Dormancy and growth vigour of seed potatoes

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Dormancy and growth vigour of seed potatoes

Proefschrift

ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen,
op gezag van de rector magnificus,
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STELLINGEN

1. Door een gewasbespuiting met gibberellinezuur en een aan het ras aangepast bewaartemperatuurregime kan de kiemrust van aardappelpootgoed aanzienlijk worden verkort en kunnen tegelijkertijd de verschillen in kiemrustduur tussen rassen teruggebracht worden van enige maanden tot enkele weken.
   -Dit proefschrift.

2. Onder Nederlandse omstandigheden heeft de temperatuur tijdens de knolgroei nauwelijks effect op de kiemrustduur van aardappelpootgoed; wel belangrijk is de temperatuur vanaf de loofdoding.
   -Dit proefschrift.

3. Bij aardappelknollen verschilt de optimumtemperatuur voor spruitgroei van de temperaturen die gunstig zijn voor opheffing van kiemrust. Dit feit is in het verleden ten onrechte vaak verwaarloosd bij de opzet en interpretatie van onderzoek naar het effect van bewaartemperatuur op kiemrust.
   -Dit proefschrift.

4. Opheffing van kiemrust en fysiologische veroudering van aardappelknollen zijn deels verschillende processen, waardoor behandelingen die de kiemrust het sterkst bekorten niet noodzakelijkerwijs behoeven te leiden tot de meest gevorderde fysiologische leeftijd en daarmee de grootste groeikracht bij het poten snel na de oogst.
   -Dit proefschrift.

5. Verkorting van de kiemrust via een gewasbespuiting met gibberellinezuur en aangepaste bewaartemperatuurregimes ten gunste van vroege export van Nederlands aardappelpootgoed zal tot logistieke aanpassingen bij de teelt, opslag, keuring en vervoer moeten leiden.

6. De positieve invloed van perioden met een hoge instraling en lage nachttemperatuur in het najaar op het suikergehalte (op basis van het versgewicht) van suikerbieten moet vooral toegeschreven worden aan een verlaging van het watergehalte van de bieten en niet aan een toename van de hoeveelheid suiker per biet.

7. Uit het oogpunt van ammoniakvervluchtiging en nitraatuitspoeling in beweid grasland is een onbemest gras/klavermengsel niet milieuvriendelijker dan een met behulp van kunstmest even produktief grassenbestand zonder klaver.

8. Na de relatief grote aandacht voor opbrengstverhoging in het consumptie-aardappelonderzoek voor de (sub)tropen, dient de aandacht nu verlegd te worden naar post-harvest onderzoek.

9. Een toegepast onderwijselement statistiek, deels in plaats van en deels bovenop het huidige onderwijsaanbod van de vakgroep Wiskunde, is onontbeerlijk voor een goede opleiding van landbouwkundige onderzoekers.

10. De aanstelling van assistenten in opleiding met behulp van externe financiële middelen is op termijn niet in het belang van de assistenten in opleiding, de onderzoeksinstellingen en de geldschieters.

11. Het is niet reëel om verdere economische groei te verdedigen met het argument dat de extra vrijkomende middelen mogelijkheden scheppen voor de financiering van milieuverbeterende maatregelen.

12. Het verdient overweging om ten gunste van het lange-termijnbeleid de perioden tussen verkiezingen tenminste te verdubbelen.

13. Een vermeend tekort aan tijd is een zeer belangrijke oorzaak van milieuvervuiling.

14. Het begin- en eindsignaal van een sportwedstrijd, in het bijzonder een voetbalwedstrijd, markeren een periode met een markante norm- en gedragsverandering van mensen.

15. De hedendaagse akkerbouwer is niet van gisteren en zal er alles aan doen geen verleden tijd te worden; hij verdient daarbij wel een beleid met duidelijke toekomstperspectieven.

Proefschrift M.K. van Ittersum
Dormancy and growth vigour of seed potatoes
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ABSTRACT

Ittersum, M.K. van, 1992. Dormancy and growth vigour of seed potatoes. Doctoral thesis, Wageningen Agricultural University, Wageningen, the Netherlands, X + 187 pp., English and Dutch summaries.

Dormancy is an important property of seed potatoes. Seed tubers planted too soon after their harvest do not produce plants because of dormancy, or produce low yields because of poor growth vigour. Potato tubers from the same cultivar vary in their duration of dormancy. The first aim of the research reported in this thesis was to predict the end of seed tuber dormancy, and to explain the variation in the duration of dormancy. The second aim was to investigate ways of curtailing the dormancy and of advancing the growth vigour of seed tubers. Tubers harvested when immature were used in the study.

After haulm pulling, the length of the axis and the number of leaf primordia of the tuber buds did not change during dormancy, and therefore these characteristics cannot be used to quantify dormancy. The longer tubers had been kept in storage, the stronger their sprouting response to a dormancy-breaking treatment with a growth-stimulating substance. This indicates that the intensity of dormancy is not constant during the dormancy period. It is concluded that this response might be used to predict the end of dormancy, but more research is necessary to develop such an application.

The variation in duration of dormancy within a seed tuber lot depended on the cultivar and was large. In cv. Diamant, this variation was found to be related to variation in tuber weight, date of tuber initiation and the position of the tuber on the plant during its growth. The effect of growth conditions such as nitrogen, temperature, light intensity and photoperiod on dormancy of progeny tubers was minor, but the effect of storage conditions immediately after the harvest was major.

Dormancy was greatly shortened by a foliar spray with gibberellic acid applied shortly before haulm killing, and by storage regimes with low temperatures (2 °C) and even much more so by those with high temperatures (28 °C). The growth vigour of the tubers was greatly advanced by both a foliar spray with gibberellic acid and by storage at 28 °C. The effects varied from a single week up to several (>3) months depending on the duration of dormancy of the cultivar, whether one or both treatments were used, and on whether a storage regime with a low or high temperature was opted for. The treatments offer very good prospects for improving the performance of seed potatoes that have to be planted soon after harvest.

Keywords: ageing, 6-benzylaminopurine, bud, cultivar, daylength, dormancy, gibberellic acid, growth vigour, heat sprouting, irradiance, light intensity, nitrate, nitrogen, photoperiod, physiological age, potato, primordium, rest, second growth, seed potato, seed tuber, shading, *Solanum tuberosum* L., sprout growth, sprouting, stolon, storage, temperature, tuber initiation, tuber weight

Reference to the contents of Sections 2.1 and 4.2 and of Chapters 3 and 5 should be made by citing the original publications.

WOORD VOORAF

De fysiologische veroudering van aardappelpootgoed heeft reeds lang internationaal de aandacht van onderzoekers. In Nederland is sinds het einde van de jaren zeventig in het kader van de werkgroep "Groeivermogen van pootaardappelen", onder voorzitterschap van dr. ir. D.E. van der Zaag, opnieuw veel onderzoek verricht omtrent dit onderwerp. Op de vakgroep Landbouwplantenteelt en graslandkunde (LUW) deden dr. ing. K. Scholte en prof. ir. L.J.P. Kupers onderzoek naar de fysiologische veroudering van aardappelpootgoed onder invloed van verschillende temperatuur- en lichtregimes en naar een toets ter karakterisering van de verouderingssnelheid van de diverse aardappelrassen. Het onderzoek was vooral gericht op bewaarperioden zoals die gebruikelijk zijn onder Nederlandse omstandigheden. In 1987 formuleerde Scholte een projectvoorstel waarin de kiemrust en de groeikracht van aardappelpootgoed na kortere bewaarperioden centraal stonden. Dit resulteerde in het onderzoek zoals beschreven in dit proefschrift. De eerste proefplannen en resultaten van het project werden uitgebreid besproken in de eerder genoemde werkgroep, die echter in 1989 zijn activiteiten beëindigde.

Een proefschrift is niet het werk van één of enkele personen, maar dat van een heel team. Graag wil ik een ieder die op enigerlei wijze heeft bijgedragen aan het totstandkomen van dit proefschrift van harte bedanken! Een aantal mensen wil ik in het bijzonder noemen.

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Mijn promotor prof. dr.ir. P.C. Struik dank ik hartelijk voor zijn bijzonder stimulerende houding en voor het feit dat hij immer bereid was een gaatje te maken in zijn volle agenda. Ik kan me niet herinneren dat ik ooit langer dan één weekend heb moeten wachten op een gefundeerde reactie op mijn manuscripten. Paul, het is voor mij een eer bij jou te mogen promoveren.

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Vele studenten en stagiair(e)s hebben meegewerkt aan het onderzoek. Zij maakten het niet alleen mogelijk om ongeveer 4.000 monsters à 30 knollen veelvuldig te controleren op kieming, maar vooral ook droegen zij bij aan discussies en aan plezier in het werk. Frank Aben, Jan Willem Berendsen, Wim Bos, Abco de Buck, Tonnie Engels, Allard Jukema, Geert-Jan Molema, Zeger van Oudheusden, Wim Stegeman, Jeen Sijtsma Poll, Marco Theunis en Cor de Vrieze

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I would like to express my deep gratitude to Mr Shimon Warshavsky from the Experiments Department of Hevel Ma'on Enterprises, Negev in Israel, for making it possible to lay out two experiments in the Negev, which were of great value to the project. I also thank Mr M. Maharshak for his skilful help and the people of the kibbutz Ze'elim for taking care of the experiments, sometimes under very difficult circumstances (January 1991!). Shimon and Gigi, thanks a lot for your hospitality and friendship!

Mevr. J. Burrough-Boenisch corrigeerde op nauwgezette en leerzame wijze de Engelse tekst van een aantal hoofdstukken.

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Vier jaar onderzoek aan één facetje van de aardappel gaven mij sòms het gevoel dat de knollen mij uitlachten, sòms het gevoel er iets van te begrijpen en váák: wat zit ook een aardappel wonderlijk en ingewikkeld in elkaar!

Martin

NOTE

Most of the papers included in this thesis are in press or have been accepted by Potato Research, American Potato Journal or Netherlands Journal of Agricultural Science. As presented in this thesis they differ from the original papers in the following ways:

1. the 'keywords' of the individual papers have been combined into one list at the end of the 'Abstract';

2. the acknowledgements are given in the 'Woord vooraf';

3. the 'References' of the individual papers, the general introduction and the general discussion have been combined into one list;

4. in Sections 4.2.1 and 4.2.3, the terms 'working hypothesis' and 'general discussion' have been added;

5. in Sections 5.2 and 5.4, Fig. 1 and Fig. 3 have been added;

6. some very minor changes were made to standardize presentation.

I thank the editorial boards of Potato Research, American Potato Journal and Netherlands Journal of Agricultural Science for their kind permission to include the papers in this thesis.

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The potato crop and its propagation

The potato (*Solanum tuberosum* L.) originates from the Andes in South America, from where it was introduced into Europe in ca 1570. Nowadays, the potato is grown in more than 70 % of all countries, which means in more countries than any other food crop except maize. The total area cropped to potato is ca 18 million ha per year (FAO, 1990). During the last decades, world potato production has been gradually shifting from the industrialized to the developing countries and from the temperate to the tropical and subtropical countries (FAO, 1990; Horton & Anderson, 1992). After wheat, rice and maize, potato is the world's fourth important crop for human consumption in terms of annual production which amounts to about 280 million tonnes (FAO, 1991). Thus, the potato is the world's most important non-graminaceous crop and the most important crop with a perishable yield.

Generally, the potato is propagated vegetatively by means of tubers. A tuber is a greatly shortened and thickened stem that bears scale leaves with axillary buds. The physiological properties of a tuber change with time; this is reflected in a changing sprouting behaviour. Since the real time scale of changes in the sprouting behaviour differs between cultivars and is influenced by storage conditions, the term 'physiological age' of tubers is commonly used (Reust, 1986). The physiological age of a planted tuber is reflected in its growth vigour (Van der Zaag & Van Loon, 1987). The growth vigour of a seed tuber is defined as its potential to produce a well developed plant within a relatively short (and defined) period of time.

Potato tubers have a dormancy period during which they show no sprout growth and their growth vigour is zero. The growth vigour of the tubers increases initially upon termination of dormancy and levels out at a maximum. After some time the growth vigour gradually declines and ultimately this leads to the inability to produce new plants. The maximum level of growth vigour extends only over a limited period of time, which depends largely on the cultivar and the storage conditions.

The physiological age of the tuber also affects the growth pattern of the plant (Van der Zaag & Van Loon, 1987). Plants grown from physiologically older seed tubers may senesce earlier than plants grown from physiologically young seed tubers. When using young seed tubers, high yields can be obtained if the growing season is very long. Within normal ranges, physiologically older seed results in high tuber yields early in the season, but in relatively low yields late in the season. To achieve the highest tuber yields at the time the harvest is planned the seed tubers should be the correct age at planting.

Dormancy and its implications for seed potatoes

From an ecological point of view, the dormancy period of a tuber is advantageous to survive a period unfavourable for growth. From an agronomical point of view, tuber dormancy is

favourable when tubers have to be stored for a certain period of time before consumption or other use, but disadvantageous when seed tubers have to be planted soon after their harvest. The duration of dormancy depends on the genotype, but may also be influenced by the conditions during growth and during storage of the tubers. The timing of the end of dormancy together with storage conditions mainly determine the degree of sprout growth at planting. It is important to know the growth factors influencing dormancy of seed tubers and to be able to predict the duration of dormancy, in order to take the appropriate measures during storage. It would be a great help if dormancy could be measured long before it ends.

Non-dormant seed tubers with a high growth vigour are not always available at each planting time. Often, seed tubers must be planted soon after their harvest, for example in regions in the world where the potato is grown more than once per year and seed tubers from the last crop have to be used for the next crop, or when seed tubers are imported from other regions or countries relatively soon after their harvest.

Consider the situation in North Africa as an example. In many countries in North Africa, a spring potato crop is grown from January to early June and an autumn crop from September to December or January. In some coastal areas a winter crop is planted in November or December. Often the environmental conditions in these regions are unfavourable for storing potatoes and cool-storage facilities are scarce. Therefore, seed tubers from the last crop have to be used for the next crop. In addition to locally grown seed tubers, imported seed tubers from Europe are used for phyto-sanitary reasons. Generally, the spring crop is planted with imported seed tubers. The autumn crop is planted with seed tubers from the spring crop, and the winter crop with either imported seed tubers or seed tubers from the spring crop (Fahem & Haverkort, 1988). Locally grown tubers from the spring crop are still rather young (about 3 months) when planting of the autumn crop starts. The Netherlands is the world's largest exporter of seed potatoes (in 1990-91 about 680,000 tonnes were exported). In the Netherlands, seed tubers are usually harvested in August and, consequently, seed tubers to be exported to North Africa for the winter crop (and for some cultivars even for the spring crop) are physiologically very young and their field performance may be suboptimal. Moreover, in many tropical or subtropical countries attempts are being made to replace part of the imported seed tubers by locally produced seed tubers. Shortening dormancy and advancing the growth vigour of the tubers could improve the performance of both local and imported seed tubers, which have to be planted soon after their harvest.

The research programme

The first aims of the research reported in this thesis were to predict the end of dormancy in seed tubers, and to explain the variation in their duration of dormancy. Many plant physiologists have investigated the phenomenon of dormancy and the processes involved. However, the biochemical and physiological backgrounds of dormancy are still poorly understood (Coleman, 1987; Burton,

1989; Burton et al., 1992). The objectives of this study were not to explore the regulation of dormancy, but to quantify its properties and responses to environmental factors. Morphological changes in tuber buds were measured during dormancy and initial sprout growth, and it was attempted to quantify dormancy by measuring the response to a dormancy-breaking method. This is described in Chapter 2. The variation in the duration of dormancy between tubers within a plant or within a seed tuber lot was quantified. The relation between several stolon and tuber characteristics and the duration of dormancy of the tuber was investigated to account for the variation in duration of dormancy within a seed lot (this is described in Chapter 3). The effects of conditions during growth of the tubers were investigated to explain the differences in duration of dormancy between tuber lots (Chapter 4).

The other aims of the research programme were to examine possible ways of curtailing dormancy and of advancing the growth vigour of seed tubers. Several techniques were investigated with cultivars differing in duration of dormancy (Chapter 5). Emphasis was put on measures that are safe, since the few chemicals that are known to be effective in breaking dormancy (Rindite and carbon disulphide) are very poisonous and dangerous to use. Attempts were made not only to curtail dormancy, but also to advance the growth vigour, since the growth vigour of the tubers may still be poor immediately after the end of dormancy.

Tubers harvested while immature, as is usual in the Netherlands when growing seed potatoes, were used in the research.

CHAPTER 2

MORPHOLOGICAL AND PHYSIOLOGICAL CHANGES DURING DORMANCY

SECTION 2.1

MORPHOLOGICAL CHANGES IN TUBER BUDS DURING DORMANCY AND INITIAL SPROUT GROWTH OF SEED POTATOES

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Summary

Potato tuber dormancy is usually defined as lasting from tuber initiation until a sprout of 2 mm long has been formed under storage conditions optimal for sprouting. We tried to find out whether there is a period during which buds of seed tubers do not grow and whether different batches of seed take the same time to grow sprouts 2 mm long.

We measured changes in number of leaf primordia and length of tuber buds of cvs Diamant and Désirée over two years. After early haulm pulling, buds did not grow for at least 60 days ('Diamant') or 95 days ('Désirée').

Buds in both cultivars and two tuber weights of 'Diamant' took about 20 days from the estimated onset of sprouting to grow 2 mm long. We question whether this period is always similar and thus whether the moment sprouts 2 mm long have formed is a good criterion for the end of dormancy.

Introduction

The accepted definition of dormancy of a potato tuber is the physiological state of the tuber in which sprout growth will not occur, even when the tuber is kept in conditions ideal for sprout growth (darkness, 15-20 °C and a high relative humidity) (Reust, 1986). Burton (1963) proposed measuring the duration of dormancy from the date of tuber initiation, that is when the stolon tip starts to swell. Dormancy is deemed to have ended when the buds on the tuber, which has been stored from harvest onwards under conditions optimal for sprouting, are seen to be sprouting. This definition of the dormancy period has various physiological and methodological implications.

Some researchers (e.g. Coleman, 1987; Burton, 1989) query whether there is a period without bud growth. Rosa (1928) and Davidson (1958) contended that the tuber apical bud is growing

slowly at the moment when the (mature) tuber is harvested and that there is no period without growth. Sadler (1961) agreed that there is no real dormancy period after harvest; she concluded that dormancy was the period during which the buds increased in length until they become visible to the naked eye. However, Goodwin (1966, 1967a) found no sustained growth during dormancy; he reported that occasionally an apical bud suddenly grew 0.1 to 0.2 mm and then stopped, and he suggested that when a group of buds displays this behaviour, their mean length gives the impression of continuous growth. Krijthe (1962a) found that the number of leaf primordia on the buds of tubers harvested when immature did not increase until the end of dormancy.

Burton (1968) stated that whether or not there is growth, the concept of dormancy has a real practical value, because there may be large differences between different tuber samples in the moment at which sprout growth becomes visible. The criterion for the end of dormancy is a tuber showing at least one sprout of a given length; this length varies between less than 1 mm and 3 mm (EAPR definition, Reust, 1986), depending on the researcher, but 2 mm is common. Clearly, if there is no growth during dormancy, then the duration of dormancy and the rate of initial sprout growth are both important when using 'a tuber showing at least one sprout of 2 mm' as the criterion for the end of dormancy. This criterion is suitable only if the time needed to produce a sprout of a certain length, after the period of no growth has ended, is similar for different treatments.

We used destructive measurements to investigate whether there is a period without bud growth, either during tuber growth or after immature-harvest, on seed tubers of two cultivars known to differ in duration of dormancy. In addition, we measured the initial sprout growth non-destructively in these two cultivars (in two tuber weights in one cultivar) in order to evaluate the appropriateness of the 2 mm criterion.

Materials and methods

Destructive measurements on apical and lateral tuber buds

Plant material. In 1989 and 1990, tubers of cvs Diamant (short dormancy) and Désirée (long dormancy) were grown on a trial field near Wageningen. Details are listed in Table 1 (Tuber Sets 1 and 2). The haulms were pulled when the tubers were still immature, at a time depending on tuber size and aphid pressure (in agreement with the dates specified by the General Netherlands Inspection Service for Agricultural Seeds and Seed Potatoes - NAK Nederland).

After final harvest, healthy tubers with a narrow range in weight (Table 1) were selected and stored in a dark controlled environment at 18 °C and 80 % RH. The duration of dormancy of these tubers was assessed by regular observations on 90 tubers of each cultivar. Dormancy of a seed lot was deemed to have ended when 80 % of the tubers had at least one sprout 2 mm long (Appendix).

