proportion of the variation in duration of dormancy. Therefore, all possible models (total number of models = 2^v; v = number of regressor terms) were calculated. The best models were selected on the basis of a measure called Mallow's C_p (Montgomery & Peck, 1982). This measure is defined as:

$$C_p = (\text{Residual sum of square}/\sigma^2) - n + 2p \qquad (1)$$

in which σ^2 = estimated variance of full model, n = total number of observations and p = number of regressor terms in the model + 1. Candidate models are the simpliest models with a C_p that equals approximately p (e.g. $C_p < p + 2$). The least significant of the non-significant variables (judged by means of the t-statistic) in these candidate models were omitted. The percentage of variance accounted for by a model is given by the adjusted R^2 statistic (Snedecor & Cochran, 1980):

$$R^2_{\text{adj}} = 100 \times (1 - (\text{Residual mean square}/\text{Total mean square})) \qquad (2)$$

First, the best models were selected from those with only main terms; then, the best alternatives were selected from all possible models with main terms and two-way linear interaction terms. Possible regressor variables/terms for the duration of dormancy were:
- all linear, quadratic and cubic terms of the variables listed in Table 1 and the cubic root of tuber weight (van Ittersum, 1992);
- all two-way interactions between linear terms of the variables.

Subsequently, multiple regression analyses were carried out with all main and two-way interaction terms of all variables as qualitative variables by grouping the values of the variables in classes (e.g. tuber weight with the classes: 0-20, 20-40, 40-60 g, etc.) as a final check whether the relation between dormancy and the variables in the candidate models was described well by the linear, quadratic, cubic or cubic root terms and whether there were important non-linear interactions between variables.

The best and simpliest candidate models of each experiment were analysed further. First, they were re-calculated without the data of those tubers with high leverages (extreme x-values; Montgomery & Peck, 1982), to analyse whether the results were affected strongly by these data. Finally, a forward selection was used to find out the relative importance of the variables of the model. This analysis started with the fit of the empty model. Then, variables were added one by one, in every step including the terms of that variable in the model that achieved the highest reduction of the residual mean square. After all variables of the best/simpliest candidate model were included, the qualitative variable 'plant' was added to analyse differences between plants not covered by the variables already in the model. This only gave a rough indication of plant effects, since for some plants some data were missing.

The statistical analyses were performed with Genstat 5, Release 2.1 (Genstat 5 Committee, 1987) and the Genstat procedure Rselect (Thissen & Goedhart, 1990).

Results

First analysis of the data

Mean haulm dry weight of the plants was higher in Expt 1 (68 g) than in Expt 2 (48 g). At haulm removal, the haulms were more senesced in Expt 1 than in Expt 2. Plants of Expts 1 and 2 also differed in some stolon and tuber characteristics (Table 1). In Expt 1, the stolons were longer and initiated at a higher position on the stem. On average tubers were initiated later, the variance in their date of initiation was larger (27 vs 19 days^2) and more tubers (46 vs 7 %) grew on stolon branches. The tuber-size distribution also differed markedly. On average tubers of Expt 1 were smaller and only 10 tubers were heavier than 70 g. Although the range of tuber weights was larger in Expt 1 than in Expt 2, the variance of individual tuber weights in the whole seed lot was smaller in Expt 1 than in Expt 2 (474 vs 753 g^2). The mean duration of dormancy hardly differed between the two experiments, but the range in duration of dormancy was much smaller in Expt 1 than in Expt 2. This was also reflected in a much smaller variance in Expt 1 (67 days^2) than in Expt 2 (342 days^2).

The correlation coefficients between the duration of dormancy and the regressor variables are given in Table 2. Since the number of observations was very large, most correlations were highly significant, although their values were not always high. Tuber weight was rather closely (negatively) correlated with dormancy in

Table 1. Means and ranges (in parentheses) of the regressor variables and the duration of dormancy for the whole seed lot comprising 260 tubers (Expt 1; 21 plants) or 355 tubers (Expt 2; 25 plants).