Measurements. From 55 (1989) or 50 (1990) days after planting (DAP) until final harvest, several plants were harvested at regular intervals (about 2 weeks) and a sample comprising 10-15 of the largest tubers per harvest was fixed in a mixture containing 5 ml formaldehyde (37 %), 85 ml ethanol (96 %) and 10 ml acetic acid per 100 ml (FAA). For the first harvest, the mean tuber weights in the samples were 17 g (1989) or 4 g (1990) for cv. Diamant and 22 g (1989) or 10 g (1990) for cv. Désirée. After final harvest until the end of dormancy of the tubers in the controlled environment (i.e. 80 % showed one sprout of 2 mm), samples of 10-15 tubers were removed from that storage at regular intervals and were also fixed in FAA.

We weighed all fixed tubers and counted their eyes (excluding the apical eye). We defined an eye as a scale leaf (with an axillary bud) separated from the apical bud in such a way that it followed the curvature of the tuber rather than that of the apical bud. We were careful to count each scale leaf either as part of an eye or as a leaf of the apical bud. Subsequently, measurements were carried out on the apical bud and on the fourth lateral bud from the heel end. Tubers from the first harvest in the field were so small that the fourth lateral bud from the heel end was not measured. The scale leaves and leaf primordia were dissected and counted under a binocular microscope (maximum magnification 40x). Any swelling on the flank of the apex was taken to be a leaf primordium. The buds were then bisected longitudinally and the length of the axis (=stem) was measured as the distance between the tip of the apex and the base of the bud, i.e. the beginning of the tuber tissue (Fig. 1).

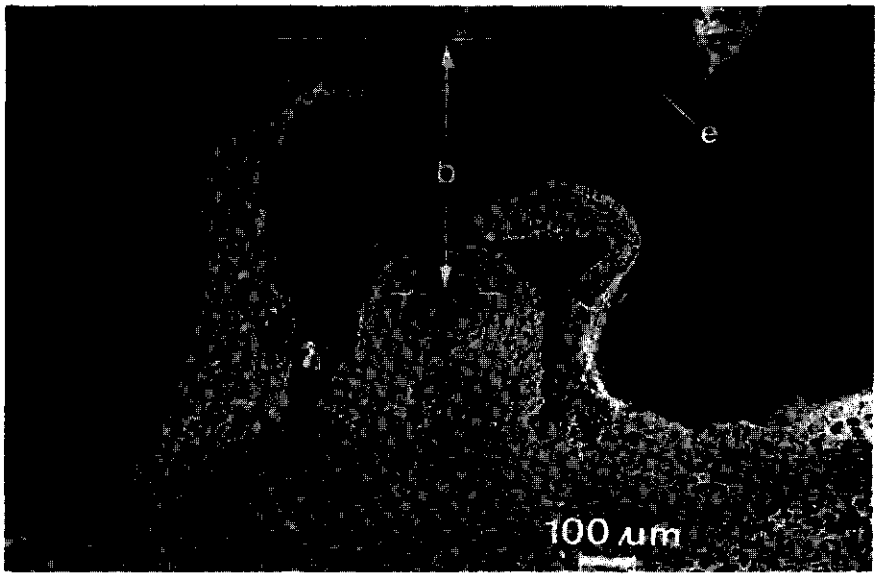

Fig. 1. Scanning electron micrograph of a longitudinal section of an apical bud (cv. Désirée - 66 days after haulm pulling). The vertical bar (a) denotes the length of the axis and bar (b) denotes the length of the rest of the bud. Part of the scale leaf of an eye is visible in the background (e).

Table 1. Details on the growth and weight of tubers used for the destructive and non-destructive measurements on initial sprout growth.

Descriptor	Measurements				
	Destructive		Non-destructive		
Tuber batch code	Set 1	Set 2	Set 3	Set 4	Set 5
Origin	Field	Field	Field	Greenhouse[a]	Greenhouse[a]
Planting date	20/4/89	23/4/90	23/4/90	5/7/90	1/12/90
Tuber initiation (DAP[b])					
cv. Diamant	48	42	42	30	36
cv. Désirée	38	38	38	26	-[c]
Haulm pulling (DAP)	81	77	77	70	74
Harvest (DAP)	102	92	92	81	90
Tuber weight in samples (g)					
cv. Diamant	45±10	40±15	25±5	25±5	25±5
			80±10	80±10	80±10
cv. Désirée	75±15	65±20	80±10	80±10	-[c]

[a]Conditions in the greenhouse: 18/12 °C - day 12 h/night. During the growth of Set 5, the daylight was augmented with artificial light (35 W/m²; 400-700 nm).
[b]DAP=days after planting.
[c]Not included in Set 5.

In practice, the lengths of *entire* buds (or sprouts) are observed when applying the '80 % and 2 mm criterion' to intact tubers. Therefore, in 1990 a second series of buds was examined by scanning electron microscope, to find out what part of the entire bud consisted of the axis. A number (5-10) of apical eyes of tubers of similar weight as those used for the light microscopy measurements were fixed in 2 % (v/v) glutaraldehyde at frequent intervals during storage until the beginning of sprouting. After dehydration in an ethanol series (10-30-50-70-90-96-100 %) and critical point drying under CO_2, the buds could be sectioned with a razor blade (Cresti et al., 1986) without deforming them. The sectioned buds were sputtered with palladium/gold, measured, and photographed in a Jeol JSM-5200 scanning electron microscope. The lengths of the entire buds and of their axes were measured. The length of the entire bud was defined as the distance between the tip of the longest scale leaf of the bud and the beginning of the tuber tissue (Fig. 1).

Non-destructive measurements on initial sprout growth

Plant material. These measurements were done on three sub-sets of tubers of cvs Diamant and Désirée (see Table 1 - Tuber Sets 3-5). For Tuber Sets 3-5 initial sprout growth was measured on 13 Diamant tubers of 25±5 g and another 13 of 80±10 g and for Tuber Sets 3 and 4 on 20 Désirée tubers of 80±10 g. The two tuber weights of cv. Diamant were used because dormancy of tubers of this cultivar is related to tuber weight, unlike that of cv. Désirée (Van Ittersum,

1992a). Only tubers with sound apical buds were selected for measurements.

After the end of dormancy, when storage has been under conditions ideal for sprouting, the apical bud is the first bud to show growth (Goodwin, 1967a).

Measurements. We measured initial sprout growth with a special set-up (Fig. 2) in a dark controlled environment at 18 °C and 80 % RH. Each selected tuber was put in a cup of dry sand, with its apical bud upwards. A brass bar with two vertical guiding holes was positioned horizontally above the cups. Through one of the two holes above each cup, a pin (weight: 0.07 g) was placed head down on top of the apical bud. In the second hole, 3 mm behind the first, a second pin with a vertically placed micrometer scale (divisions of 0.1 mm) was placed on the tuber tissue next to the apical bud. Twice a week, the position of the tip of the first pin was determined relative to the micrometer scale of the second, using a horizontally positioned binocu-

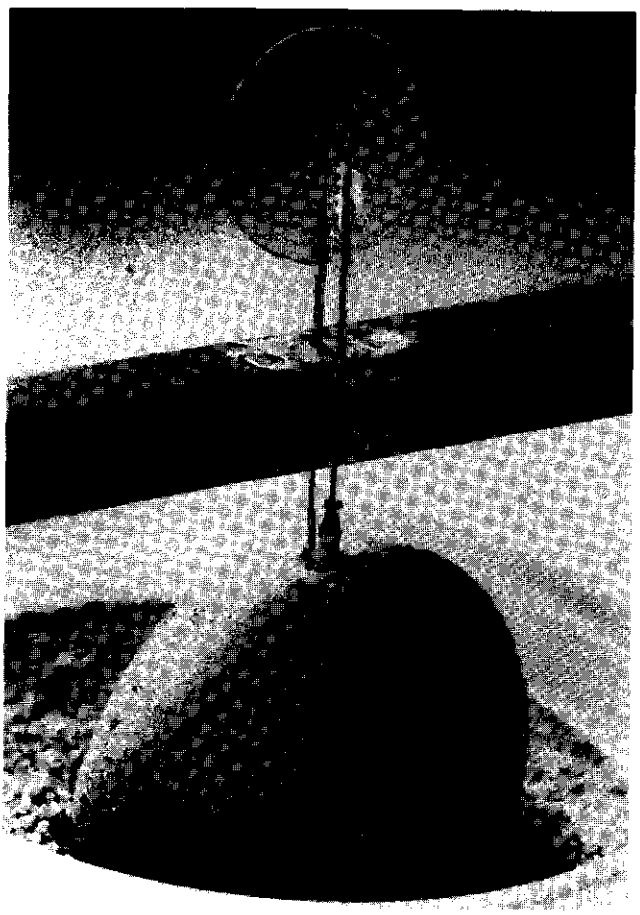

Fig. 2. The set-up for the non-destructive measurements on initial sprout growth. The front pin was placed on the apical bud and the rear pin, holding a micrometer scale, on the tuber tissue.

lar microscope. The measurements on a tuber were stopped when its sprout was about 4 mm long. Any swelling or shrinking of the tuber was accounted for, because the pin with the scale was positioned on the tuber tissue. Tubers were omitted from analysis if the sprout missed the head of the pin or if apical dominance was lost.

The start of sprouting was estimated retrospectively, as the last observation date before the first sprout growth of at least 0.1 mm was observed. The observation date before the one on which the first growth of 0.05 mm was recorded, was considered to be the start of sprouting only if it was followed by another increase in length of at least 0.05 mm at the next observation.

Results

Destructive measurements on apical and lateral tuber buds

The duration of dormancy (according to the '80 % and 2 mm criterion') of the batches of tubers in the controlled environments hardly differed between 1989 and 1990 (cv. Diamant: 100 and 103 days after haulm pulling=DAH; cv. Désirée: 149 and 145 DAH).

cv. Diamant. In 1989, there was no discernible trend in the mean length of the axis of the apical bud until ca 60 DAH (Fig. 3a). In 1990, before haulm pulling, the average length of the axis of the apical bud decreased in time slightly but significantly ($P<0.01$; Fig. 3b). From haulm pulling until ca 60 DAH, there was no change in the average length of the axis. The average length during this period of no change was 0.43 ± 0.22 mm (1989) or 0.28 ± 0.08 mm (1990). The larger mean and spread in 1989 were partly caused by one bud in the 42 DAH sample with an axis 1.2 mm long and one in the 57 DAH sample with an axis 1.7 mm long. After ca 60 DAH, the mean length and the range in length increased rapidly, especially in 1990. During the period from 0 to 57 (1989) or 66 (1990) DAH, there was no significant positive correlation within the tuber samples between the weight of an individual tuber and the length of its apical bud axis, but thereafter there was ($P<0.01$).

From 26 days before haulm pulling until haulm pulling, the average number of eyes per tuber increased significantly ($P<0.01$) from 7.2 to 9.1 in 1989 and from 5.7 to 9.4 in 1990. It was difficult to count the scale leaves or primordia per bud. Older tubers with growing buds often had some scale leaves broken off, or that were shrivelled up or damaged. Therefore, we may have underestimated the true number of primordia in older tubers. There appeared to be no clear trend in the number of leaf scales or primordia, until about 100 (1989) or 90 (1990) DAH (Fig. 3c,d).

There was no increase in the average length of the axis of the lateral bud, before and after haulm pulling until about 70 (1989) or 85 (1990) DAH (Fig. 3e,f). During these periods, the average lengths were 0.22 ± 0.05 mm (1989) and 0.24 ± 0.08 mm (1990). The number of leaf primordia of the lateral bud (not shown in Fig. 3) did not change until about 90 (1989) or 100 (1990) DAH.

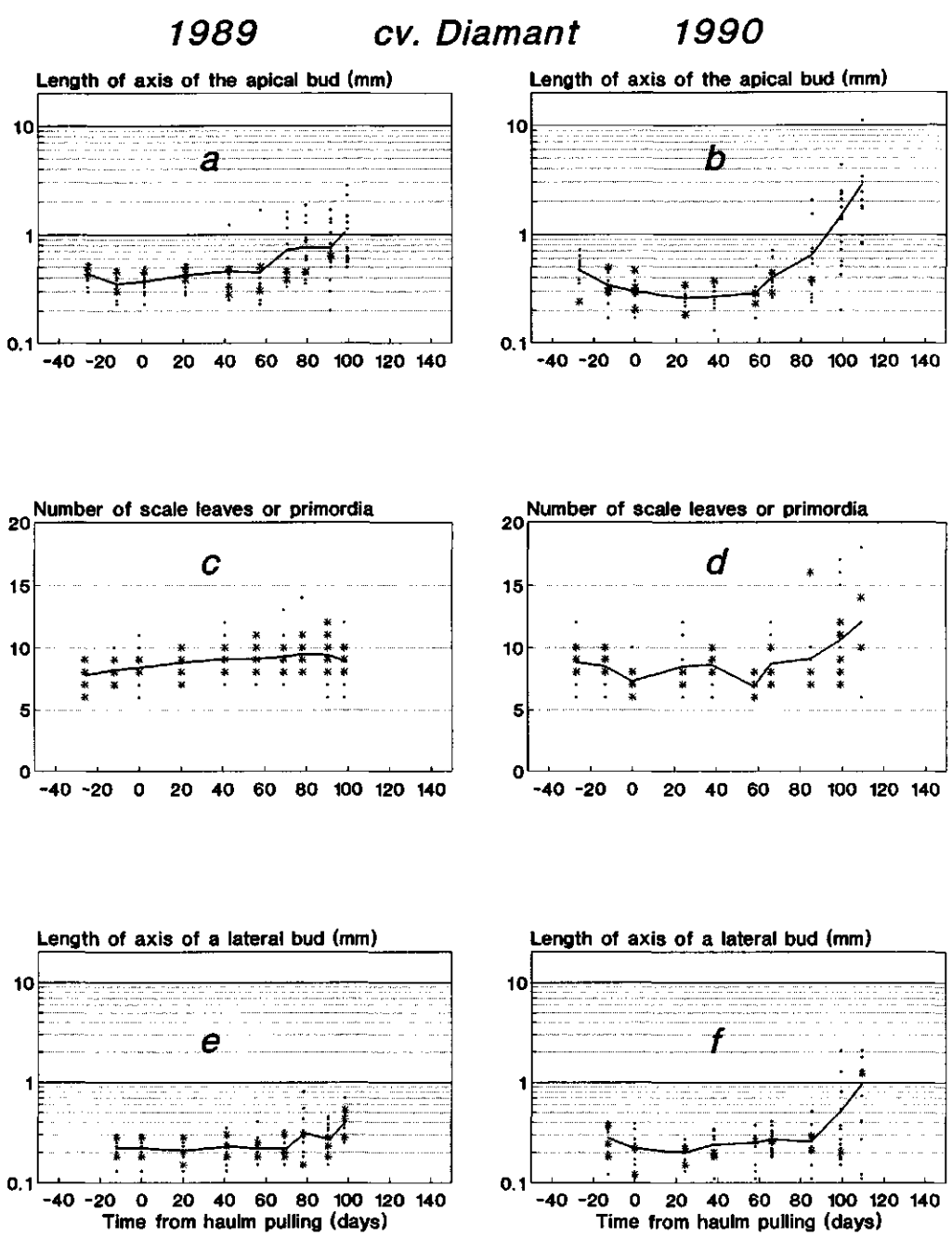

Fig. 3. The length of the axis of the apical bud (a and b), the number of scale leaves or primordia of the apical bud (c and d) and the length of the axis of the fourth lateral bud from the heel end (e and f) in time from haulm pulling (days). The lengths of the axes were plotted on a log-scale, in order to improve the visualization of possible small changes in length. Cv. Diamant - grown in 1989 (a,c,e) or 1990 (b,d,f); ·=one bud; *=two or more buds.

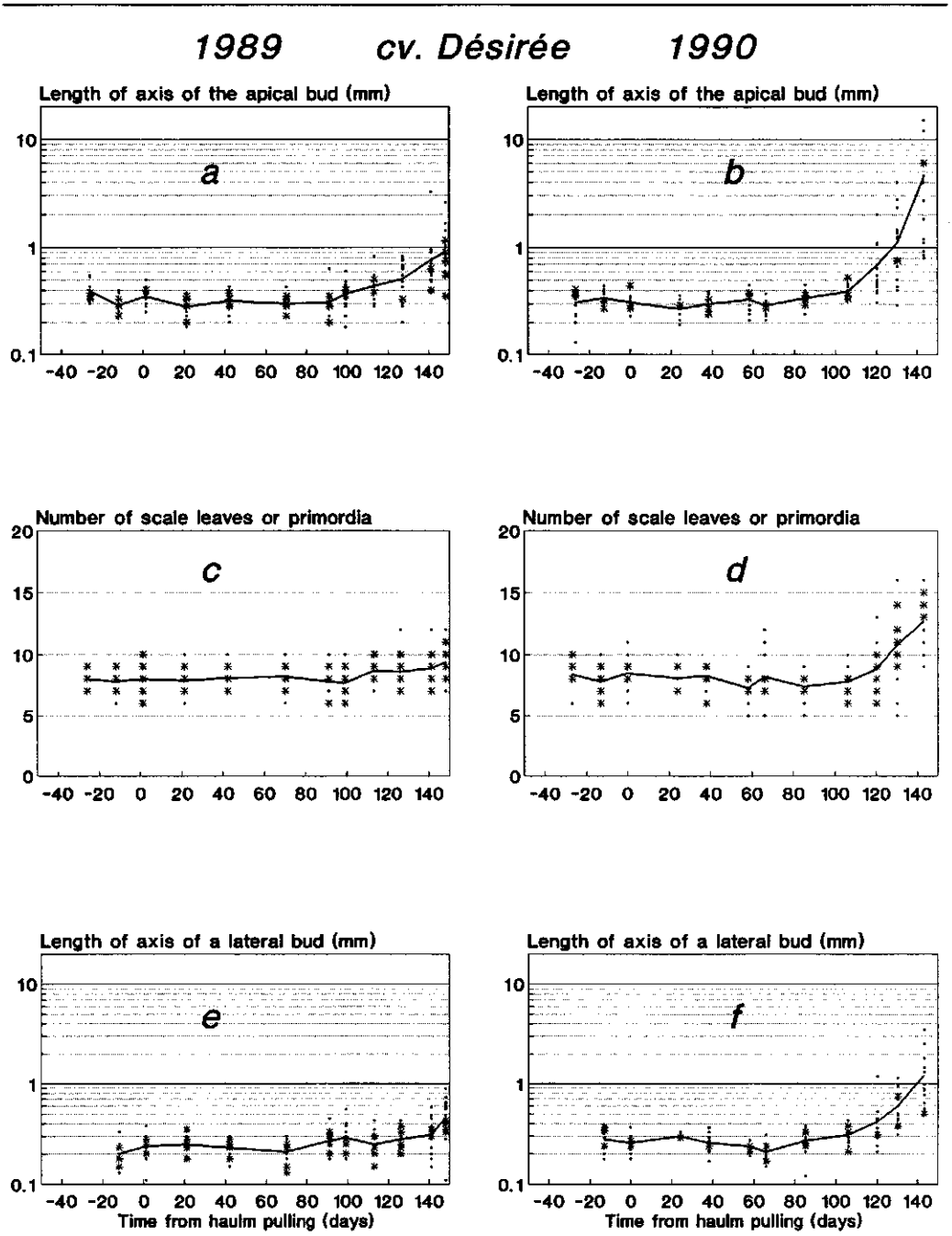

Fig. 4. The length of the axis of the apical bud (a and b), the number of scale leaves or primordia of the apical bud (c and d) and the length of the axis of the fourth lateral bud from the heel end (e and f) in time from haulm pulling (days). The lengths of the axes were plotted on a log-scale, in order to improve the visualization of possible small changes in length. Cv. Désirée - grown in 1989 (a,c,e) or 1990 (b,d,f); ·=one bud; *=two or more buds.

cv. Désirée. From before haulm pulling until about 95 (1989) or 100 (1990) DAH, there was no appreciable change in the average length of the axis of the apical bud (Fig. 4a,b). The mean length during this period was 0.32 ± 0.08 mm (1989) or 0.31 ± 0.07 mm (1990). After this period, the mean length and range in length increased rapidly. There was no significant positive correlation within the tuber samples between the weight of an individual tuber and the length of its apical bud, during the periods monitored.

Until haulm pulling, the average number of eyes per tuber increased significantly ($P < 0.01$) from 9.6 to 10.9 (1989) or 8.6 to 11.8 (1990). There was no increase in the mean number of scale leaves or primordia per apical bud until about 110 DAH (mean number = 8; Fig. 4c,d).

The average length of the axis of the lateral bud did not show a clear trend until about 120 (1989, mean 0.25 ± 0.07 mm) or 100 (1990, mean 0.26 ± 0.06 mm) DAH (Fig. 4e,f). The mean number of primordia of the lateral bud (not shown in Fig. 4) did not change until 140 (1989) or 120 (1990) DAH.

Length of the entire apical buds. There was no significant correlation, for either cultivar, between the length of the axis of the bud (or sprout) and the length of the rest of this bud, i.e. from the apex to the tip of the topmost emerging leaf (Fig. 1). In other words, the length of the part of the bud above the apex did not differ for different axis lengths (maximum axis length in the samples: about 3 mm). The average length of the part of the apical bud above the apex was 0.43 ± 0.13 mm in cv. Diamant and 0.46 ± 0.17 mm in cv. Désirée. Using the 1990 data, we estimated the mean length of the entire apical bud for the period without a discernible trend in the mean length as 0.28 mm (from tuber to apex) + 0.43 mm (above apex) = 0.71 mm, for cv. Diamant. For cv. Désirée, this mean length was $0.31 + 0.46 = 0.77$ mm.

Non-destructive measurements on initial sprout growth

The mean number of days (after haulm pulling) to the start of sprouting differed significantly between the two tuber weights of cv. Diamant (Table 2). For the Tuber Sets 3-5, the mean difference to the start of sprouting between the two weights was 17 days. Within the cultivar or size classes, tubers showed a rather large variation in the number of days to the start of sprouting (standard deviations in Table 2).

The time taken for the first few millimetres of sprout growth differed little between the two tuber weights of cv. Diamant and was statistically significant only for Tuber Set 4 (Table 3). Neither did the mean time taken for the first 2 mm of sprout growth differ between cvs Diamant and Désirée for tubers of the same weight. However, Désirée sprouts grew faster from 2 mm to 3 mm than Diamant sprouts.

Generally, the tubers that started sprouting first were also the first to reach a certain sprout length. However, in cv. Diamant there was a tendency for a negative correlation (not always significant) between the time taken for the first few millimetres of a tuber's sprout growth and the

Table 2. Estimated start of sprouting (days after haulm pulling), for two tuber weights of cv. Diamant and one tuber weight of cv. Désirée; Tuber Sets 3-5 (see Table 1).

Tuber Set	cv. Diamant		cv. Désirée
	Tuber weight 25 g	Tuber weight 80 g	Tuber weight 80 g
3	92±7.7	65±5.8***	119±7.5
4	66±7.4	56±2.0**	100±6.7
5	69±9.7	54±6.8**	-[a]
Mean	75	58	110

**, ***The difference in moment of start of sprouting between the two tuber weights of cv. Diamant was statistically significant at $P<0.01$ and $P<0.001$, respectively.
[a]Not carried out.

Table 3. Time lapse (days) between the estimated start of sprouting (see Table 2) and 1, 2 or 3 mm sprout growth, for two tuber weights of cv. Diamant and one tuber weight of cv. Désirée; Tuber Sets 3-5 (see Table 1).

Sprout growth (mm)	Tuber Set	cv. Diamant		cv. Désirée
		Tuber weight 25 g	Tuber weight 80 g	Tuber weight 80 g
1	3	15±3.4	17±7.0	18±6.0
	4	17±3.2	13±3.3**	15±5.8
	5	17±3.9	18±5.9	-[a]
	Mean	16	16	16
2	3	21±3.8	23±7.1	22±8.2
	4	22±4.4	17±3.3**	18±6.4
	5	24±6.0	23±6.8	-[a]
	Mean	22	21	20
3	3	25±4.8	28±7.3	23±9.0
	4	27±4.4	21±3.5**	19±6.5
	5	30±6.3	27±7.1	-[a]
	Mean	27	25	21

**The difference in time lapse between the two tuber weights of cv. Diamant was statistically significant at $P<0.01$.
[a]Not carried out.

moment it started to sprout.

Initial sprout growth in time (from the estimated start of sprouting until the sprout was about 4 mm long) for individual tubers was described well by exponential functions. The mean percentage of variance accounted for was 98 % (cv. Diamant) or 97 % (cv. Désirée). For some tubers, however, the function that gave a good fit for the period of initial growth was unrealistic beyond that period.

Discussion

Bud growth during tuber growth. Although the number of eyes per tuber increased until haulm pulling, the number of scale leaves and primordia in the apical bud did not decrease. This means that, until haulm pulling, the formation of leaf primordia by the apical bud keeps pace with the number of leaves of this bud that differentiate into an eye (= leaf with axillary bud) on the tuber. This fully agrees with the findings of Krijthe (1946, 1962a) and Sadler (1961). The apical buds of very young tubers may appear to be slightly longer than those of older and larger tubers (Fig. 3b) because, in very small tubers, the apical bud has not yet sunk into the tuber (Sadler, 1961).

No conclusions about the growth of the lateral buds during tuber growth can be drawn from our measurements. Krijthe (1946) found a rather rapid increase in the number of leaf primordia of the first bud from the heel end until some weeks after tuber initiation. Sadler (1961) stated that lateral buds grew relatively rapidly soon after differentiation until they had attained about 10-12 primordia.

The period without bud growth. We described the changes in *average* lengths and numbers. Generally, the apical bud was the first to increase in mean length during storage. We propose calling the period after haulm pulling with no increase in mean length of the apical axis 'the period without bud growth' (comparable with the rest period; Reust, 1986), even though a few buds may have started to grow some time before the end of this period (Fig. 3a: at 42 and 57 DAH, one bud axis per sample was more than 1 mm long). After the period without bud growth, the increase in the averages was clearly caused by larger values in only some of the buds in the sample (Figs 3 and 4).

The period without bud growth was much longer in cv. Désirée (about 95 days) than in cv. Diamant (about 60 days). This means that most of the difference in duration of dormancy between the two cultivars according to the '80 % and 2 mm criterion' is attributable to the difference in the period without bud growth. Rosa (1928) and Davidson (1958) reported that there was no period without bud growth for tubers harvested mature. However, Rosa's evidence was based on only a few buds. Davidson (1958) measured the length of ten axes of apical buds of tubers harvested mature and stored at 4 °C and of tubers stored at 27 °C. From a regression analysis he concluded that the buds grew continuously after harvest. However, the buds of the tubers stored at

4 °C could not have done so. The buds of tubers stored at 27 °C may have grown continuously, but as Davidson analysed the means of ten tubers (and did not plot any individual lengths), the buds of some tubers may have grown while others did not.

The fact that we measured no growth of the buds does not mean that the buds are physiologically inactive. Macdonald & Osborne (1988) demonstrated that protein, RNA and DNA were continuously synthesized in dormant potato tuber buds in the absence of cell growth (storage temperature 22-25 °C).

The dormant buds in our experiments were similar in length to those on tubers harvested mature examined in other studies (Davidson, 1958; Sadler, 1961; Goodwin, 1967a,b). According to Sadler (1961), a tuber seems to reach its maximum number of eyes before it has reached its maximum size. Therefore, it seems likely that in tubers harvested mature there is also a period with no bud growth, and that this period begins before harvest if the differentiation of eyes stops.

The numbers of scale leaves plus primordia of the apical bud remained unchanged for a longer period than the length of the apical bud. The average number per bud during the dormancy period was about 8, which agrees with the number found by Kirk et al. (1985), but is less than the number found by others (8-13 primordia per bud; Krijthe, 1946; Sadler, 1961; Goodwin, 1967b). This discrepancy might be due to differences in the definition of an eye.

The (re)growth of the buds during storage. Our set-up for non-destructive measurements of sprout growth was satisfactory, although cv. Désirée sometimes caused problems because axillary buds of the apical bud also started to grow. The exact moment of onset of sprouting could not be determined with this set-up. The accuracy was 0.05-0.10 mm and the onset of bud growth may not have been observed if cavities occurred between the scale leaves (Fig. 1). Therefore, small increases in bud length before the estimated start of sprouting cannot be excluded.

Using the measurements made with the scanning electron microscope, we estimated the mean length of the entire apical bud to be 0.7-0.8 mm. Only part of this length is visible on intact tubers and therefore the buds have to grow about 1.5 mm until the sprout is visibly 2 mm long. The time needed for this growth hardly differed between the two tuber weights of cv. Diamant or between the two cultivars; it was about 20 days. Comparable measurements should be done for all kinds of treatments to confirm the validity of the 2 mm criterion as an indicator of the end of dormancy. We doubt whether the time taken to form a sprout 2 mm long is always about 20 days. For instance, storage temperature regimes with storage at 18 °C preceded by a short period of low (0-2 °C) or high (28 °C) temperature may result in a period different from 20 days (Van Ittersum & Scholte, 1992a). Moreover, the period will be longer than 20 days if sprouting takes place under conditions not optimum for sprout growth (e.g. temperatures below 15 °C, Burton, 1989). In these cases, the 2 mm criterion may still be convenient to apply, but it is questionable whether differences between treatments are caused by differences in dormancy and/or differences in rate of sprout growth.

The rate of sprout growth for cvs Diamant and Désirée was similar until the sprout was about 2 mm long. Thereafter, the sprouts on cv. Désirée grew appreciably faster. This underlines how critical it is to choose an appropriate sprout length for the criterion for the end of dormancy.

The clear difference in estimated start of sprouting between the two tuber weights of cv. Diamant suggests there is a real difference in the moment when their dormancy ends (cf. Van Ittersum, 1992a). This is contrary to Krijthe's (1962b) observations on cv. Bintje. She observed a similar moment of onset of sprouting, but found differences in rate of sprout growth: large (40-45 mm) tubers had grown sprouts 3 mm long several weeks earlier than had the smaller (28-35 mm) tubers.

Conclusions

1) During tuber growth, the formation of leaf primordia by the apical bud keeps pace with the number of leaves of this bud that differentiate into an eye on the tuber.
2) After haulms have been pulled at an immature stage of tuber development, both apical and lateral tuber buds have a period without growth. For apical buds, this period was at least 60 days for cv. Diamant and 95 days for cv. Désirée.
3) The difference in dormancy between cvs Diamant and Désirée according to the '80 % and 2 mm criterion' is mainly attributable to the difference in the period with no bud growth, since the time taken for an apical bud to grow from its initial length to a length of 2 mm was about 20 days for both cultivars.
4) This time lapse hardly differed between small (25 g) and large (80 g) tubers of cv. Diamant. However, the moment when sprouting started differed significantly between tuber weights.

Appendix

In this thesis, the duration of dormancy is expressed in days after haulm removal, except in Section 4.2. In this section, the duration of dormancy is expressed in days after tuber initiation, to allow comparison of the duration of dormancy of treatments with different dates of tuber initiation.

SECTION 2.2

CAN THE INTENSITY OF DORMANCY BE MEASURED WITH A BIO-ASSAY?

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Summary

It was investigated whether the 'intensity' of dormancy of seed potatoes could be measured with a bio-assay. In the assay, attempts were made to break dormancy by dipping lateral eye plugs in different concentrations of growth substances. Several cultivars were used and their intensity of dormancy was measured at various times.

The results indicated that the longer the tubers are stored, the easier it is to break dormancy. Generally, the cultivars with a shorter dormancy responded more strongly to the assay than cultivars with a long dormancy. However, the assay seemed to be very sensitive to external conditions, and thus some results were hard to interpret. If the variability in response to the treatments in the bio-assay is caused by variation in external conditions and if this variability can be reduced by better control of the environment, a bio-assay would be a promising method for assessing the intensity of dormancy and for estimating the duration of the remaining dormancy period of a certain cultivar.

Introduction

Dormancy is defined as the physiological state of the tuber in which autonomous sprout growth will not occur, even when the tuber is kept in conditions ideal for sprout growth (Reust, 1986). Burton (1963) suggested that dormancy starts at tuber initiation, when extension growth of the stolon tip ceases. Dormancy has ended when sprouts are formed from buds on the tuber during storage. During the dormancy of a seed tuber harvested while immature, no changes occur in simple morphological characteristics of the tuber buds (Van Ittersum et al., 1992). Nevertheless, various biochemical and physiological processes take place in the tuber and endogenous concentrations of substances change (Coleman, 1987; Van der Plas, 1987; Macdonald & Osborne, 1988; Burton et al., 1992). Consequently, it can be assumed that dormancy is not constant during the dormancy period.

Some reseachers mentioned that concentrations of sprout stimulators needed to break dormancy may differ between years (Bruinsma et al., 1967; Carls & Caesar, 1979), and that the response to

a sprout stimulator differs over time during growth and storage (Bruinsma & Swart, 1970; Turnbull & Hanke, 1985a). In literature the terms 'depth' and 'intensity' were used to indicate that differences in dormancy exist (Bruinsma & Swart, 1970; Sikka, 1982). In this chapter, the term 'intensity' will be used. It is both of scientific and practical interest if the intensity of dormancy were measurable: it would be possible to assess effects of growth or storage conditions on dormancy and the remaining duration of dormancy could be predicted. Subsequently, tubers could be stored or treated according to their intensity of dormancy and their planned date of planting.

Hypothetical scheme for the intensity of dormancy of seed tubers. As a working hypothesis, a hypothetical scheme was drafted for the development over time of the intensity of dormancy of seed tubers, harvested while immature (Fig. 1).

The first part of the scheme (dashed line) concerns the tuber attached to the mother plant. This part of the line is based on knowledge and ideas about the degree of induction to tuberize, the induction of second growth and the effect of the haulm killing date on the duration of dormancy. Moreover, Szalai (1959) found that the concentration of Rindite (a sprout-stimulating mixture of ethylene chlorhydrin, ethylene dichloride and carbon tetrachloride, 7:3:1 by volume, respectively) needed to break dormancy was lower at immature harvest than at mature harvest, and Bruinsma et al. (1967) stated that tubers harvested very early are often barely dormant when treated with gibberellic acid (GA). Turnbull & Hanke (1985a) found that during the first weeks after tuber ini-

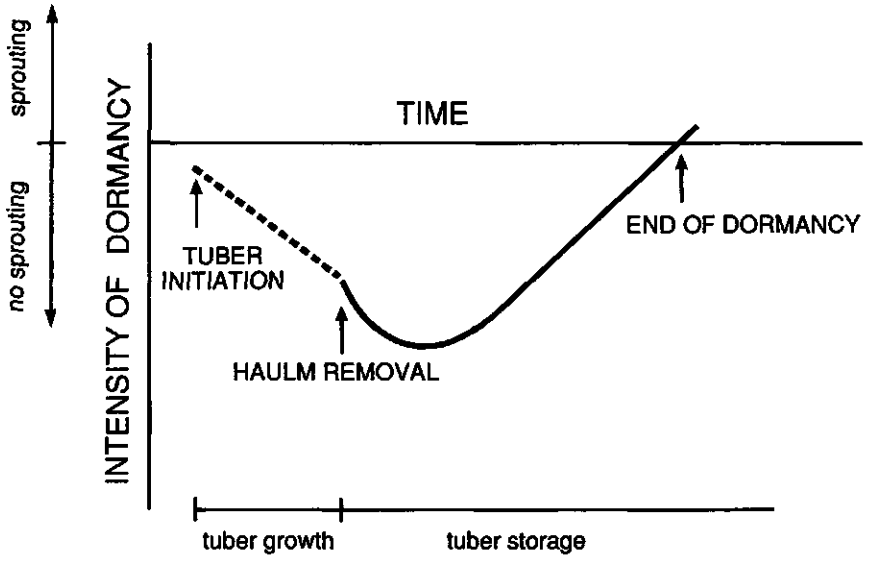

Fig. 1. Hypothetical scheme for the intensity of dormancy of seed tubers harvested while immature.

tiation, the tuber buds of cv. Majestic could be induced to grow out by supplying cytokinins (CK). Thereafter, the response to exogenous CK disappeared.

Haulm pulling results in removal of an important source of all kinds of substances for the tuber. This might lead to sudden biochemical and physiological changes in the tuber. Heat sprouts (sprouts grown from tuber buds prior to harvest due to high temperatures during tuber bulking) do not continue to grow when tubers are harvested (Van Ittersum & Scholte, 1992b). These arguments made me suppose that dormancy might intensify at haulm pulling. Bruinsma & Swart (1970) showed that the response to their dormancy-breaking method increased during the first weeks of storage of the tubers, although not in a regular way. During storage until dormancy release, endogenous concentrations of hormones that may be related to dormancy change gradually (Van der Plas, 1987).

Much about processes and endogenous substances regulating dormancy is still unknown. Therefore, the intensity of dormancy is poorly defined and cannot be measured directly. I tried to quantify dormancy by measuring the response to a dormancy-breaking treatment (cf. Bruinsma & Swart, 1970).

Measuring dormancy with a bio-assay. It was tried to break dormancy by dipping eye plugs in solutions that differed in concentration of growth substances. It was hypothesized that the less intensive dormancy was, the easier it would be to break it. In the bio-assay, eye plugs of tubers could only be measured while detached from the mother plant.

Dormancy was measured at different times during tuber growth and during storage in different cultivars. On the basis of some data, I will demonstrate that the results indicate that it becomes easier to break dormancy during storage, but that the assay was very sensitive to external conditions resulting in data that were hard to interpret.

Material and methods

Plant material. In 1989 and 1990, several cultivars (for 1989, see Table 1) were grown on an experimental field near Wageningen (52 °N lat.). The plant material for cvs Diamant and Désirée was identical to that used for the morphological measurements (Van Ittersum et al., 1992). Planting took place at 20 April 1989 or 23 April 1990 and tuber initiation started between 35-50 days after planting. Haulm pulling took place 81 (1989) or 77 (1990) days after planting and tubers were harvested 2-3 weeks later. Healthy 40-55 mm tubers were selected and stored in darkness at 18 °C and 80 % RH. The duration of dormancy of intact tubers was assessed on 90 tubers per cultivar. Dormancy of these tubers ended, by definition, when 80 % of the tubers showed at least one sprout 2 mm long.

Bio-assay. The following bio-assay was developed, based on preliminary experiments with eye

plugs, dipped in different concentrations of gibberellin A_3 or 6-benzylaminopurine (BAP) and the subsequent sprouting response during 21 days of incubation.

For each cultivar, at frequent intervals (see Fig. 2) samples of 25 tubers were taken from the field or from the storage chamber. Lateral eye plugs (diameter=2.5 cm) were taken with the fourth eye from the heel end of the tuber (Lallu & McWha (1976) showed that lateral and apical eye plugs of the same tubers responded similarly to plant growth regulators, whereas lateral eye plugs have the advantage that they contain just one eye). Each sample was dipped in one solution of a range of solutions of BAP (see legend Fig. 2). Subsequently, the eye plugs were put on humid quartz sand. The samples were placed in a dark controlled environment at 18 °C and 90 % RH for one week. The entire procedure was replicated twice. After the first replication, each solution was renewed. The two replications of one date will be called a run of the assay.

Three to four times a week the sprouted eye plugs were counted. The criterion for the end of dormancy was a sprout of about 1 mm. The percentage of sprouted eye plugs 7 days after the start of a run of the assay was considered as the dormancy-breaking action of a solution. From such values from successive runs, the date was deduced that a solution resulted for the first time in 80 % sprouted eye plugs in 7 days after the start of an assay run.

In 1989 (Expt 1), runs of the bio-assay were carried out only after haulm pulling. In 1990 (Expt 2) several runs were also conducted before haulm pulling by digging up plants, and runs were conducted more frequently shortly before and shortly after haulm pulling.

Examples of results and evaluation

Some data for cvs Diamant (short dormancy) and Désirée (long dormancy) are shown in Fig. 2. Figs 2a and 2b show that, generally, the later the start of a run of the assay, the higher the percentage of sprouting. The assay of 46 days after haulm pulling (DAH) showed a remarkable lack of response in both cultivars. This was probably (partly) due to a lower relative humidity (about 85 in stead of 90 %) in the controlled environment during the first days after the start of this run. There were more indications that the humidity is of crucial importance in the assay.

Table 1 was deduced from Figs 2a and 2b and similar figures for the other cultivars. For each solution the date was estimated (by interpolation) that 80 % sprouting was obtained for the first time (intersection between the response lines and the dotted 80 % line in Figs 2a and 2b; the data from 46 DAH were discarded: dashed lines). Table 1 shows that: 1) the later the starting date of an assay run, the lower the concentration of the solution necessary for 80 % response; 2) the shorter the duration of dormancy of intact tubers of a cultivar, the earlier eye plugs of a cultivar responded; cv. Draga was an exception in that it responded earlier than cv. Désirée, whereas dormancy of intact tubers of cv. Draga is longer.