Variable		Mean (range)	
		Experiment 1	Experiment 2
SI	(date of stolon initiation; DAP[a])	not observed	28 (21-43)
SL	(stolon length; cm)	7.3 (0.8-18)	3.2 (0.0-14)
SP	(stolon position; cm from mother tuber)	3.1 (0.0-9.0)	1.2 (0.0-7.0)
TI	(date of tuber initiation; DAP)	40 (28-57)	33 (28-51[b])
TP	(tuber position[c])	0.46 (0-1)	0.07 (0-1)
TS	(tuber shape, length/width; cm cm^{-1})	1.5 (0.8-2.6)	1.5 (0.9-2.4)
TW	(tuber weight; g)	27 (0.9-145[d])	38 (0.2-116)
Duration of dormancy (DAH[e])		95 (80-126)	98 (66-139)

[a]DAP = days after planting. [b]Only 11 out of 355 tubers were initiated 40 days after planting or later. [c] Tubers on main stolons: TP = 0; tubers on stolon branches: TP = 1. [d]Only 10 out of 260 tubers were heavier than 70 g. [e]DAH = days after haulm cutting.

Table 2. The correlation coefficients between the duration of dormancy and some stolon and tuber variables varying within a plant for Expt 1 (n = 260) and Expt 2 (n = 355).

Variable		Correlation coefficient	
		Expt 1	Expt 2
TW	(tuber weight)	−0.51***	−0.82***
TI	(tuber initiation)	0.44***	0.51***
SI	(stolon initiation)	not observed	0.41***
TS	(tuber shape)	−0.38***	−0.32***
TP	(tuber position)[a]	0.37***	0.27***
SL	(stolon length)	0.20**	−0.19***
SP	(stolon position)	−0.04	−0.02

** and *** indicate statistically significant at $P < 0.01$ and $P < 0.001$, respectively. [a]The mean duration of dormancy of tubers on main stolons (TP = 0) was significantly ($P < 0.001$) shorter than that of tubers on stolon branches (TP = 1).

both experiments. The correlations with the date of tuber initiation and with the date of stolon initiation (Expt 2) were also rather clear. In both experiments, the length/width ratio of a tuber (tuber shape) and the duration of dormancy were negatively correlated. Tubers on main stolons had a shorter duration of dormancy than tubers on stolon branches. The correlation between dormancy and stolon length in Expt 1 was contrary to that in Expt 2. The stolon position showed no significant correlation with dormancy.

Selection of the models

The results of the selection of the models describing the duration of dormancy are summarized in Table 3.

For Expt 1, the models with terms of the five variables stolon length, tuber initiation, tuber position on the stolon, tuber shape and tuber weight were the best models with only main terms. There were a number of models with these variables having rather similar C_p-values; the simpliest model (and also the one with one of the lowest C_p-values) is given in Table 3. The best model with a different set of variables had a C_p-value of 16.5, which was much larger than the criterion ($p + 2 = 9$). In this model the variable tuber shape did not occur. The models with interaction terms were not clearly better than the ones without. Therefore, we conclude that the model with the terms: SL, SL^2, TI, TI^2, TP, TS, TS^2, and $TW^{0.33}$ is the best and simpliest candidate descriptive model in Expt 1, accounting for 49.0 % of the variation in the duration of dormancy of the tubers.

For Expt 2, the model with the variables stolon length, stolon position on the stem, tuber initiation, tuber position on the stolon, tuber shape and tuber weight gave the best description of the duration of dormancy of all models with main terms only. The percentage of variance accounted for was 77.5 %. Models with an essentially different set of variables were poorer ($C_p = 12.4 > 7 + 2$). The

Table 3. The terms and the C_p and R^2_{adj} values of the candidate models (without and with interaction terms) for the description of the duration of dormancy. The best alternatives with an essentially different set of regressor variables are given.

Terms[a] of candidate models	$p + 2$[b]	C_p-value[c]	R^2_{adj} (%)
Experiment 1			
Terms of models with only main terms			
SL,SL^2 TI,TI^2 TP TS,TS^2 TW$^{0.33}$	11	6.0	49.0
SL,SL^2 TI,TI^2 TP TW$^{0.33}$	9	16.5	46.4
Terms of models with linear interaction terms			
SL,SL^2 TI,TI^2 TP TW$^{0.33}$ TP*TS	10	5.6	49.1
SL,SL^2 TI,TI^2 TW$^{0.33}$ TI*TP TP*TS	10	6.4	48.9
Experiment 2			
Terms of models with only main terms			
SL SP,SP^2 TI TP TS TW$^{0.33}$	10	6.5	77.5
SL SP,SP^2 TI TP TW$^{0.33}$	9	12.4	77.1
Terms of models with linear interaction terms			
SP,SP^2,SP^3 TP TW$^{0.33}$ SL*TS SL*TW TI*TS TI*TW	12	5.9	78.5
SP,SP^2,SP^3 TW$^{0.33}$ SL*TP SL*TS SL*TW TI*TS TI*TW	12	7.1	78.4
SP,SP^2,SP^3 TP TS TW$^{0.33}$ SL*TI SL*TS SL*TW	12	7.9	78.4
SP,SP^2,SP^3 TS TW$^{0.33}$ SL*TI SL*TS SL*TW TP*TS	12	8.0	78.4