Figs 2c and 2d illustrate that the results in 1990 were less clear than those in 1989. Besides the variable response in time, sometimes there also was a large spread between the two replications

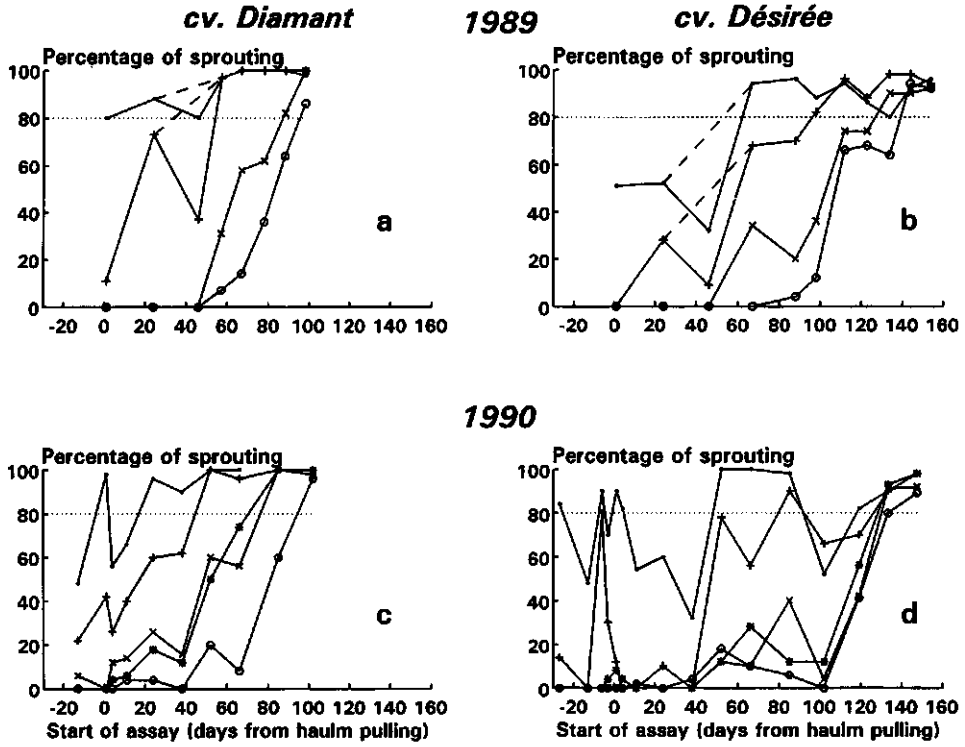

Fig. 2. The percentage of sprouted eye plugs 7 days after the start of the bio-assay runs with different solutions, for cv. Diamant 1989 (a), cv. Désirée 1989 (b), cv. Diamant 1990 (c) and cv. Désirée 1990 (d). The dashed lines in Figs a,b represent the estimated response when the data from the run of 46 days after haulm pulling were discarded. Dipping solutions: (·) 50 μM BAP for 60 min.; (+) 10 μM BAP for 60 min.; (*) 2 μM BAP for 60 min. (1990 only); (x) water for 60 min.; (o) undipped.

Table 1. Estimated date (days from haulm pulling) at which 80 % sprouting within 7 days after the start of a run was achieved in successive bio-assay runs with different solutions and for various cultivars. The last column shows the duration of dormancy (days after haulm pulling) of intact tubers; data from 1989.

Cultivar	Solution (μM)				Duration of dormancy of intact tubers
	50 BAP	10 BAP	Water	Undipped	
Diamant	1	34	87	95	100
Jaerla	1	78	101	101	130
Désirée	54	97	127	139	149
Draga	19	90	117	114	162
Average	19	75	108	112	135

within an assay run. It is impossible (especially for cv. Désirée) to deduce a table like Table 1 from these figures. It is not clear whether the high variation was due to the sensitivity of the assay to small differences in external conditions (e.g. humidity) or whether it had other causes.

For cv. Diamant, the response at 1 DAH was remarkably high (Fig. 2c), as was the response for cv. Désirée at 6 days before haulm removal (Fig. 2d). However, in the runs shortly before or after haulm pulling the buds of the sprouted eye plugs often did not continue to grow after they had reached a length of about 1-2 mm (cf. Madec & Perennec, 1969; Turnbull & Hanke, 1985a). In later runs of the assay, the sprouts showed continuous and more rapid sprout growth. Therefore, the length of the sprouts perhaps also gives an indication about the intensity of dormancy.

Thus, there are indications that a bio-assay can give an impression of the intensity of dormancy of a tuber batch, but it is also obvious that the assay should be improved. A good control of the humidity seems to be very important. Therefore, an improvement could be that eye plugs are also covered with humid sand instead of resting on a sand bed. Moreover, the appearance of a sprout of 1 mm does not suffice as a criterion for the response to the assay; the length of the sprout should also be taken into account.

Conclusions

1. The longer the tubers are stored, the easier it is to break dormancy.
2. Generally, the cultivars with a short dormancy responded more strongly to the assay than cultivars with a long dormancy.
3. The bio-assay seems to be very sensitive to small differences in external conditions. The relative humidity seems to be especially important. If this variation in external conditions can be reduced by better control of the environment, it would be worth assessing the intensity of dormancy as the response to the bio-assay. Besides the appearance of a sprout about 1 mm long, the continuation of the growth of the sprout should also be taken into account as one of the criteria for the response to the assay.

CHAPTER 3

VARIATION IN THE DURATION OF DORMANCY WITHIN A SEED TUBER LOT

SECTION 3.1

VARIATION IN THE DURATION OF TUBER DORMANCY WITHIN A SEED POTATO LOT

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Summary

The variation in duration of dormancy within a seed tuber lot was studied over three years by harvesting individual plants of cvs Diamant and Désirée from field plots and by storing the tubers at 18 °C. The variation in dormancy within a tuber lot was large (especially for cv. Diamant) and was mainly caused by variation within plants.

For cv. Diamant there was a close negative relation between dormancy and the cube root of tuber weight, whereas for cv. Désirée a relation with tuber weight was almost absent.

The duration of dormancy of a seed lot comprising tubers with a narrow range in weight can be well described by two parameters. It is proposed to maintain the moment of 80 % sprouting as the criterion for the end of dormancy of a tuber lot and to characterize the spread in dormancy duration by the time lapse between 10 % and 90 % sprouting.

Introduction

Dormancy of tubers of potato (*Solanum tuberosum* L.) varies among genotypes. Within a genotype, the duration of dormancy may vary between tuber lots of different origin or year. It may also vary within a seed lot of one cultivar from a particular origin and year. This latter variation is of both scientific and practical interest, but there are hardly any data on it. Emilsson (1949) reported that the range in duration of dormancy of individual tubers (50-90 g) within a sample of ten tubers could vary from 1 to 8 weeks in extreme cases. Krijthe (1962c) found that the variation within a tuber sample was larger for small tubers than for larger tubers. The time lapse between 50 % and 90 % sprouting at 15-20 °C was about 15-20 days for cv. Bintje (40-45 mm).

One of the causes of variation in dormancy within a seed lot may be difference in tuber size. Emilsson (1949) and Krijthe (1962b,c) found that the duration of dormancy of 40-50 mm tubers was about 4 weeks shorter than that of 28-35 mm tubers. Reust (1982) also found that large tubers usually had a shorter dormancy than small tubers, but that with some cultivars or sources the

difference in dormancy between the tuber sizes was not significant.

The EAPR definition for the end of the dormancy period of a tuber lot is the moment when 80 % of the tubers have formed sprouts (Reust, 1986). This characterization of the duration of dormancy is rather incomplete. For a better characterization, more information is necessary on the probability distribution of the duration of dormancy of individual tubers.

In this paper, the variation in duration of dormancy within a seed tuber lot is analysed for two cultivars differing in length of dormancy by quantifying the variation between and within plants. The relation between the duration of dormancy and tuber weight is described, and a way of characterizing the duration of dormancy of a tuber sample is proposed.

Materials and methods

Three experiments (abbreviated to Expts 1-3) were carried out on sandy soils near Wageningen (52 °N lat.) during the years 1988-90. Individual plants of cvs Diamant (short dormancy period) and Désirée (long dormancy period) were harvested. Presprouted basic-seed was used; in Expt 1, 80 g tubers with multiple sprouts were planted, whereas in Expts 2 and 3 small (25 or 20 g) and single-sprouted tubers were used. Before haulm removal, the number of stems per plant was recorded. The haulms were removed (by cutting or pulling) at a time depending on aphid pressure and tuber size. Care was taken to collect all tubers of an individual plant. Detailed information is summarized in Table 1.

After harvest, each tuber was weighed and then stored in a dark chamber at 18 °C and 80 % RH to assess the duration of dormancy. Dormancy was defined as having ended when a tuber had at least one sprout 2 mm long. The number of sprouted tubers was counted at least three times a week. The duration of dormancy of a tuber was defined as the period between haulm removal and the end of dormancy (for further definitions and details on the way of storage, see Van Ittersum, 1992b).

For each experiment and cultivar, all tubers of all harvested plants were considered to be one tuber lot. Possible differences in the duration of dormancy between plants within the lots were tested statistically by means of an analysis of variance with plant (on which a tuber grew) as a random factor (analysis of components of variance; Snedecor & Cochran, 1980). The relation between the duration of dormancy and tuber weight was analysed by means of regression analysis. The proportion of variance accounted for by the model is given by the adjusted R^2 statistic (Snedecor & Cochran, 1980) based on mean squares: R^2_{adj} = 100 x [1 - (Residual mean square/Total mean square)].

The frequency distribution of the duration of dormancy of tubers with a narrow range in weight was tested for skewness by calculating the coefficients of skewness (Snedecor & Cochran, 1980) for many tuber samples of cvs Diamant and Désirée. These samples consisted of seven weight classes (0-5, 5-20, 20-40, 40-60, 60-80, 80-100 and 100-120 g) of tubers from Expts 1-3. More-

Table 1. Details of the experiments with individually harvested plants.

Descriptor	Expt 1	Expt 2	Expt 3
Year	1988	1989	1990
Seed tuber weight (g)	80	25	20
Planting date	April 18	April 20	April 19
Plant spacing (cm)	25x75	25x75	18x75
Nitrogen application (kg N/ha)	140	175	150
Number of stems per m^2			
cv. Diamant	18.5	5.3	7.4
cv. Désirée	11.9	5.3	7.4
Tuber initiation (DAP[a])			
cv. Diamant	45	48	46
cv. Désirée	39	38	34
Haulm removal (DAP)	93	93	78
Harvest (DAP)	115	107	99
Number of harvested plants per cultivar	26	30	33
Total number of tubers per lot			
cv. Diamant	324	194	198
cv. Désirée	244	140	206
Standard deviation tuber weight within tuber lot (g)			
cv. Diamant	40	49	43
cv. Désirée	49	65	47
Mean duration of dormancy (DAH[a])			
cv. Diamant	80	72	110
cv. Désirée	139	130	156

[a]DAP=days after planting; DAH=days after haulm removal.

over, analyses were carried out on 100 samples comprising 30 healthy and undamaged tubers of 50-90 g each, stored at 18 °C and grown on field plots in 1989 (haulm pulling and harvest: 91 and 111 days after planting, respectively). Consequently, the cumulative percentage with time of sprouted tubers of each of the samples was analysed with a probit regression analysis. It is not possible to give a measure (mean scaled deviance; McCullagh & Nelder, 1989) for the goodness-of-fit of these analyses since the data of a sample concerning the cumulative number of sprouted tubers with time were not mutually independent. Therefore, the goodness-of-fit was assessed by eye.

The statistical analyses were performed with Genstat 5, Release 2.1 (Genstat 5 Committee, 1987).

Results and discussion

Variation between and within plants

The variance of the duration of dormancy within the three tuber lots of cv. Diamant amounted to 239-485 days² (Table 2). This variance can be split into two components: the variance between plants and the variance within plants. The latter was the most important one: 86 % or more of the variation within a lot was accounted for by the variation within plants. Nevertheless, the variation caused by differences between plants was statistically significant for cv. Diamant in all experiments. The range in duration of dormancy within a single plant was 38-51 days on average in the three experiments. There was no clear relation between the variation in duration of dormancy and the mean duration of dormancy of a tuber lot.

For cv. Désirée, the variance of the duration of dormancy within a tuber lot amounted to 82-104 days², which was much less than that of cv. Diamant. Again, more than 84 % of this variation was accounted for by the variation within plants. The variation between plants was statistically significant only in Expt 1. The range in duration of dormancy within a single plant amounted to 19-24 days on average in the three experiments.

These results imply that the variation in duration of dormancy within a tuber lot is large, but cultivar dependent. Most of the variation within a lot is caused by variation within a plant and much less by differences between plants.

Table 2. Variation in the duration of dormancy within a tuber lot of individually harvested plants; Expts 1-3.

Parameters on duration of dormancy	Expt 1		Expt 2		Expt 3	
cv. Diamant						
Total variance within a tuber lot (days²)	239	**	485	**	313	**
Component of variance between plants (days²)	14		71		40	
Component of variance within plants (days²)	225		418		276	
Variation in tuber lot accounted for by plants (%)	6		14		12	
Average range within a single plant (days)	47		51		38	
cv. Désirée						
Total variance within a tuber lot (days²)	82	***	97		104	
Component of variance between plants (days²)	13		10		3	
Component of variance within plants (days²)	69		88		101	
Variation in tuber lot accounted for by plants (%)	16		9		3	
Average range within a single plant (days)	24		19		21	

, * Indicate that the component of variance between plants differs statistically from zero at $P<0.01$ and $P<0.001$, respectively.

Relation to tuber weight

For cv. Diamant, tuber weight and duration of dormancy were closely related (Fig. 1). The heavier the tubers the shorter the dormancy. The relation was not linear, since for small tubers dormancy was shortened more with increasing tuber weight than it was for larger tubers. Of all simple terms of tuber weight, the cube root gave the best relation to the duration of dormancy for all experiments (Table 3). The percentage of variance accounted for by these models varied from 39 to 72 %. The difference in mean duration of dormancy between small tubers of around 10 g and heavier tubers of around 150 g was about 37 days on average. The difference between two more practical weights for seed tubers, e.g. 50 g and 100 g, was about 11 days on average.

For cv. Diamant, the variation in individual tuber weights within the seed lot was lowest in Expt 1 and highest in Expt 2 (Table 1). In Expt 1, the stem density was much higher than in the other experiments (Table 1) because much heavier seed tubers with multiple sprouts were used. Consequently, the number of tubers per m^2 was also highest in Expt 1. MacKerron et al. (1988) showed that there is a negative correlation between the relative variability in individual tuber weight and the number of tubers per unit area. Because of the relation between dormancy and tuber weight for cv. Diamant, the variance in duration of dormancy within the seed lot was also lower in Expt 1 than in Expt 2 (Table 2).

For cv. Désirée, the duration of dormancy hardly changed with a change in tuber weight (Fig. 1), though the relation between both variables was significant because of the high numbers of tubers in the analyses. The percentage of variance accounted for by the models was only 7-15 %, and the relation also varied slightly between the experiments. In Expt 2, there was a significant trend for dormancy of the heaviest tubers to be slightly shorter than that of lighter tubers (R^2_{adj}=15 %), but in Expts 1 and 3, dormancy of very small tubers was sometimes even shorter than that of heavier tubers.

The relation between the duration of dormancy and tuber weight appears to be cultivar dependent. Several researchers have found that dormancy was shorter for large tubers than for smaller ones (Emilsson, 1949; Krijthe, 1962b; Abeygunawardena et al., 1964; Reust, 1982), but

Table 3. The relation between the duration of dormancy and tuber weight for cv. Diamant in three experiments (see also Fig. 1).

Experiment	Regression equation[a]	R^2_{adj} (%)	*F*-value[b]
cv. Diamant			
1	$D = 109 - 8.7TW^{0.33}$	39.2	209^{***}
2	$D = 127 - 14.0TW^{0.33}$	41.3	141^{***}
3	$D = 156 - 12.8TW^{0.33}$	72.0	504^{***}

[a]D=duration of dormancy (days after haulm removal); TW=tuber weight (g).
[b]*F*-value of regression.
***Indicates significance at $P<0.001$.

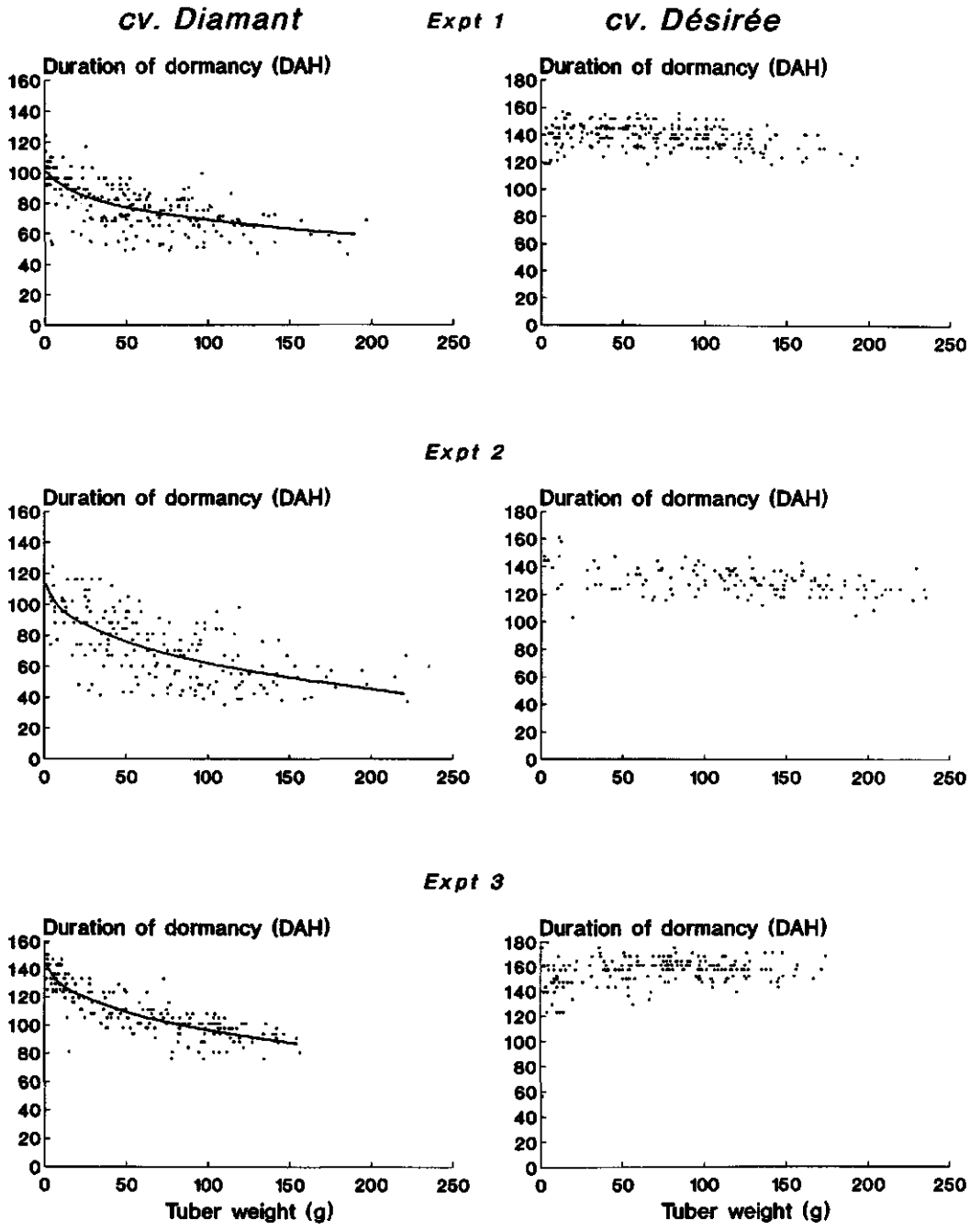

Fig. 1. Relation between the duration of dormancy (DAH=days after haulm removal) and tuber weight, for cvs Diamant and Désirée in Expts 1-3. Curves were fitted by means of regression analysis. For regression equations see Table 3.

they compared only two practical seed sizes (ca 40-50 vs 28-35 mm). Even for cv. Désirée, dormancy of large tubers tended to be shorter than that of small tubers in Expts 1 and 2 (Fig. 1). Lommen & Struik (1990) compared different weights of minitubers and also found a shorter dormancy for the heavier tubers. The current results and the data in the literature indicate that for most cultivars the duration of dormancy (expressed in days after haulm removal or harvest) decreases with increasing tuber weight, but the magnitude of the decrease is cultivar dependent and probably there are cultivars that show hardly any relation between dormancy and tuber weight.

Since dormancy is defined as ending when the tuber has formed a sprout of at least 2 mm long (or 3 mm by other researchers), differences in dormancy defined in this way may partly be differences in the rate of initial sprout growth. Krijthe (1962b) observed that small and larger tubers of cv. Bintje started their sprout growth at about the same time, but the rate of sprout growth of the larger tubers was higher, leading to differences of several weeks to the time when a sprout of 3 mm (her criterion for the end of dormancy) was formed. However, my results with cv. Diamant (Van Ittersum et al., 1992) did not support this observation. The rate of sprout growth up to 2 mm hardly differed between tubers of 25 g and tubers of 80 g, but the moment when sprouting started did differ. Therefore, it can be assumed that for cv. Diamant, dormancy (expressed in days after haulm removal) of heavy tubers ends earlier than that of lighter tubers.

The relation between the duration of dormancy (in days after haulm removal) and the cube root of tuber weight for cv. Diamant is descriptive and not necessarily causal. Tuber weight may be related to other tuber characteristics. For example, the smallest tubers may have been initiated later than larger tubers, although not necessarily so (Struik et al., 1991). Therefore, the relation between the duration of dormancy and tuber weight could be different when the duration of dormancy is expressed in days after tuber initiation of the individual tubers (not recorded in the current experiments). However, it is unlikely that differences in date of initiation were so large that the relation between dormancy and tuber weight would disappear (cf. Van Ittersum & Struik, 1992).

A high variation in duration of dormancy is relevant when tubers are planted soon after harvest, since it may cause an irregular emergence. Cv. Diamant showed a much larger variation in duration of dormancy within a tuber lot than did cv. Désirée. However, a large part of the variation of cv. Diamant is accounted for by tuber weight and this characteristic of tubers is very easy to select for.

Characterization of the duration of dormancy of a tuber lot

Since dormancy in cv. Diamant was closely related to the tuber weight, the frequency distribution of the duration of dormancy of individual tubers of a seed lot was highly dependent on its tuber-size distribution. Therefore, the frequency distribution was analysed only on tuber samples within a narrow range in weight.

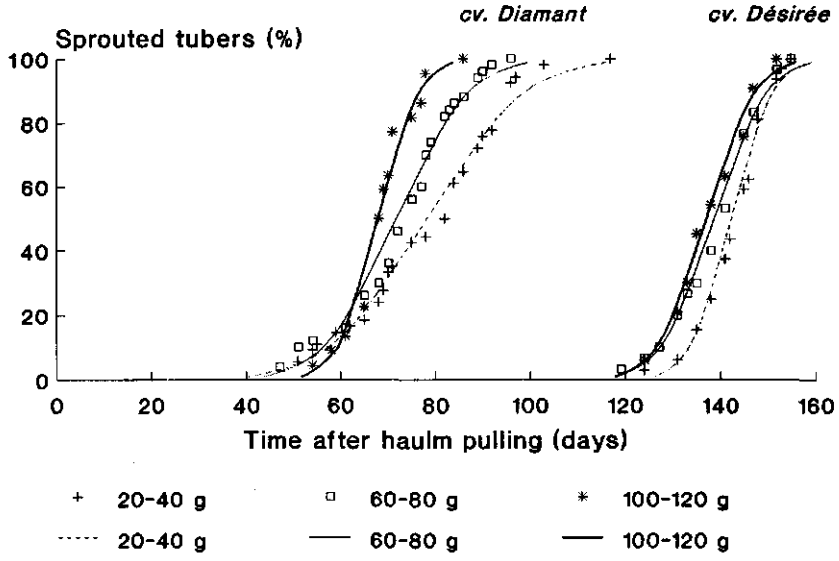

Fig. 2. The cumulative percentage of sprouted tubers in time for different tuber weight classes of cvs Diamant and Désirée in Expt 1. The curves were fitted by means of probit regression analysis.

For cv. Diamant, the coefficient of skewness was significant ($P<0.05$) only for the lowest weight classes (0-5 and 5-20 g) of Expt 1 and for the weight class 5-20 g of Expt 3. For cv. Désirée, the skewness was significant for the weight class 60-80 g of Expt 3. In all these cases, the skewness was negative and caused by one to three relatively early sprouting tubers.

The general absence of skewness in the frequency distribution of the duration of dormancy of individual tubers of a seed lot was confirmed in the analyses of samples of cvs Diamant and Désirée from the field plots of 1989.

The percentage of sprouted tubers in time was described well by a cumulative normal distribution for most of the samples, although the fit was poorer for those samples with a significant skewness. As an illustration, the data and the fitted probit curves for some weight classes of both cultivars in Expt 1 are given in Fig. 2. One of the causes of the (small) deviations from normality is that the ranges in weight of the classes/samples are still too large.

From the foregoing, it may be concluded that the duration of dormancy of a tuber lot is well characterized by only two parameters, the mean and the standard deviation. In case of a normal distribution, the mean equals the median and therefore the mean duration of dormancy equals the moment at which 50 % of the tubers has ended dormancy. The EAPR (Reust, 1986) defined the end of dormancy of a sample as the moment at which 80 % of the tubers has sprouted (which equals the mean duration of dormancy + 0.84σ, if the duration of dormancy of individual tubers is normally distributed). Instead of the standard deviation, the time lapse between 10 % and 90 %

sprouting (which equals 2.56σ, with a normal distribution) is proposed as a practical measure for the spread in duration of dormancy within a sample or lot. Thus dormancy of a tuber sample or lot can be characterized by its duration/end (EAPR definition: 80 % sprouting) and its spread (time lapse between 10 % and 90 % sprouting).

Several research-workers used probit analysis to estimate the moment of 80 % sprouting (e.g. Cho et al., 1983; Saunders & Hutchinson, 1984). This seems to be justified for many samples with a narrow range in weight, but there might be some systematic skewness or other deviations from normality for the frequency distribution of the duration of dormancy of tubers stored at fluctuating temperatures (e.g. with cold or hot pre-treatments) or treated with dormancy-breaking chemicals causing a final sprouting percentage lower than 100 % (data not shown). In these cases more than two parameters are necessary to account for attributes such as the skewness or the lower ultimate sprouting percentage. Brown & Mayer (1988a,b) discussed several models with one to four parameters describing the cumulative germination of non-dormant true seeds of *Aristida armata*. Their conclusion was that the Weibull function was the most suitable function for describing cumulative germination, because it provided a consistently close fit to the data, as it also did in cases with an asymmetric germination curve and for samples not achieving 100 % germination.

Conclusions

1. The duration of dormancy varies greatly within a seed tuber lot, but this variation is cultivar dependent.
2. Most of this variation is caused by variation in duration of dormancy within plants.
3. The relation between the duration of dormancy and tuber weight is cultivar dependent. For cv. Diamant, there was a good negative relation to the cube root of tuber weight, but for cv. Désirée a relation was not clear.
4. The duration of dormancy of a tuber lot can be described well by two parameters, provided that the tubers have a narrow range in weight.
5. The moment of 80 % sprouting can be maintained as a parameter to characterize the end of dormancy, although the moment of 50 % sprouting would be more logical. The time lapse between 10 and 90 % sprouting is proposed as a spread parameter for the duration of dormancy of a tuber lot.

SECTION 3.2

RELATION BETWEEN STOLON AND TUBER CHARACTERISTICS AND THE DURATION OF TUBER DORMANCY IN POTATO

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Summary

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 the duration of 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.

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, 1992a). 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, 1992a). For this cultivar, the observed relation between the duration of dormancy and tuber weight is in line with earlier research (e.g. Krijthe, 1962b). 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 glasshouses, 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 glasshouse 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.

Pre-sprouted 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 (a curing period at 15-20 °C for 1 month, storage at 4 °C for 6 months and a pre-sprouting period at 15 °C for 1½ month). After the roots had reached a length of about 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 about 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 about 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 (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 2 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 2 weeks before harvest. Temperature during the hardening period was 18 °C.

Observations. Tuber (Expt 1) or stolon and tuber (Expt 2) initiation were recorded about 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 % RH 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 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:

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

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):

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

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, 1992a);
- 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,

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])		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.

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 $days^2$).

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)		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

**, ***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).

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 both experiments. The correlations with the date of tuber initation 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 duration of dormancy of the tubers.

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).

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 R^2_{adj}'s of the models with linear interaction terms were slightly, but significantly, higher than those with only main terms. However, these models with 3-5 interaction terms are extremely complex and do not comprise variables other than those with only main terms. 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.

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

*, **, *** Indicate statistically significant at $P<0.05$, $P<0.01$ and $P<0.001$, respectively.

[a] Statistically significant at $P=0.07$.

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 the duration of 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 by 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:

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

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

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 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 (about 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 with 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, 1992a). 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 (about 50 %) than in Expt 2 (about 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, 1992a).

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 about 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 the date of tuber initiation were positively correlated (Table 2), partly because tuber weight showed a negative correlation with the date of tuber initiation (r=-0.28 ($P<0.001$; Expt 1) or -0.46 ($P<0.001$; Expt 2)). Differences in dormancy between tubers of similar weight and different dates of initiation were small, especially in Expt 2 (Fig. 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

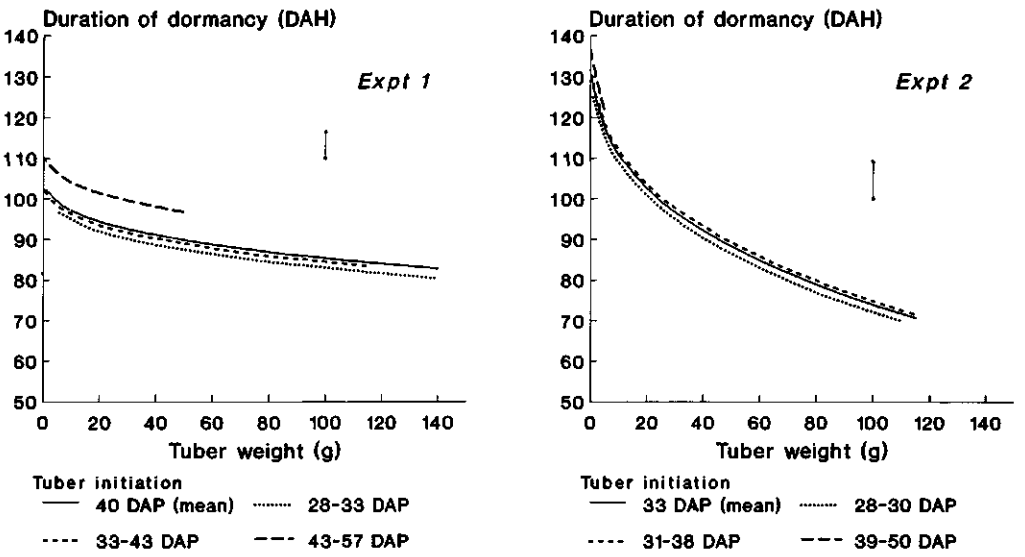

Fig. 1. The relation between the duration of dormancy (DAH = days after haulm cutting) and tuber weight for the mean date of tuber initiation and different classes of the date of initiation, as estimated by a model with only the variables tuber weight and date of tuber initiation. The vertical bars represent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

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. 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, 1992a). 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.

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, some tubers were removed. 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).

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.
, * Indicate statistically significant at $P<0.01$ and $P<0.001$, respectively.

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

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

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

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 not 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).

CHAPTER 4

VARIATION IN THE DURATION OF DORMANCY BETWEEN SEED TUBER LOTS

SECTION 4.1

4.1 QUANTIFICATION AND POSSIBLE SOURCES OF VARIATION IN DURATION OF DORMANCY BETWEEN SEED TUBER LOTS

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Introduction

The dormancy period primarily depends on the genotype but it may also be influenced by the growing conditions and cultural practices. In order to quantify the effects of these conditions and practices, the duration of dormancy of tuber lots, grown at different sites, seasons or years will be compared (literature and own results). After this quantification, possible sources of the variation in duration of dormancy are summarized.

Methodological problems. At least two methodological problems ought to be mentioned, before reviewing the literature. The first is the expression of the end of dormancy or the duration of dormancy: days after planting, days after tuber initiation, days after haulm killing, days after harvest or calendar date. When tuber lots from different years are compared, dormancy may end at different calendar dates (e.g. because of differences in planting dates and thus differences in dates of tuber initiation), whereas the duration of dormancy expressed in days after tuber initiation or days after haulm killing may not be different. Often information about the dates of tuber initiation is lacking. The second methodological problem is that the duration of dormancy was assessed at different storage temperatures in different studies. This may be a problem, since there is an interaction between the effects of growth conditions and storage temperatures on the duration of dormancy (see below).

Review of literature. Literature on the assessment of dormancy of a range of cultivars for several years is abundant. However, only a few cases are known in which differences in duration of dormancy between years were consistent for most of the cultivars examined (Wright & Whiteman, 1949; Krijthe, 1962b; Burton, 1963). During three consecutive years, Wright & Whiteman (1949) stored tubers of 35 cultivars at various temperatures. When stored at 21 °C, dormancy (in days after harvest) was about 10 days longer in 1947 than in 1945 and 1946. At lower storage temperatures the differences between years were larger.

Krijthe (1962b) also found consistent differences in the end of dormancy (in calendar date)

between years. Most cultivars sprouted about 9 weeks later in 1958 than in 1959. However, controlled storage started about 8 weeks later in 1958 than in 1959. In Krijthe's experiments, tubers were stored at 2 °C and transferred to 20 °C for sprouting. She defined the end of dormancy as the calendar date of that transfer to 20 °C that resulted in 80 % sprouting within 3 weeks. The difference in the start of controlled storage at 2 °C between both years as well as the low storage temperature itself, possibly resulting in cold pre-treatment effects on dormancy (Van Ittersum & Scholte, 1992a), may have affected her results.

Burton (1963) stored six cultivars at 10 °C during 5 years. He did not find large differences in the duration of dormancy (weeks after harvest) between most years, but in 1956 dormancy lasted at least one month longer for all cultivars.

Several studies indicate that differences in duration of dormancy between different years were not consistent for all cultivars, in other words there was an interaction between cultivar and year (Emilsson, 1949; Lindblom, 1970). Averaged over all cultivars, they found no differences between years, but for some cultivars the duration of dormancy differed up to 6 weeks between years.

Schippers (1956a) found a statistically significant interaction between year and storage temperature. When stored at 5 °C, averaged over 40 cultivars, dormancy (in calendar date) ended about 3.5 weeks later in 1954 than in 1953. When stored at 20 °C, the mean date of end of dormancy did not differ between the 2 years. However, in 1954 in some cultivars dormancy ended about 4 weeks earlier and in other cultivars about 4 weeks later than in 1953.

In Israel, Susnoschi (1981a) compared tuber lots produced in spring with lots produced in autumn. The duration of dormancy (weeks after harvest) of tubers from the autumn crop was about 13 weeks longer than of the spring crop when stored at 4 °C and 3 weeks longer when stored at 22 °C.

Some researchers compared dormancy of tubers grown in different regions. Emilsson (1949) compared tubers lots grown in different parts of Sweden. Although differences in planting date, temperature and latitude were fairly large, no large differences were observed in the duration of dormancy (weeks after harvest). Lindblom (1970) also did not find a consistent effect of site of production over several cultivars, but within cultivars location effects were up to 4 weeks.

Schippers (1955) compared tubers from crops grown in different regions of the Netherlands. For all crops seed of the same tuber lot was used and planted on the same date. Progeny tubers in the south of the country had ended dormancy (in calendar date) 2-3 weeks earlier than progeny tubers from the west or north of the country. The storage temperature was 20 °C.

Krijthe (1962c) stored tuber lots of cv. Bintje from different origins at various temperatures. In 1956, differences between origins were 4 weeks maximum at 16-20 °C, but at low storage temperatures (5 °C or lower) they were larger. In 1957, she observed that the difference between tuber lots of various origin was about 10 days at 20 °C.

Table 1. Details of the experiments with 19 cultivars at Swifterbant and Wageningen.

Descriptor	Swifterbant	Wageningen
Soil		
Soil type	marine clay	sand
Clay fraction (% < 2μm)	27	< 8
Organic matter (%)	3.4	4.0
pH(KCl)	7.5	4.7
$CaCO_3$-concentration (%)	10.9	1.5
1989		
Planting date	May 3	April 25
Tuber initiation (DAP[a])	32-45[b]	36-49[b]
Haulm pulling (DAP)	69-82[c]	70-86[c]
Harvest (DAP)	98	78-87[c]
Air temperatures during 1/6-1/8 (°C)		
Mean minimum	11.2	10.5
Mean maximum	21.3	21.9
Mean daily	16.4	16.7
1990		
Planting date	April 10	April 27
Tuber initation (DAP[a])	38-50[b]	31-43[b]
Haulm pulling (DAP)	72-87[c]	59-73[c]
Harvest (DAP)	93-101[c]	87-90[c]
Air temperatures during 1/6-1/8 (°C)		
Mean minimum	11.6	10.7
Mean maximum	20.0	20.3
Mean daily	15.8	15.8

[a]DAP=days after planting.
[b]The range of dates includes the range for the different cultivars.
[c]Haulm pulling and harvest took place per cultivar at a time depending on tuber size, aphid pressure and maturity class of the cultivar.

Own experiments. In 1989-90 the duration of tuber dormancy was determined for 19 cultivars grown at two locations, to quantify possible differences in dormancy between years and locations. The next sections describe the experiments and their results.

Materials and methods

In 1989 and 1990, 19 cultivars were grown in small plots at two sites, i.e. Swifterbant and Wageningen. In each year, pre-sprouted certified seed of the same origin was planted by hand at both sites. Some details of the sites and experiments are listed in Table 1. Nitrogen was applied at such rates that the total available amount of nitrogen in the soil was 110-150 kg N/ha at planting.

The usual cultural practices were carried out. The experiments in Wageningen were irrigated more often than those in Swifterbant. Temperatures and solar radiation were recorded at a meteorological station near each site. During June and July (=period after tuber initiation until harvest), the temperature differences between the different years and sites were very small (Table 1). Irradiance was slightly higher in 1989 than in 1990 and hardly differed between Swifterbant and Wageningen (data not shown).

Haulm pulling took place at a time depending on size of the tubers, aphid pressure and maturity class of the cultivar. After a hardening period of 2-3 weeks the tubers were harvested by hand. For each cultivar, two samples comprising 30 tubers with a limited range in weight were stored in a dark controlled environment at 18 °C and 80 % RH for assessing the duration of dormancy. It was not possible to take always tubers of the same weight class in the samples of each cultivar across years. In 1990, for some cultivars tubers in the samples of Wageningen were heavier than those in the samples of Swifterbant. By definition dormancy ended when 80 % of the tubers had at least one sprout 2 mm long.

Results and discussion

Experiments with 19 cultivars. The interaction year*origin*cultivar was statistically significant ($P < 0.001$) for the end of dormancy (calendar date). However, for nearly all cultivars dormancy ended significantly earlier for tubers from Swifterbant than from Wageningen and for all cultivars dormancy ended significantly earlier in 1990 than in 1989 (Table 2).

The interaction year*origin*cultivar was also statistically significant ($P < 0.001$) for the duration of dormancy (days after haulm pulling). Again, for all cultivars dormancy was shorter for tubers produced in Swifterbant than for tubers produced in Wageningen (Table 3). The mean difference in dormancy between the two sites was 16 days. For many cultivars dormancy was shorter in 1990 than in 1989, but for some cultivars the difference was not significant or dormancy was longer in 1990 than in 1989. Differences between the years in the duration of dormancy (days after haulm pulling) were much smaller than the differences in end of dormancy (calendar date), because in Swifterbant planting took place 23 days earlier in 1990 than in 1989 and in Wageningen the haulms were pulled earlier in 1990 than in 1989 (Table 1). Early planting and early haulm pulling, generally, result in an earlier end of dormancy (calendar date; see below).

It is unlikely that the differences in tuber weight between tubers from Swifterbant and Wageningen caused the difference in duration of dormancy between Swifterbant and Wageningen in 1990, since the tubers of the Wageningen samples were at least as heavy as those in the Swifterbant samples (cf. Van Ittersum, 1992a).