[a]SL = stolon length; SP = stolon position on the stem; TI = date of tuber initiation; TP = tuber position on the stolon; TS = tuber shape (length/width ratio); TW = tuber weight. [b]p = number of regressor terms in the model + 1. [c]C_p-values are comparable only per experiment for models with the same type of terms (either without or with interaction terms).

R^2_{adj}'s of the models with linear interaction terms were slightly, but significantly, higher than those with main terms only. However, these models with 3-5 interaction terms are extremely complex and do not comprise variables other than those with main terms only. Therefore, the model with only main terms is preferred for this first effort to describe the variation in duration of dormancy within a seed lot.

The multiple regression analyses with the values of all regressor variables grouped in classes (qualitative variables) did not reveal any important kind of non-linear relations between the duration of dormancy and the regressor variables than already in the candidate models, nor did it reveal important non-linear interactions between the variables.

The sets of selected terms did not change when omitting the data of those tubers with a high leverage. For Expt 1, one extremely oblong tuber (length/width ratio 2.6) had a rather large influence on the regression coefficients for the terms of the variable tuber shape. It was decided to omit this tuber in the further analysis (this raised the R^2_{adj} of the model to 49.4 %). For Expt 2, the regression coefficients hardly changed when re-calculated without the data of those tubers with high leverages. In both experiments, there were no tubers causing high standardized residuals.

Further analysis of the selected models

In order to get more insight in the relative importance of the variables in the best/simpliest models, the results of the forward selection are summarized in Table 4. For Expt 1, tuber weight accounted for 27.1 % of the variation in the duration of dormancy. The date of tuber initiation was the second important variable of the model describing together with tuber weight 38.0 % of the variation in dormancy. The position of the tuber on the stolon was the third variable appearing in the model and stolon length and tuber shape were the last selected variables. The final addition of the qualitative variable plant to the selected model raised the percentage of variation accounted for statistically significantly with another 9.4 %.

When the forward selection was started with the date of tuber initiation the R^2_{adj} was: 19.3 %. The total percentage of variance accounted for by the best/simpliest model without a term with tuber weight was 34.8 % without the variable plant and 45.7 % with this variable.

In Expt 2, tuber weight was by far the most important variable, accounting for 75.3 % of the variation in the duration of dormancy. Adding other variables only slightly increased this percentage. Again, the date of tuber initiation was the second variable appearing in the model. A final addition of the variable plant to the model increased the total percentage of variance accounted for to 81.4 %.

When the forward selection was started with the date of tuber initiation, the R^2_{adj} was 26 %. The percentage of variance accounted for was 36.3 % for the best/simpliest model without a term with tuber weight.

The best and simpliest descriptive models for the duration of dormancy (D) with only variables varying within plants were:

$$D = 145 - 4.2TW^{0.33} - 0.93TI + 0.016TI^2 + 4.7TP - 1.7SL + 0.076SL^2 - 24.8TS + 6.4TS^2 \qquad \text{(Expt 1) (3)}$$

$$D = 123 - 14.4TW^{0.33} + 0.38TI + 9.0TP - 0.95SL + 6.3TS - 3.10SP + 0.58SP^2 \qquad \text{(Expt 2) (4)}$$

According to these models the variables were related to the duration of dormancy as follows (provided that only one variable is varying and the other variables do not change in value). The heavier the tubers the shorter the duration of dormancy, but the relation was not linear. The duration of dormancy decreased more with increasing tuber weights at low than at higher tuber weights and more in Expt 2 than in Expt 1. The cubic root of tuber weight gave the best description even if the duration of dormancy of a tuber was expressed in days after its initiation (data not shown). In both models there was a positive correlation between the duration of dormancy and the date of tuber initiation. The later a tuber was initiated the longer its duration of dormancy in days after haulm cutting, however, a delay in tuber initiation did not result in the same delay in end of dormancy. Tubers grown on stolon branches had a longer duration of dormancy. Tubers grown on longer stolons had a shorter dormancy than tubers on very short stolons. In Expt 1, tubers with a higher length/width

Table 4. Results of the forward selection of regressor terms for the duration of dormancy. The qualitative variable 'plant' was added finally to the best/simpliest model. The R^2_{adj}'s for the same models without the tuber weight (TW) term are also given.