Tubers of some cultivars produced in Wageningen, especially cvs Bildtstar and Saturna in 1989, were severely infested with *Helminthosporium solani*. Sprout growth of these cultivars was probably inhibited by this infection.

Table 2. End of dormancy (calendar date) of 19 cultivars grown at Swifterbant and Wageningen in 1989 and 1990. The interaction year*origin*cultivar was statistically significant ($P<0.001$); LSD=4.6 ($P=0.05$).

Cultivar	Swifterbant		Wageningen	
	1989	1990	1989	1990
Eigenheimer	16/9	3/9	23/9	15/9
Procura	9/10	15/9	24/10	3/10
Saskia	30/9	8/9	3/10	15/9
Diamant	1/10	27/9	21/10	14/10
Sirtema	8/10	26/9	22/10	10/10
Sirco	1/11	3/10	9/11	22/10
Mansour	25/10	4/10	27/10	18/10
Saturna	2/11	16/10	2/12	14/11
Prevalent	3/11	17/10	13/11	4/11
Irene	7/11	20/10	16/11	11/11
Bintje	23/10	14/10	5/11	25/10
Vivaks	25/11	23/10	16/11	7/11
Morene	8/11	26/10	20/11	6/11
Bildtstar	31/10	24/10	8/12	14/11
Marfona	28/11	24/10	3/12	9/11
Astarte	28/11	5/11	1/12	26/11
Jaerla	12/11	22/10	25/11	5/11
Désirée	9/12	8/11	20/12	4/12
Draga	24/12	27/11	23/12	12/12
Mean	2/11	14/10	13/11	30/10
Mean (per origin)	Swifterbant: 24/10		Wageningen: 6/11	
Mean (per year)	1989: 8/11		1990: 22/10	

Possible factors causing variation in duration of dormancy. In addition to storage conditions the following factors may cause differences in the duration of dormancy or the end of dormancy between tuber lots (with similar individual tuber weights):

- planting date (Wurr, 1978; Cho et al., 1983; Gillison et al., 1987);
- pre-sprouting of the mother tubers (Holmes & Gray, 1972; Saunders, 1979; Saunders & Hutchinson, 1984);
- growing conditions, including fertilization (Section 4.2);
- date of haulm removal (Emilsson, 1949; Burton, 1963; Hutchinson, 1978a; Wurr, 1978; Cho et al., 1983; Gillison et al., 1987);
- duration of the hardening period in the field (Emilsson, 1949; Schippers, 1955; Hutchinson, 1978a);
- diseases (Burton, 1963).

Table 3. Duration of dormancy (days after haulm pulling) of 19 cultivars grown at Swifterbant and Wageningen in 1989 and 1990. The interaction year*origin*cultivar was statistically significant ($P<0.001$); LSD=4.6 ($P=0.05$).

Cultivar	Swifterbant		Wageningen	
	1989	1990	1989	1990
Eigenheimer	67	62	81	82
Procura	77	70	96	86
Saskia	81	74	91	82
Diamant	76	86	101	97
Sirtema	89	91	110	106
Sirco	113	98	128	119
Mansour	100	101	107	108
Saturna	108	101	143	128
Prevalent	102	102	116	118
Irene	113	105	127	125
Bintje	98	109	116	115
Morene	107	118	122	127
Vivaks	137	118	135	135
Bildtstar	106	119	149	128
Marfona	134	119	144	130
Astarte	127	121	134	140
Jaerla	124	122	144	133
Désirée	145	134	161	155
Draga	166	153	172	170
Mean	109	105	125	120
Mean (per origin)	Swifterbant: 107		Wageningen: 123	
Mean (per year)	1989: 117		1990: 113	

The planting date may have at least two possible consequences. Firstly, by shifting the whole growth cycle of the crop on the calendar and, secondly, by changing the circumstances under which the crop will grow (e.g. temperature and photoperiod). Pre-sprouting the seed will have partly the same effect as advancing the planting date. The effects of growing conditions, such as nitrogen fertilizer, temperature, light intensity and photoperiod have been poorly investigated. The effect of the date of haulm removal, by contrast, has been studied frequently. Removing the haulm has two effects. The first effect is that the tubers are separated from the rest of the plant. The second effect is caused by a change in environmental conditions either in the soil or in storage when the tubers are harvested. Generally, an earlier haulm removal date results in an earlier end of dormancy (calendar date), but in a longer duration of dormancy in days after haulm removal. Exceptions to this rule, however, are known.

After haulm removal, the duration of the hardening period in the field may affect dormancy,

because the conditions in the soil differ from those in storage (e.g. temperature and humidity). Infection with diseases may have a shortening effect on dormancy (e.g. *Phytophthora infestans*), but own observations suggest that fungal infection with *Helminthosporium solani* may also prolong the duration of dormancy.

The effects of conditions during growth of the tubers on the duration of dormancy have been poorly investigated and are of scientific interest. Therefore, my research focused on the effects of these conditions (Section 4.2).

Conclusions

Review of literature revealed that the difference in the duration of dormancy (calendar date or days after haulm removal) between tuber lots from different years, seasons or sites, stored at moderate temperatures (15-22 °C), is generally less than 4 weeks. The difference in the duration of dormancy is larger when the constant storage temperature is below this range. Only a few cases are known where interaction between cultivar and year, season or site of production was absent.

In my experiments, the duration of dormancy of tubers grown in Wageningen was always 2-3 weeks longer than that of tubers grown in Swifterbant.

SECTION 4.2.1

RELATION BETWEEN GROWTH CONDITIONS AND DORMANCY OF SEED POTATOES. 1. WORKING HYPOTHESIS AND EFFECTS OF NITROGEN

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Summary

The duration of dormancy of seed potatoes varies between years and between origins. Therefore, the effects of conditions during crop growth on dormancy of progeny tubers were studied. The effect of nitrogen during tuber bulking on the duration of dormancy was investigated in three field experiments with two cultivars. In addition to an application of 125 kg N/ha at planting, top dressings of 0-150 kg N/ha were given about 2 weeks after tuber initiation. Haulm was pulled about 4 weeks later. The effect of nitrogen rate at planting was also examined in one experiment.

Nitrogen top dressings shortened dormancy in all experiments by 5-8 days. An increased nitrogen rate at planting resulted in a shorter dormancy when the duration of dormancy was expressed in days after tuber initiation, but not when it was expressed in days after haulm pulling, probably because extra nitrogen also delayed tuber initiation.

Introduction

Dormancy is a favourable factor for ware potatoes and for seed tubers that have to be stored for a long period before use or planting. However, it is a great disadvantage for seed tubers that have to be planted soon after harvest. In either case, an accurate prediction of the duration of dormancy is required to be able to treat tubers appropriately.

Dormancy depends on the genotype. However, storage conditions, especially temperature, affect this dormancy period greatly (Burton, 1978). The duration of dormancy under similar storage conditions can also vary between years and between origins, sometimes for several weeks (Burton, 1963; 1978). The temperature during growth has been suggested as the most important factor causing this variation. However, data in the literature are fragmentary and few systematic studies have been undertaken to quantify the effect of growth conditions on the duration of dormancy. A systematic quantitative approach is the essence of a series of papers of which this is the first. The effects of several growth conditions on dormancy were investigated within the framework of the following working hypothesis.

Working hypothesis. At tuber initiation, elongation growth of the apical bud of the stolon/tuber stops until sprouting starts during storage. Krijthe (1946) stated that both the apical buds of tubers and the axillary buds of stems are second-order buds of stems. This could imply that conditions favourable for growth of axillary buds of the haulm are also favourable for growth of buds on the tubers. Burton (1968) suggested that dormancy of the tubers might be affected via the foliage by weather conditions, if they were such as to lead to the cessation and subsequent resumption of foliage growth.

If dormancy of tubers starts at tuber initiation, as suggested by Burton (1963), then dormancy may be induced by factors associated with tuber initiation. It might be assumed that, once tuber initiation (and dormancy) starts, factors lowering the level of tuberization stimulus shorten dormancy of the tubers.

Temporary re-growth of the apical bud during growth of the tubers occurs during second growth or heat sprouting (for describtions of these terms see Ewing & Struik, 1992). Lugt et al. (1964) and Bodlaender et al. (1964) stated that conditions favourable for delaying tuber formation and promoting vegetative growth make the plant more susceptible to induction of second growth. Although it is not clear whether the induction of second growth and the onset of sprouting during storage are related, it has been observed that the primary tubers of second growth tubers are physiologically older than their secondary tubers (Bodlaender & Lugt, 1962) and than tubers without second growth (Jefferies & MacKerron, 1987).

On the basis of these arguments the working hypothesis was adopted that conditions unfavourable for tuber initiation and favourable for inducing second growth or conditions favourable for growth of axillary buds of the haulm, might shorten the dormancy period of the progeny tubers. Such conditions are high nitrogen rates, high temperatures, low light intensities and long photoperiods. Therefore, the effects of these factors on the duration of dormancy of seed tubers were studied. Treatments generally started after tuber initiation, to avoid complications due to possible variations in the time of tuber initiation and the start of dormancy.

Nitrogen. Nitrogen fertilization plays a role in tuberization, although its effects on the time of initiation are small within the range of usual agronomic practice (Ewing & Struik, 1992). High nitrogen applications can also induce second growth and favour haulm growth (Ewing & Struik, 1992). It was therefore hypothesized that high nitrogen rates shorten the dormancy of progeny tubers.

There have been many reports on the effects of applying nitrogen fertilizer to the crop on the growth of progeny tubers, but most of them pertain to observations started long after dormancy was over (e.g. Volkart, 1948; Schepers et al., 1969; Thow, 1970; Gray, 1974). In other studies the possible effects of nitrogen, phosphorus and potassium were confounded (Pfeffer, 1959; Walker, 1974). The few reports on the effect of nitrogen fertilizer on the duration of dormancy seem to point to no or inconsistent effects (Emilsson, 1949; O'Brien & Allen, 1986).

In the present research, the effect of nitrogen was mainly investigated using top dressings applied after tuber initiation. Thus the effects of nitrogen on the date of tuber initiation were excluded.

Materials and methods

Experimental details and treatments. In 1988-90 three field experiments (Expts 1-3) were conducted near Wageningen (52 °N lat.) on a sandy soil with a very low mineralisation potential of nitrogen, a pH-KCl of 4.8, and 2.3 % organic matter. Two mid-late maturing cultivars were used: Diamant with a short dormancy and Désirée with a long dormancy period. The experimental design was split-plot with cultivars as the main factor and nitrogen treatments as the split factor. Six (Expt 1) or four (Expts 2 and 3) replications were used.

In all experiments pre-sprouted basic seed was planted by hand and local cultural practices were observed. Some of the agronomic and experimental details are listed in Table 1. In 1989 and 1990, frequent irrigations were necessary from tuber initiation to maintain the balance between evaporation and availability of water. Despite irrigation, conditions were drier in 1989 than in 1988 and 1990.

Table 1. Experimental details of field experiments.

	Expt 1	Expt 2	Expt 3
Year	1988	1989	1990
Planting date	April 18	April 18	April 20
Seed size (mm)	35-40	35-40	35-40
Plant spacing (cm)	25x75	25x75	18x75
Gross plot dimensions (m)	3.75x3.75	4.5x3	9x3
Net plot dimensions (m)	2x2.25	3x1.5	8.1x1.5
K-application (kg K/ha)	276	117	122
P-application (kg P/ha)	49	34	73
Tuber initiation cv. Diamant (DAP[a])	43	49	42 or 47[b]
Tuber initiation cv. Désirée (DAP)	38	42	33 or 35[b]
Haulm pulling (DAP)	84	91	77
Harvest (DAP)	98	111	95
Soil temperature at -5 cm (°C)[c]			
Mean temperature	17	21	20
Mean minimum temperature	14	15	16
Mean maximum temperature	20	27	24

[a]Days after planting.
[b]The second date for the high basal dressing of 225 kg N/ha.
[c]Soil temperatures were recorded at a meteorological station in Wageningen; data are for the period between haulm pulling and harvest.

Table 2. Times and rates of nitrogen application (kg N/ha) in Expts 1-3.

Code of N-level	Time of nitrogen application (days after planting) Expt 1		Expt 2			Expt 3	
	0	58	0	58	69	0	55
N1	125	0	125	0	0	125	0
N2	125	75	125	75	0	125	100
N3	125	150	125	0	75	225	0
N4	-	-	125	75	75	-	-

The nitrogen treatments (of calcium ammonium nitrate) are summarized in Table 2. In all experiments, a basal dressing was given at planting and a top dressing about 2 weeks after the start of tuber initiation. Flattened ridges were used to ensure that the top dressing would affect plant growth and the experiments were irrigated before and after the fertilizer was applied.

In Expt 2, the effect of nitrogen top dressings was investigated together with the effect of shading the crop (no shading, shading from 70-80 days after planting (DAP), 80-90 DAP or 70-90 DAP). Only means over the four shading levels are presented in this paper, since no significant interactions occurred between nitrogen top dressings and shading. The effects of the shading treatments are presented in a companion paper (Van Ittersum, 1992c).

Procedures and observations. The dates of tuber initiation were assessed by digging up ten plants per cultivar (and in Expt 3, ten plants for each of the two basal dressings of nitrogen) every other day. Tuber initiation was defined as the moment at which at least six of the plants showed tubers (with a minimum diameter of twice the diameter of the stolon) on at least half the stolons.

The haulms were pulled by hand when the tubers were still immature, at a time depending on tuber size and aphid pressure (in agreement with the haulm killing dates of seed potatoes specified by the General Netherlands Inspection Service for Agricultural Seeds and Seed Potatoes). The colour of the foliage was scored at haulm pulling. Haulm weights and nitrogen concentrations in the haulm were assessed for Expts 2 and 3.

After a hardening period of about 2 weeks, the tubers were harvested by hand. Tuber yields and tuber-size distributions were determined and the shape of the tubers was recorded. From each field plot, a sample comprising 30 tubers free from damage, disease, greening or deformations, and with a narrow range in weight, was taken from the most frequently occurring class of tuber sizes. The weight ranges of the tubers in the samples were 40-80 g (Expt 1), 55-95 g (Expt 2) or 40-80 g (Expt 3). These tubers were stored in egg trays with the apical bud upwards (one sample per tray) in a dark controlled environment at 18 °C and 80 % RH. The trays were arranged according to the plot numbers and blocks of the experiment in the field. A possible effect on dormancy of illumination during the time when observations were made in the storage chambers

Table 3. The effect of nitrogen top dressings on tuber parameters, averaged over two cultivars. Expt 1.

Parameter	Top dressing (kg N/ha)			
	0	75	150	
Fresh weight (g/m²)	2990	2890	2840	
Dry-matter concentration (g/kg)	190	185	186	
N concentration (g/kg)	10.8	12.2	12.7	***
$N\text{-}NO_3$ concentration (g/kg)	0.06	0.11	0.11	***
Duration of dormancy (DAT[a])				
cv. Diamant	120	116	115	
cv. Désirée	200	194	193	
Mean[b]	160	155	154	***
Spread in dormancy (days)	21	19	19	

***Indicates statistically significant effects of the nitrogen top dressings at $P<0.001$.
[a]DAT=days after tuber initiation.
[b]The interaction between cultivar and nitrogen was not statistically significant.

was accounted for by the block factor in the statistical analysis.

Dormancy of an individual tuber was taken to have ended when at least one sprout 2 mm long had been formed. The numbers of sprouted tubers were counted at least twice a week, using as little light as possible. The end of the dormancy period of a sample was defined as the moment that 80 % of the tubers had ended dormancy (Reust, 1986). The duration of dormancy was expressed in days after tuber initiation (DAT). The spread in duration of tuber dormancy for a sample was defined as the time lapse between 10 % and 90% sprouting (Van Ittersum, 1992a).

Dry-matter, nitrogen and nitrate concentrations in tubers from the same weight class as those in the dormancy samples were measured as described in Biemond & Vos (1992).

In Expt 1 the sprouts ($\geq$2mm) per tuber were counted for cv. Diamant about 4 weeks after the end of dormancy. In Expt 3 they were counted for both cultivars 3 weeks after the end of dormancy of each treatment.

Results

Experiment 1. The control treatment (no top dressing) did not show a clear symptom of nitrogen deficiency, although its foliage was a lighter green than that of the other treatments.

Values for tuber parameters are averaged over the two cultivars because no significant interactions occurred between cultivar and nitrogen. The effect of nitrogen top dressings on tuber yield and dry-matter concentrations in the tubers was statistically significant only at the ten percent

Table 4. The effect of nitrogen top dressings (75 kg N/ha) on crop parameters. Expt 2.

Parameter	Cultivar	Time of nitrogen top dressing (days after planting)				LSD P=0.05
		-	58	69	58 + 69	
Haulm						
Dry weight (g/m²)	Mean	259	288	292	301	16.6
N concentration (g/kg)	Mean	23.2	31.6	31.7	37.1	1.43
Tuber						
Fresh weight (g/m²)	Diamant[a]	3000	2630	2960	2810	147
	Désirée	3270	3220	3140	3010	147
Dry-matter conc. (g/kg)	Diamant[a]	215	212	211	212	4.2
	Désirée	205	193	192	192	4.2
N concentration (g/kg)	Diamant[a]	11.4	12.9	13.1	13.7	0.45
	Désirée	12.5	15.2	15.3	16.2	0.45
$N\text{-}NO_3$ concentration (g/kg)	Diamant[a]	0.07	0.07	0.08	0.10	0.022
	Désirée	0.06	0.13	0.14	0.18	0.022
Duration of dormancy	Diamant	116	112	111	109	
(days after tuber	Désirée	200	195	195	191	
initiation)	Mean	158	153	153	150	1.6
Spread in dormancy (days)	Mean	19	20	19	21	ns

[a]The interaction between cultivar and nitrogen was statistically significant.

level of probability (Table 3). Nitrogen concentration in the tubers increased markedly. Top dressing doubled the nitrate concentration. However, the differences between the two rates of top dressing were not significant. The shape of the tubers was not affected (data not shown).

Dormancy was shortened by 5-6 days by the top dressings. There was no effect of nitrogen top dressings on the spread in duration of dormancy (time lapse between 10 % and 90 % sprouting: 22 days (cv. Diamant) and 17 days (cv. Désirée)). For cv. Diamant, 4 weeks after the end of dormancy, the number of sprouts per tuber was not affected by nitrogen (mean: 1.0 sprouts per tuber).

Experiment 2. Nitrogen top dressings considerably increased the haulm weights and nitrogen concentration in the haulm (Table 4). The interaction between cultivars and nitrogen top dressings was statistically significant for tuber parameters. The yield and dry-matter concentration of the tubers were reduced slightly by top dressings. For cv. Diamant, the early single top dressing gave

Table 5. Effect of nitrogen on crop parameters, averaged over two cultivars (except for the dry-matter concentration in tubers, where interaction between cultivar and nitrogen was statistically significant). Expt 3.

Parameter	Nitrogen (kg N/ha)[a]			LSD P=0.05
	125 + 0	125+100	225 + 0	
Haulm				
Dry weight (g/m²)	338	355	387	27.5
N concentration (g/kg)	23.2	30.0	31.1	1.92
Tuber				
Fresh weight (g/m²)	2760	2720	2520	166
Dry-matter concentration (g/kg)				
cv. Diamant	193	188	193	8.4
cv. Désirée	193	183	175	8.4
N concentration (g/kg)	12.9	15.7	16.3	1.03
$N\text{-}NO_3$ concentration (g/kg)	0.04	0.09	0.09	0.016
Duration of dormancy (DAT[b])				
cv. Diamant	136	131	130	
cv. Désirée	194	189	188	
Mean	165	160	159	2.9
Spread in dormancy (days)	16	16	16	ns
Number of sprouts per tuber	1.8	1.6	1.6	ns

[a]The first quantity was given at planting and the second at 55 days after planting as a top dressing.
[b]DAT=days after tuber initiation.

the lowest yield, whereas for cv. Désirée the double top dressing had the largest negative effect on yield. Nitrogen and nitrate concentrations were higher after one or two top dressings. Concentrations in cv. Désirée increased more than those in cv. Diamant.

Nitrogen top dressings shortened dormancy by 5 days (one top dressing) or 8 days (two top dressings) on average. The spread in duration of dormancy was not affected by nitrogen (means: 22 and 18 days for cvs Diamant and Désirée respectively).

Experiment 3. Tuber initiation was delayed by 2 days (cv. Désirée) or 5 days (cv. Diamant) by the higher basal dressing (Table 1). Crop growth was more affected by extra nitrogen at planting than by a top dressing (Table 5). Haulm dry weight increased and tuber weight decreased significantly after extra nitrogen at planting. High nitrogen levels reduced the dry-matter concentration in the tubers of cv. Désirée, but that of cv. Diamant was not affected. Nitrogen and nitrate concentrations did not differ between the treatment with a top dressing and the treatment

with a high basal dressing, but both treatments had significantly higher concentrations than the control treatment (125 kg N/ha only).

Dormancy was shortened significantly by 5-6 days by high nitrogen applications. The spread in duration of dormancy was not affected by nitrogen (means: 15 and 18 days for cvs Diamant and Désirée respectively). The number of sprouts 3 weeks after the end of dormancy did not differ between the treatments.

Discussion

In all experiments, the duration of dormancy was shortened by 5-8 days after nitrogen top dressings. Effects of rate (Expt 1), time or frequency (Expt 2) of top dressings were small. In Expt 3 a higher basal dressing also resulted in a significantly shorter dormancy.

The date of initiation of a tuber is correlated with the date of the end of dormancy: tubers initiated later end their dormancy later (Van Ittersum & Struik, 1992). Therefore, a possible effect of higher basal dressings of nitrogen on dormancy cannot be observed if tuber initiation is delayed and if the duration of dormancy is expressed in days from harvest or if the end of dormancy is expressed in calendar dates. The results of Expt 3 seem to support this assumption: the higher basal dressing delayed tuber initiation by 2-5 days and significantly shortened dormancy (expressed in days after tuber initiation) by 6 days. However, calculated in days from haulm pulling or in calendar dates, the higher basal dressing shortened dormancy non-significantly by 2 days only. This may be the reason why O'Brien & Allen (1986) did not always observe that nitrogen shortened dormancy. Their experiments were carried out on soils probably high in N, and all the nitrogen was generally applied at planting. In one of their experiments tuber initiation was delayed after very high (304-608 kg N/ha) nitrogen applications at planting, and the dormancy of progeny tubers (in days from harvesting) was prolonged.

The dormancy shortening effect of nitrogen is of scientific interest, but its practical implications are probably limited. The soil in my experiments was very poor, so the effects of nitrogen top dressings would be expected to have been relatively large. Moreover, although the top dressings were rather large for seed potatoes their effects were only seen for up to 8 days.

From Expts 2 and 3, it could be surmised that there is a negative correlation between haulm growth and the duration of dormancy, and a positive correlation between the dry-matter concentration in the tubers and the duration of dormancy. However, these relations did not hold in my experiments with different light intensities during growth of the tubers (Van Ittersum, 1992c).

In both experiments where nitrogen and nitrate concentrations were measured, there was an association between these concentrations and the duration of dormancy. Because dormancy was defined to end when a 2 mm sprout had been formed, the effect of nitrogen could be a direct effect on sprout growth. Headford (1961) suggested that a low nitrogen content in the tuber might limit sprout growth during storage. However, Davies (1984) concluded that nitrogenous

compounds were not major factors limiting sprout growth. Moreover, in my experiments the differences in dormancy between treatments were not smaller when a sprout length of 1 mm was considered as the criterion for the end of dormancy (data not shown).

The dormancy of potato tubers is probably related to a balance of growth-inhibiting (e.g. abscisic acid (ABA)) and growth-promoting (e.g. gibberellins (GA) and cytokinins (CK)) hormones (Van der Plas, 1987). Krauss (1985) observed that a continuous nitrogen supply to the potato plant led to a relatively low ABA and high GA concentration in the shoot. Interruption of the nitrogen supply increased the ABA and decreased the GA concentration, and tuberization occurred. Restoring the nitrogen supply decreased the ABA and increased the GA concentration greatly in shoots, and slightly in tubers, and was often accompanied by second growth. CK activity increases at high nitrogen levels (Sattelmacher & Marschner, 1978; Darrall & Wareing, 1981). Vincent & Roberts (1977) and Hilhorst (1990) found that both endogenous and exogenous nitrate can stimulate germination of true seed of several plant species, an effect probably related to synthesis of or sensitivity to gibberellins (Hilhorst, 1990). It seems possible that nitrogen shortens dormancy directly or indirectly, because of a shift in the hormone balance of the tubers in favour of sprouting.

SECTION 4.2.2

RELATION BETWEEN GROWTH CONDITIONS AND DORMANCY OF SEED POTATOES. 2. EFFECTS OF TEMPERATURE

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Summary

In two indoor experiments under short day conditions, the effect of temperature during tuber bulking on dormancy of tubers was investigated for cvs Diamant and Désirée. Temperature treatments started after tuber initiation and lasted for 4 weeks, after which the haulm was removed.

In Experiment 1, the day/night temperature regimes 18/12, 22/22, 26/18 and 32/12 °C (T18/12 etc.) were compared. In Experiment 2, three day temperatures (18, 24 and 30 °C) were combined with three night temperatures (12, 18 and 24 °C), resulting in nine treatments.

The dormancy of cv. Diamant was shortest after very high day temperatures (30-32 °C), but intermediate day temperatures (22-26 °C) had no shortening effect compared to T18/12. Dormancy of cv. Désirée was not shortened, but rather tended to be prolonged by high temperatures (22-32 °C) during growth.

High temperatures during growth resulted in more sprouts per tuber after dormancy had ended.

Introduction

In a previous paper (Van Ittersum, 1992b), it was suggested that growth conditions that delay tuber initiation and favour the induction of second growth or conditions that stimulate haulm growth might reduce the duration of dormancy of the tubers. High temperature is such a condition, since it can delay, hamper or impede tuber initiation (Struik et al., 1989a), induce second growth (Bodlaender et al., 1964) and stimulate haulm growth (Marinus & Bodlaender, 1975). Therefore, we examined the effect of temperature during growth on the duration of tuber dormancy.

Circumstantial evidence indicates that dormancy is shorter after warmer conditions during growth. The results of Krijthe (1962b) suggest a markedly shorter dormancy after a hot dry season. Burton (1963) found a longer dormancy period after a cold wet season, and Susnoschi (1981a) showed that tubers which developed in spring under higher temperatures had a

significantly shorter dormancy than tubers grown in autumn under cooler conditions. However, Allen et al. (1992) found no association between temperature at the site of production and the duration of dormancy. Reust (1982), expressing duration of dormancy in accumulated temperature during growth and storage, found that dormancy ended after a lower temperature sum for tubers produced at higher altitudes than for those produced at lower altitudes.

Unequivocal evidence on the effect of temperature during growth on the duration of dormancy is scarce. Susnoschi (1976) compared a low (20 °C day/12 °C night) and a high (32/16 °C) growth temperature regime at two daylengths and subsequent storage at 22 °C with cv. Up-to-date. He found dormancy to be 2-4 weeks shorter after the high temperature regime.

Dormancy is hypothesized to start at tuber initiation, and since high temperatures can delay initiation, temperature treatments were imposed about 2 weeks after tuber initiation.

Materials and methods

Experiment 1. Four temperature regimes were compared at two levels of nitrogen for the two mid-late maturing cultivars Diamant and Désirée (short and long dormancy period, respectively). On 27 September 1989 three single-sprouted physiologically young tubers, each 30 g, were planted in black 20-litre pots filled with quartz sand. Plants grew in growth chambers (14 m^2 each) at a day/night temperature regime of 18/12 °C (12 h daylength) and a light intensity of 70 W/m^2 (400-700 nm) measured at plant level.

Tuber initiation was assessed on additional plants and started about 48 (cv. Désirée) or 54 (cv. Diamant) days after planting (DAP). Sixty-eight DAP, four day/night temperature regimes were started: 18/12 °C, 22/22 °C, 26/18 °C and 32/12 °C at 12 h daylength and 70 % RH (T18/12, T22/22, etc.). There was one growth chamber for each temperature regime. Each growth chamber was divided into five blocks. Within each block the four cultivar nitrogen treatments were randomized: two pots per experimental unit in blocks 1-4 and one in block 5. A factorial nested design was used. Between haulm removal (98 DAP) and harvest (12 days later), the temperature was maintained at 18 °C day and night for all treatments.

The temperature of the air and in the pots at tuber level was measured with thermocouples and recorded with a data recorder (Fluke 2240/A). Air temperatures almost reached their target values within 2 h after a temperature switch and fluctuated < 1 °C. Temperatures at tuber level reached their maximum and minimum values by the end of the day and night, respectively. These maximum and minimum values differed not more than 2 °C from the maximum and minimum air temperatures.

Until 54 DAP, a total of 2.2 g N per pot was given in four applications. From 61 DAP until haulm cutting, two nitrogen levels were maintained. For the low regime 0.9 g N (as $Ca(NO_3)_2$) was applied in five weekly applications and for the high regime 2.7 g N (as $Ca(NO_3)_2$) was applied in ten applications (two applications per week). Total nitrogen rates for the low and high

regime were 3.1 and 4.9 g N per pot, respectively, and total calcium rates were 1.7 and 3.0 g Ca per pot.

From planting until haulm removal, the following total amounts of other nutrients were applied per pot, apportioned over nine applications: 1.0 g P, 6.0 g K, 0.5 g Mg and 12 ml of a trace element solution containing 20 g $MnSO_4.H_2O$, 30 g H_3BO_3, 5 g $ZnSO_4.7H_2O$, 1 g $CuSO_4.5H_2O$ and 1 g $Na_2MoO_4.2H_2O$ per litre of water.

Experiment 2. Nine temperature regimes were compared in three glasshouses for cvs Diamant and Désirée. On 11 May 1990, one tuber (20-25 g; optimum physiological age) with two sprouts was planted in each of 270 black 12-litre pots filled with a mixture of peat and quartz sand. Plants grew at a day/night temperature regime of 18/12 °C, with 12 h daylength (maintained by means of a power driven roof).

Tuber initiation started at about 26 (cv. Désirée) or 30 (cv. Diamant) DAP. From 48 DAP until haulm removal (76 DAP), the glasshouses were adjusted to different day/night temperature regimes: 18/12 °C, 24/18 °C and 30/24 °C (12 h daylength; T18/12, T24/18, etc.). All pots of each cultivar were randomized and placed on barrows. By moving two third of the barrows every morning at 08.00 h and every evening at 20.00 h, nine different temperature regimes were obtained. At one time, in each glasshouse, plants of three temperature regimes were present. Each glasshouse was divided into five blocks ('replications'). Each block comprised three barrows (three temperature regimes), each with three pots of cv. Diamant and three pots of cv. Désirée. The experimental design was a factorial nested design. From haulm removal until harvest (95 DAP), the temperature was maintained at 18 °C day and night. Target temperatures were mostly well maintained, although on sunny days the maximum temperature in the glasshouses was 2-4 °C higher than desired for some hours.

From planting until haulm removal, the following total amounts of nutrients were applied per pot: 2.8 g N, 0.7 g P, 4.0 g K, 0.5 g Ca, 0.3 g Mg and 9 ml of the trace element solution (see Expt 1).

Observations. Plant heights were measured 77, 90 and 97 DAP (Expt 1) or 47, 56, 69 and 76 DAP (Expt 2). The increase in plant height during the temperature treatments gave an indication of the growth of apical axillary haulm buds, since the main axis of most plants started flowering or showed aborted flower initials at the start of the temperature treatments. The haulm was weighed when it was removed, and the individual weights of all tubers heavier than 2.5 g were recorded at harvest. In Expt 2 the length and width of tubers were measured in two replications. By harvest, some tubers from treatments with a high temperature had formed heat sprouts, i.e. sprouts grown from tuber buds prior to harvesting. These sprouts were removed before storage. After harvest, all tubers were stored in the dark at 18 °C and 80 % RH, to assess dormancy parameters. The end of dormancy of a sample was defined as when 80 % of the tubers showed at

least one 2 mm sprout. Definitions and further details about determining dormancy are given in an earlier report (Van Ittersum, 1992b). The present paper will deal with dormancy of all tubers heavier than 25 g.

In Expt 1, the numbers of sprouts (≥2mm) per tuber were counted, 4 weeks after the end of dormancy of T22/22 of each cultivar. In Expt 2, for cv. Diamant the sprouts (≥2 mm) on each tuber were counted 4 weeks after the end of dormancy of each treatment. Sprouts of cv. Désirée were very hard to count because of branching due to calcium deficiency. Therefore, only the main sprouts (not the branches) were counted for T18/12, T24/12, T30/18 and T30/24, about 4 weeks after the end of dormancy of all treatments.

Statistical analysis. The growth chambers (Expt 1) and glasshouses (Expt 2) were each of one make and of the same age. The temperature conditions could be controlled very well (±0.5 °C), so it may be assumed that effects on the plants due to differences between growth chambers (or glasshouses) were negligible compared to the effects of the different temperature treatments. Therefore, if the analysis of variance showed statistically significant differences between plant populations in the various growth chambers (or glasshouses), these differences were attributed to the temperature treatments.

A multiple regression analysis was carried out for Expt 1 (cv. Diamant, T32/12) and Expt 2 (cv. Diamant, T30/12, T30/18 and T30/24 and cv. Désirée, T30/24). This analysis was carried out to verify whether tubers that had formed heat sprouts during growth differed in their duration of dormancy from tubers grown at the same temperature without heat sprouts, also taking into account tuber weight.

Table 1. The effect of nitrogen application and day and night temperature during tuber bulking on the duration of dormancy (days after tuber initiation) for cvs Diamant and Désirée. The interaction between cultivar and temperature is statistically significant ($P < 0.001$). Expt 1.

Cultivar	Nitrogen (g/pot)	Day/night temperature (°C)				Mean
		18/12	22/22	26/18	32/12	
Diamant	3.1	127	135	127	112	125
	4.9	124	127	119	101	117[a]
	Mean	125	131	123	107	
Désirée	3.1	187	208	203	190	197
	4.9	179	201	191	171	185[a]
	Mean	183	204	197	180	

[a]The nitrogen effect was statistically significant ($P < 0.001$).

Table 2. Effect of temperature regime during tuber bulking on various crop parameters of cvs Diamant and Désirée, averaged over two nitrogen levels. Expt 1.

Parameter	Day/night temperature (°C)				LSD P=0.05
	18/12	22/22	26/18	32/12	
cv. Diamant					
Haulm					
Increase in plant height[a] (cm)	3.1	9.9	8.5	5.3	2.32
Dry weight (g/pot)	30.2	32.0	31.9	28.0	2.11
Tuber					
Fresh weight (g/pot)	825	769	726	700	38.7
Mean tuber weight >25 g (g/tuber)	82.8	78.1	74.5	74.2	8.60
Dormancy and sprouting behaviour					
Duration of dormancy (DAT[b])	125	131	123	107	5.6
Spread in dormancy (days)	27	36	33	28	7.6
Number of sprouts per tuber[c]	1.1	1.0	1.4	2.9	0.49
cv. Désirée					
Haulm					
Increase in height[a] (cm/plant)	8.8	16.5	24.4	22.1	7.70
Dry weight (g/pot)	21.2	26.4	29.4	29.3	4.22
Tuber					
Fresh weight (g/pot)	745	760	698	690	38.7
Mean tuber weight >25 g (g/tuber)	73.3	74.4	63.9	74.9	8.60
Dormancy and sprouting behaviour					
Duration of dormancy (DAT[b])	183	204	197	180	5.6
Spread in dormancy (days)	21	23	28	34	7.6
Number of sprouts per tuber[c]	1.2	1.5	1.4	1.6	0.20

[a]During 77-97 days after planting.
[b]DAT=days after tuber initiation.
[c]Four weeks after the end of dormancy of the 22/22 °C treatment.

Results

Experiment 1

The higher nitrogen application shortened dormancy signicantly for both cultivars (Table 1). There was no interaction between nitrogen and temperature, but that between cultivar and temperature was statistically significant for the duration of dormancy and other important variables. Moreover, variances differed between cultivars for some variables, so the effects of temperature are presented

by cultivar averaged over the two nitrogen applications (Table 2). The effects of nitrogen on dormancy corroborate those already presented (Van Ittersum, 1992b).

cv. Diamant. Haulm growth was only slightly affected by temperature, but tuber yields decreased with increasing day temperatures. The mean tuber weight of tubers heavier than 25 g tended to decrease for treatments with higher day temperatures.

T32/12 was the only treatment where dormancy was significantly shorter than T18/12 (18 days shorter). The dormancy of T22/22 was significantly longer than that of T26/18 and T32/12. The spread in duration of dormancy (time lapse between 10 % and 90 % sprouting) of T22/22 was larger than that of T18/12 and T32/12.

Some 14 % of the tubers of T32/12 showed heat sprouts at harvest. The duration of dormancy of these tubers did not differ from that of tubers without heat sprouts. The number of sprouts per tuber was much higher for T32/12 than for the other treatments. The apical dominance of tubers of T32/12 was broken for 80 % of the tubers.

cv. Désirée. Haulm height and haulm weight increased considerably at higher temperatures. Total tuber weights were significantly lowest for T26/18 and T32/12, but differences were small. T26/18 produced slightly more tubers heavier than 25 g and T32/12 slightly fewer than the other treatments (data not shown). This resulted in a significantly lower mean tuber weight for tubers of T26/18 heavier than 25 g.

Dormancy was significantly longest for T22/22 and shortest for T32/12 and T18/12, which did not differ. The spread in duration of dormancy was largest for T32/12. About 5 % of the tubers of T32/12 showed heat sprouts at harvest. The number of sprouts per tuber was lowest for T18/12.

Experiment 2

The interaction between cultivars and day or night temperature was statistically significant for many important variables, such as haulm weight, tuber weight and the duration of dormancy. Variance differed between cultivars for many variables, so results for the two cultivars are presented separately.

cv. Diamant. There were no significant effects of temperature during growth on the increase in plant height between 47 and 76 DAP (Fig. 1a). Haulm weight decreased slightly at higher night temperatures (data not shown). Total tuber weight was not influenced significantly by temperatures during tuber bulking (Fig. 1b). The average weight of tubers heavier than 25 g was slightly lower for treatments with a night temperature of 24 °C (55 vs 62 g). Temperature did not affect the length/width ratio of tubers (data not shown).

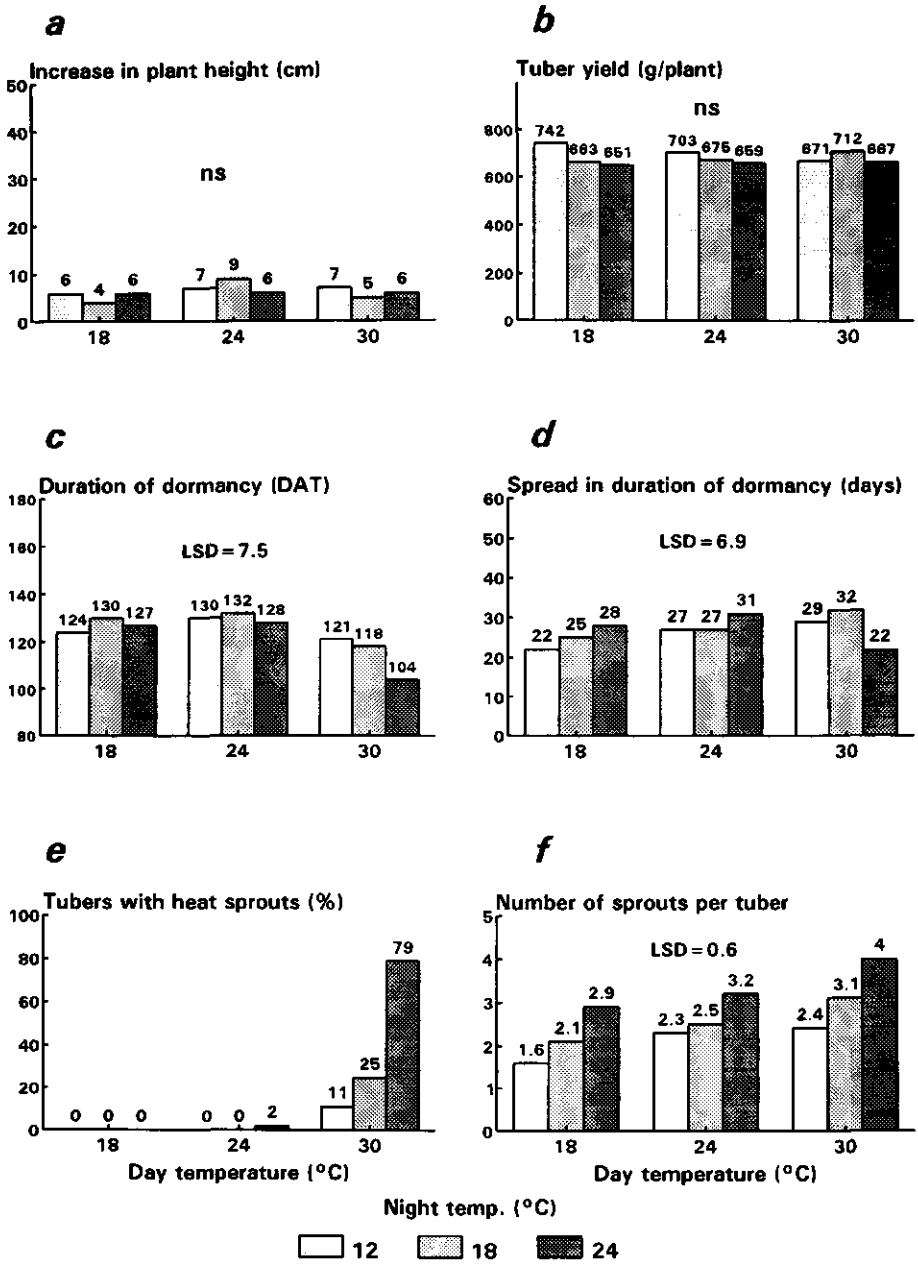

Fig. 1. Effect of day and night temperatures on growth, yield and dormancy parameters of cv. Diamant (Expt 2). (a) increase in plant height during the temperature treatments, (b) tuber yield, (c) the duration of dormancy (DAT=days after tuber initiation), (d) spread in duration of dormancy, (e) percentage of tubers with heat sprouts, (f) number of sprouts per tuber 4 weeks after the end of dormancy. The figures at the top of each bar denote the actual values; ns=not significant.