Added term	F-value	R^2_{adj} (%)	R^2_{adj} (%) same model without TW
Experiment 1			
$TW^{0.33}$ (tuber weight)	96.7***	27.1	–
TI, TI^2 (tuber initiation)	23.7***	38.0	19.3
TP (tuber position on stolon)	23.9***	43.1	28.0
SL, SL^2 (stolon length)	10.8***	47.2	30.0
TS, TS^2 (tuber shape)	6.43**	49.4	34.8
Qualitative variable plant	3.85***	58.8	45.7
Experiment 2			
$TW^{0.33}$ (tuber weight)	1078***	75.3	–
TI (tuber initiation)	11.9***	76.0	26.0
SP, SP^2 (stolon position)	3.99*	76.4	26.8
TP (tuber position on stolon)	3.54[a]	76.6	32.9
SL (stolon length)	8.50**	77.1	36.1
TS (tuber shape)	7.98**	77.5	36.3
Qualitative variable plant	3.98***	81.4	38.5

*,**and*** indicate statistically significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.
[a]Statistically significant at $P = 0.07$.

ratio had a shorter dormancy period than tubers with a very low ratio. In Expt 2, the relation was the opposite: tubers with a high length/width ratio had a longer duration of dormancy than tubers with a lower ratio. Finally, in Expt 2, tubers that grew on stolons at an intermediate distance from the mother tuber (ca 3 cm) had the shortest duration of dormancy, whereas tubers had a longer duration of dormancy when grown on stolons near the mother tuber or much higher on the stem.

Discussion

Comparison of Expts 1 and 2

The difference in concentration of the nutrient solutions and the removal of some tubers in Expt 1 induced extra differences in stolon and tuber characteristics between the two experiments. The later mean date of tuber initiation (Werner, 1934; Krauss, 1985) and the longer stolons in Expt 1 compared to Expt 2 may have been caused by the higher nitrogen concentration in Expt 1. The higher percentage of tubers grown on stolon branches may have been caused by the removal of some tubers on main stolons (cf. Oparka, 1987); this removal undoubtedly also increased the growth rates of the remaining tubers (Marschner et al., 1984; Engels & Marschner, 1986). The lower mean tuber weight in Expt 1 was probably caused by the higher number of tubers per plant and the earlier senescence of the haulms in this experiment.

The variance of the duration of dormancy within the tuber lot was much lower in Expt 1 than in Expt 2 and than in tuber lots of cv. Diamant from field plots (van Ittersum, 1992). This was partly caused by the low variability in tuber weight in Expt 1. Because of the lower total variance in Expt 1, the percentage of variance accounted for by the best models was also much lower in Expt 1 (ca 50 %) than in Expt 2 (ca 75 %). The final models of Expts 1 and 2 also differed in some other respects. Tuber weight was much less dominant in Expt 1 than in Expt 2 and the regression coefficient of the tuber weight term was much lower for Expt 1. The coefficient in Expt 2 was similar to those found for seed lots from field plots (van Ittersum, 1992).

Stolon and tuber characteristics related to variation in tuber dormancy

Despite the differences, the main conclusions from both experiments are the same. Tuber weight was the variable by far the best related to the duration of dormancy. The models without tuber weight explained ca 35 % of the variation in dormancy, whereas the other variables did not increase the R^2_{adj} that much when added to a model with only tuber weight. This shows that tuber weight is also related to some other variables. Dormancy and tuber initiation date were positively correlated (Table 2), partly because tuber weight showed a negative correlation with the date of tuber initiation (r = –0.28*** (Expt 1) or –0.46*** (Expt 2)). Differences in dormancy between tubers of similar weight and different dates of initiation were small, especially in Expt 2 (Figure 1).

Besides the weight of a tuber and its date of initiation, the position of a tuber on the plant during its growth also appeared to be related to the duration of dormancy, although this did not add much to the percentage of variation in duration of dormancy accounted for when tuber weight and the date of tuber initiation were already in the model. In this context it is interesting, that Wurr (1980) found a relation between the sprout growth (total sprout length and sprout number) of a tuber and the node of origin of the tuber.

The causes of the large variation in tuber size within one plant are still largely unknown. The variation seems to be partly determined already before tuberization by stolon characteristics and by the position of the tuber on the stolon, but differences in tuber size are also partly explained by differences in rate of tuber growth (Struik et al., 1991). The larger tubers are more likely to be found at the tip of main stolons on the lower or intermediate parts of the below-ground stem part. Generally, these stolons are initiated relatively early and they are long. Marschner et al. (1984) found that rapidly growing tubers have a low abscisic acid (ABA) and a high indol acetic acid concentration. For young tubers, Krauss (1981) found very weak negative and positive correlations between the growth rate of the tubers and the concentrations of ABA and gibberellic acid (GA), respectively.

Burton (1963) suggested that heavier tubers might have a shorter dormancy because an inhibitor produced by the foliage may be more diluted in large tubers.

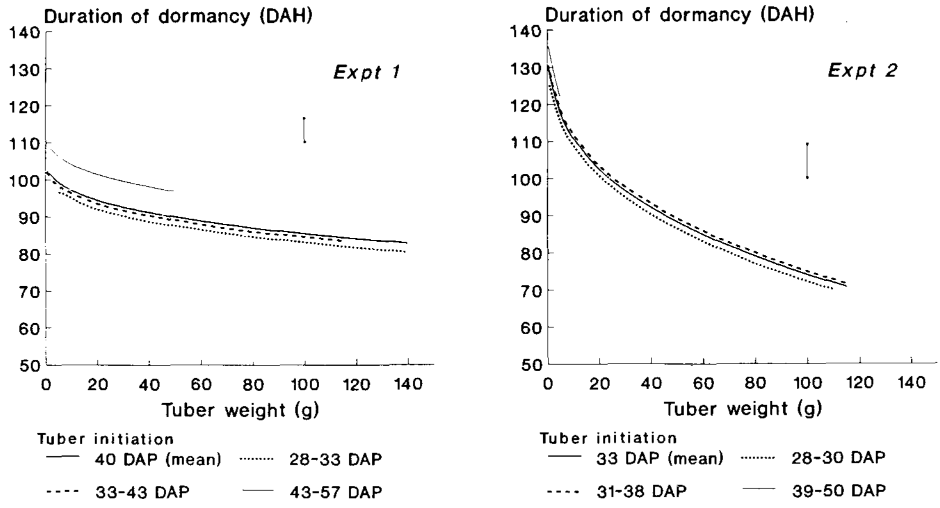

Fig. 1. The relation between the duration of dormancy (DAH = days after haulm cutting) and tuber weight for the mean date of tuber initiation and different classes of the date of initiation, as estimated by a model with only the variables tuber weight and date of tuber initiation. The vertical bars represent the square root of the residual mean square of this model.

Dormancy is believed to be related to a high ratio between growth inhibiting (ABA) and growth stimulating (e.g. GA) substances (Bielińska-Czarnecka & Białek, 1972; Białek & Bielińska-Czarnecka, 1975; van der Plas, 1987). Therefore, it is unlikely that the dilution of one factor explains the relation between dormancy and tuber weight.

The above mentioned correlations between tuber growth rate and hormone concentrations (assuming that initially rapidly growing tubers are the heaviest tubers at harvest) and between tuber dormancy and hormone concentrations suggest a physiological basis for the relation between tuber weight and tuber dormancy which is consistent with the results in our experiments with cv. Diamant. However, not all cultivars show a clear relation between dormancy and tuber weight (van Ittersum, 1992). More research is necessary on the relation between growth substance activity, tuber growth rate and the duration of dormancy for *different cultivars*, to find possible physiological explanations for the interaction between cultivars and the relation between dormancy and tuber weight.

The practical consequences of the relation between dormancy and tuber weight are obvious and important. The variation in duration of tuber dormancy, and in emergence after planting of very young tubers, can be reduced easily, by using seed with a limited range in weight.

Conclusions

For cv. Diamant:
1) the duration of dormancy is closely related to tuber weight, even for tubers initiated at the same date and grown at the same position on the plant;
2) later initiated tubers end their dormancy later than ones earlier initiated, although these differences in dormancy are small for tubers of similar weight;
3) dormancy is also related slightly to the position of the tuber on the plant.

Acknowledgements

We thank Ir A. J. G. Engels, Ir G. J. Molema and Ing. S. van Doorn for their substantial share in carrying out the experiments and Dr Ing. K. Scholte for his advices during the experiments. We are also much indebted to Drs J. H. Oude Voshaar for his valuable advice on the statistical analysis.

Appendix

Comparison of the batches with tubers from plants with relatively few (0-4 per plant; Few) and many (≥5 per plant; Many) tubers removed in Expt 1

The duration of dormancy did not differ between the batches 'Few' and 'Many' (Table I). Mean tuber weight and (naturally) its variance was higher for batch 'Many'. The number of tubers per plant became too high (to carry out the observations properly) particularly for plants with a large spread in date of tuber initiation and consequently, tubers were removed especially for these plants. Therefore, the batch 'Few' showed a much lower variation in dates of tuber initiation than batch 'Many'. The tuber batches hardly differed in the other stolon and tuber characteristics.

The correlations between dormancy and the regressor variables did not contradict each other for the two batches (Table I).

The final models for the duration of dormancy (D) were:

Few tubers removed

$$D = 146 - 3.3TW^{0.33} + 6.2TP - 2.2SL + 0.11SL^2 - 42.1TS + 11.4TS^2 \quad (1)$$

$$R^2_{adj} = 44.2\ \%$$

Many tubers removed

$$D = 156 - 4.9TW^{0.33} - 1.65TI + 0.024TI^2 + 3.6TP - 0.94SL + 0.032SL^2 - 20.3TS + 5.0TS^2 \quad (2)$$

$$R^2_{adj} = 56.2\ \%$$

Table I. Mean and variance (in parentheses) of all variables, and the correlation coefficients between the duration of dormancy and the regressor variables for the batches with tubers from plants with relatively few (= Few; n = 131) and many (= Many; n = 129) tubers removed and for the entire tuber lot (Few + Many; n = 260). Expt 1.

Variable	Tuber batch		
	Few	Many	Few + Many
Mean (and variance) of important variables			
D (duration of dormancy; DAH[a])	95 (65)	94 (68)	95 (67)
TW (tuber weight; g)	25 (394)	30 (548)	27 (474)
TI (tuber initiation; DAP[b])	40 (15)	39 (39)	40 (27)
TS (tuber shape; cm cm^{-1})	1.5 (0.09)	1.5 (0.10)	1.5 (0.10)
TP (tuber position[c])	0.44	0.47	0.46
SL (stolon length; cm)	7.7 (18)	7.0 (18)	7.3 (18)
SP (stolon position; cm)	3.0 (4)	3.1 (7)	3.1 (5)
Correlation coefficients with duration of dormancy			
TW (tuber weight)	−0.42***	−0.58***	−0.51***
TI (tuber initiation)	0.32***	0.52***	0.44***
TS (tuber shape)	−0.34***	−0.46***	−0.38***
TP (tuber position)	0.48***	0.37***	0.37***
SL (stolon length)	0.29***	0.10	0.20**
SP (stolon position)	−0.10	0.00	−0.04

[a]DAH = days after haulm cutting. [b]DAP = days after planting. [c]Tubers on main stolons: TP = 0; tubers on stolon branches: TP = 1. **and*** indicate statistically significant at $P < 0.01$ and $P < 0.001$, respectively.

Batch Few + Many

$$D = 145 - 4.2TW^{0.33} - 0.93TI + 0.016TI^2 + 4.7TP - 1.7SL + 0.076SL^2 - 24.8TS + 6.4TS^2 \quad (3)$$

$$R^2_{adj} = 49.4\ \%$$

Since the spread in date of tuber initiation was very low in batch 'Few', the regression coefficients of the variable tuber initiation were non-significant for the final model of this tuber batch. The final percentage of variance accounted for was higher for batch 'Many', probably because the spread of the most important regressor variable (tuber weight) was larger in this batch. Further, the models of the two tuber batches were essentially similar (differences in the other regression coefficients are mainly caused by the presence or absence of the variable tuber initiation).

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