The interaction between day and night temperature was statistically significant for the duration of dormancy. Dormancy was shortest after a day temperature of 30 °C, especially in combination with the highest night temperature (20 days shorter compared with T18/12; Fig. 1c). There were few significant differences in dormancy between the regimes with a day temperature of 18 and 24 °C. Trends in the spread in duration of dormancy were not clear (Fig. 1d). The spread was smallest after T18/12 and T30/24.

Heat sprouting occurred in T24/24 and especially in all treatments with a day temperature of 30 °C (Fig. 1e). The proportion of tubers with heat sprouts increased greatly with the night temperature. Tubers with heat sprouts had a significantly shorter dormancy than tubers of the same temperature treatment without heat sprouts. The mean difference was 7 (T30/12), 11 (T30/18) or 6 (T30/24) days ($n \geq 155$; $P < 0.01$).

High day or high night temperatures significantly increased the number of sprouts per tuber 4 weeks after the end of dormancy (Fig. 1f).

cv. Désirée. Plants of cv. Désirée grown at the higher day temperatures showed clear symptoms of heat stress. Evaporation on hot days was often too high compared to the uptake of water and partial wilting was observed.

Haulm heights increased significantly with day and, to a smaller extent, with night temperatures (Fig. 2a). This was reflected in significantly higher haulm dry weights after high day or night temperatures (data not shown). The effects on tuber yields were small (Fig. 2b). Temperature during growth did not affect the average weight and length/width ratio of tubers heavier than 25 g (data not shown).

The interaction between day and night temperature was significant for the duration of dormancy. Dormancy at T18/12 and T18/18 was significantly shortest and differences between the other regimes were small (Fig. 2c). The spread in the duration of dormancy of T30/24 was more than twice as large as that of most other treatments (Fig. 2d).

T30/24 was the only treatment that showed heat sprouting at harvest (26 % of the tubers). The tubers with heat sprouts had a significantly shorter dormancy than tubers without heat sprouts ($n = 157$; $P < 0.01$). This difference in dormancy was greater for smaller tubers (15 days) than for larger ones (7 days). The difference in dormancy between tubers with or without heat sprouts partly caused the higher spread in duration of dormancy for T30/24.

The number of sprouts per tuber was slightly higher for T30/24 (1.9) than for T18/12 (1.5).

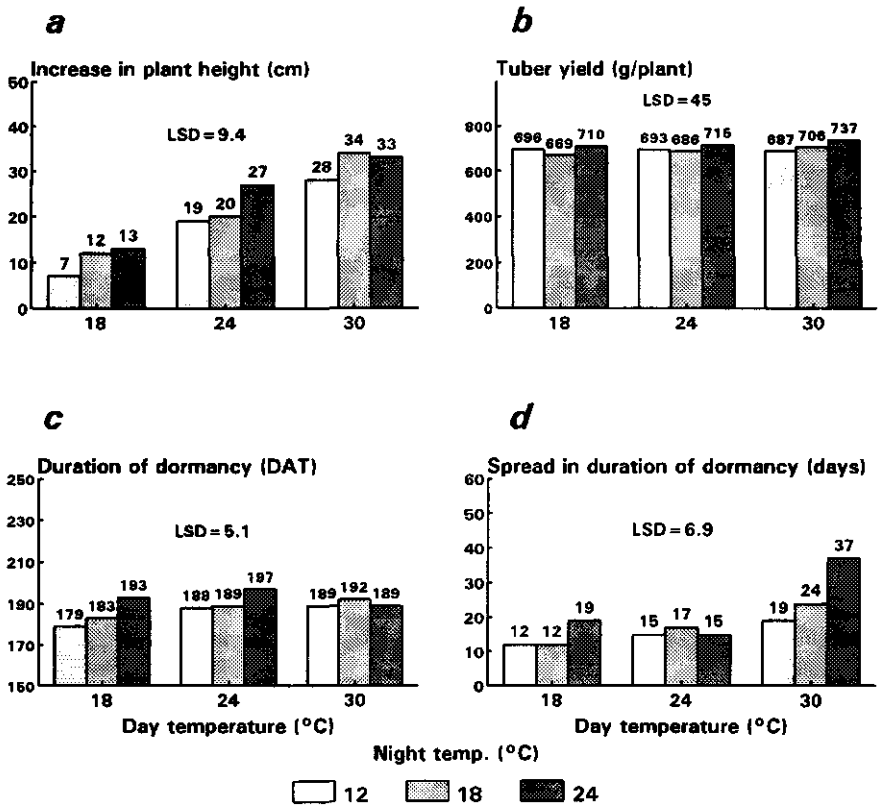

Fig. 2. Effect of day and night temperatures on growth, yield and dormancy parameters of cv. Désirée (Expt 2). (a) increase in plant height during the temperature treatments, (b) tuber yield, (c) the duration of dormancy (DAT=days after tuber initiation), (d) spread in duration of dormancy. The figures at the top of each bar denote the actual values.

Discussion

Effects of temperature on dormancy

Controlled conditions. Some authors report a shorter dormancy after high temperatures during tuber growth (see Introduction and Susnoschi, 1976). However, our results show that the relationship between dormancy and temperature during growth is rather complex. Effects of temperature during growth on the duration of dormancy depended on the cultivar and differed to some extent between the two experiments. Compared with T18/12, only the dormancy of cv. Diamant was shortened after the regimes with the highest temperatures (30-32 °C) during growth. Moreover, intermediate day temperatures (22-26 °C) did not shorten the dormancy of cv. Diamant and prolonged that of cv. Désirée. Clearly, our results are contrary to general ideas about the effect of temperature during growth on tuber dormancy.

There was no evident relationship between the duration of dormancy and the mean daily temperature. T22/22, T26/18 and T32/12 (Expt 1) all had a mean daily temperature of 22 °C, but dormancy differed greatly. Moreover, for some of these treatments the duration of dormancy did not differ from that of a treatment with a mean daily temperature of 15 °C (T18/12). The amplitude of day and night temperature also did not seem to be of crucial importance (compare e.g. T18/18 with T24/12; Fig. 1c).

Extrapolation to field conditions. Since our experiments were carried out in growth chambers or glasshouses and under short day conditions, it is not easy to extrapolate the results to local field conditions. For instance, temperatures at tuber level were almost as high as the air temperatures in Expt 1 and, although not measured, very probably also in Expt 2. This will not occur under field conditions, when ground cover is near to 100 %. Nevertheless, it can be argued that before haulm pulling the effect of temperature on the dormancy of seed tubers harvested immature is not important in a temperate climate. This agrees with the reservations of Allen et al. (1992) concerning the importance of the growth temperature on dormancy. In contrast, the influence of storage temperatures immediately after haulm pulling or harvest is very distinct (Van Ittersum & Scholte, 1992a). It can be assumed that green foliage has a controlling influence on dormancy of the tubers, whereas environmental conditions become much more important when the foliage is more mature or removed.

Recent literature reviews (e.g. Burton, 1989) still use data of Krijthe (1962b) and Burton (1963) to illustrate the importance of the temperature during growth on the dormancy of progeny tubers. However, it seems unlikely that the 9 weeks earlier end of dormancy in the year 1959 compared to the year 1958 in the Netherlands (Krijthe, 1962b) can be attributed to the much higher temperatures before haulm killing in 1959. Krijthe stored the tubers at 2 °C and every week placed samples at 20 °C for sprouting. This way of storing the tubers (in fact with cold pre-treatments) and the difference in the start of storage between both years (about 8 weeks later in 1958) may have interacted with her results. Moreover, differences in temperature between haulm killing and harvest might have caused part of the difference. It is hard to decide whether the longer dormancy in 1956 in Great Britain can be (partly) ascribed to lower temperatures during growth, as was claimed by Burton (1963). Seed potatoes in Great Britain used to be harvested when more mature than in the Netherlands. Consequently, the foliage may have lost part of its controlling influence on dormancy and the environmental conditions would have become the more important determinants of dormancy. However, differences in the duration of dormancy because of temperature differences between tubers grown in autumn and in spring, as in Israel (Susnoschi, 1981a), may indeed be expected for some cultivars. At the end of the growing periods, the temperatures are much higher (and the days are much longer) in the spring season than in the autumn season.

Relation between dormancy and haulm growth. Haulm growth of the two cultivars was affected differently by increasing temperature: for cv. Diamant these effects were very small, whereas for cv. Désirée haulm height and weight increased with higher day and night temperatures. The fact that cultivars differ in growth response to temperature is well known (cf. Marinus & Bodlaender, 1975). The effects on tuber yield were small (less than 15 %) for both cultivars. In our experiments, temperature treatments started after tuber initiation, but effects (on haulm and tuber growth) of high temperature treatments started *before* tuber initiation are much greater (Marinus & Bodlaender, 1975; Struik et al., 1989a).

The negative correlation between haulm growth and duration of dormancy, as surmised in the working hypothesis (Van Ittersum, 1992b), was not observed; in fact the opposite took place. Cv. Diamant showed no increase in haulm growth in response to very high temperatures, but dormancy was much shorter after these treatments. Cv. Désirée showed a distinct increase in haulm growth at higher temperatures, and dormancy was not shorter - rather it tended to be longer.

Relation between dormancy and second growth. In an unpublished experiment concerning the effect on dormancy of temperature during growth, we carefully harvested tubers with heat sprouts. In storage, these sprouts did not continue their growth until the desprouted tubers of the same treatment also started to sprout again. This suggests that the removal of heat sprouts at harvest did not affect our results on the duration of dormancy. Contrary to Expt 1, in Expt 2 there was a negative correlation between the formation of heat sprouts and the duration of dormancy. However, the duration of dormancy of a sample with some heat sprouted tubers (cv. Désirée, T30/24) was not always shorter than that of a sample without them.

Perennec (1966) concluded that heat sprouting in the soil and sprouting of tubers in storage differed in their mechanism, but the results of Expt 2 might imply that there is some relation between both processes.

Dormancy and physiological ageing

In contrast to the relationship between dormancy and temperature during growth, the relationship between the number of sprouts per tuber and temperature was rather clear. Higher day or night temperatures during growth increased the numbers of sprouts per tuber after dormancy was over, especially for cv. Diamant. This increase can be partly ascribed to the removal of heat sprouts at harvest, thus breaking apical dominance. However, treatments that did not show heat sprouts at harvest also showed an increase in sprout numbers (Fig. 1e,f). Tubers grown at higher temperatures may be physiologically different from those grown under lower temperatures, although the duration of dormancy is little affected. Several researchers (e.g. Went, 1959; Bodlaender, 1973; Carls & Caesar, 1979) found that tubers grown at higher temperatures or lower altitudes produced lower yields when used as seed. Dormancy and physiological ageing are apparently affected differently by temperature during growth of the tubers.

SECTION 4.2.3

RELATION BETWEEN GROWTH CONDITIONS AND DORMANCY OF SEED POTATOES. 3. EFFECTS OF LIGHT AND GENERAL DISCUSSION

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Summary

The effects on the dormancy of progeny tubers of the timing and level of shading during plant growth were investigated in three field experiments. The tubers were harvested while immature. Shading (50-75 %) the crop shortly before haulm pulling shortened dormancy by 5-7 days in two experiments. However, dormancy was hardly affected by 50 % shading in one experiment, carried out in a sunny dry period.

The effects of the photoperiod during tuber bulking on dormancy were studied in two indoor experiments. Plants were grown at 18/12 °C (day 12h/night) and a 12 h photoperiod. Shortly after tuber initiation, the photoperiod was extended to 18 h for 4-6 weeks by photosynthetically inactive incandescent light, or kept at 12 h. The effects of the photoperiod on dormancy were up to 9 days, but differed between the cultivars and experiments.

Generally, the effects on tuber dormancy of differences in growth conditions, as reported in this series of papers, were limited.

Introduction

Seed potatoes are grown over a wide range of latitudes and in different seasons and thus at different levels of irradiance and at different photoperiods. These differences in growth conditions might result in differences in tuber dormancy. It is often assumed that tubers produced at lower latitudes have a shorter dormancy than those produced at higher latitudes (Beukema & Van der Zaag, 1990), although data to support this hardly exist. On the other hand, at low northern latitudes tubers produced in autumn and winter have a longer dormancy period than those produced in spring (Susnoschi, 1981a). Besides temperature, light intensity and photoperiod may have contributed to this effect.

There is no published information concerning the influence of light intensity on the duration of dormancy, or concerning the influence of the photoperiod (at the same level of photosynthetically active radiation, PAR) on dormancy. Emilsson (1949) compared a short and a long daylength (and consequently different amounts of PAR). He did not find a significant effect of daylength on the

duration of dormancy, although for some cultivars the short daylength caused the plants to be more mature at harvest. For these cultivars dormancy was shorter after the short daylength. Tsukamoto et al. (1960) compared two different daylengths after tuber initiation and found dormancy to be shorter after a short daylength.

In the first paper of this series (Van Ittersum, 1992b), it was hypothesized that the following factors during tuber growth might shorten the dormancy of progeny tubers: factors which delay tuber initiation, those which favour the induction of second growth or those which stimulate growth of axillary buds of the haulm. Low levels of irradiance and long photoperiods decrease tuber induction and are more favourable for haulm growth than tuber growth (Ewing & Struik, 1992). Moreover, long photoperiods may enhance the induction of second growth (Madec & Perennec, 1962). We therefore investigated the effect of shading as well as of the photoperiod after tuber initiation (at the same level of accumulated PAR) on the dormancy of seed tubers. The tubers were harvested while immature. At the end of this paper, the relationship between growth conditions and dormancy, as reported in this series of papers, is discussed.

Materials and methods

Experiments on light intensity

Experimental details and treatments. In 1988-90 three field experiments (Expts 1-3) were carried out near Wageningen (52 °N lat.). Two mid-late maturing cultivars were used: Diamant (short dormancy) and Désirée (long dormancy). The experimental design was split-plot with cultivars as the main factor and shading treatments as the split factor and four (Expts 1 and 2) or five (Expt 3) replications. Soil and cultural practices were the same as those already described (Van Ittersum, 1992b; see also Table 1). Despite frequent irrigations, conditions were drier in 1989 than in 1988 and 1990.

Shading nets were hung at about 30 cm above the crop to create different light intensities. They reduced intensity by 70 % in Expt 1 and 50 % in Expts 2 and 3. The experimental treatments are summarized in Table 2. In Expt 3 there were two levels of shading, 50 % and 75 %; the 75 % light reduction was achieved by fixing two nets one above the other. The solar radiation was recorded at a meteorological station in Wageningen. Light intensity was highest in 1989 and lowest in 1988 (Table 2).

Temperatures at crop level (Expts 2 and 3) and in the soil (Expt 2) were recorded with thermocouples. In Expt 2 the temperature was hardly affected by the nets. In Expt 3, however, on sunny days the maximum temperature was 2.5 °C lower with 75 % shading than in the control and the minimum temperatures in the shaded plots were 1.5 °C higher than in the unshaded plots. On cloudy days the nets hardly affected the temperature.

Table 1. Experimental details of Experiments 1-3

	Expt 1	Expt 2	Expt 3
Year	1988	1989	1990
Planting date	April 18	April 18	April 20
Nitrogen application (kg N/ha)	140	125	150
Seed size (mm)	45-50	35-40	35-40
Plant spacing (cm)	25x75	25x75	18x75
Gross plot dimensions (m)	5x3	4.5x3	4.5x3
Net plot dimensions (m)	3x1.5	3x1.5	3.6x1.5
Tuber initiation cv. Diamant (DAP[a])	45	49	46
Tuber initiation cv. Désirée (DAP)	39	42	34
Haulm pulling (DAP)	91	91	76
Harvest (DAP)	107	111	94
Soil temperature at -5 cm (°C)[b]			
Mean temperature	18	21	20
Mean minimum temperature	14	15	16
Mean maximum temperature	24	27	24

[a]DAP=days after planting
[b]Soil temperatures were recorded at a meteorological station in Wageningen; data are for the period between haulm pulling and harvest.

Table 2. Period (days after planting) and level (% reduction in light) of shading treatments and the average irradiance (MJ m^{-2} day^{-1}) during the shading period in Expts 1-3.

Expt		Shading treatment			
		Control	Early	Late	Long
1	Period	66-88	66-77	77-88	66-88
	Shading level	0	70	70	70
	Irradiance	13.6	4.0	4.2	4.1
2	Period	70-90	70-80	80-90	70-90
	Shading level	0	50	50	50
	Irradiance	17.2	9.3	8.0	8.6
3	Period	55-76	-[a]	-[a]	55-76
	Shading level	0	-	-	50 /75[b]
	Irradiance	16.6	-	-	8.3/4.2[b]

[a]Not carried out in Expt 3.
[b]Light reductions of 50 and 75%.

In Expt 2, the effect of light intensity was investigated together with the effect of different nitrogen top dressings (no top dressing, 75 kg N/ha 58 days after planting (DAP), 75 kg N/ha 69 DAP and 75 kg N/ha 58 DAP plus 75 kg N/ha 69 DAP). These dressings were given in addition to one of 125 kg N/ha at planting. Because no statistically significant interaction occurred between light intensity and nitrogen, only means over the four nitrogen levels are presented. The effects of nitrogen supply are presented in a companion paper (Van Ittersum, 1992b).

Procedures and observations. The procedures concerning tuber initiation, haulm pulling, harvest, haulm (Expts 2 and 3 only) and tuber yield, dry-matter concentration in the tubers, and dormancy were similar to those described in Van Ittersum (1992b). The colour and elongation of the foliage was scored prior to haulm pulling. From each field plot, a sample of 30 tubers with individual tuber weights of 40-80 g (Expt 1), 55-95 g (Expt 2) or 30-60 g (Expt 3) was taken to assess dormancy parameters.

In Expt 1, the sprouts (≥2mm) per tuber were counted for cv. Diamant about 3 weeks after the end of dormancy and in Expt 3 they were counted for both cultivars 3 weeks after the end of dormancy.

Experiments on photoperiod

Treatments and experimental design. During the summers of 1989 and 1990 two pot experiments (Expts 4 and 5) were carried out in glasshouses on cvs Diamant and Désirée. The plants were grown in black 10-litre pots containing a mixture of equal volumes of peat and quartz sand.

The glasshouses were kept at a day temperature of 18 °C (day 12 h) and a night temperature of 12 °C. Until the start of the photoperiod treatments, the daylength (PAR) and photoperiod were kept at 12 h by an automatic power driven roof. After tuber initiation, the plants were randomized over the two identical glasshouses and for the rest of the growing period the photoperiod of one glasshouse was extended to 18 h by one incandescent lamp (75 W) per 2.3 m² (light intensity at plant level about 1.5 W/m², 400-700 nm). Each glasshouse was divided into 15 (Expt 4) or six (Expt 5) blocks ('replications') of six pots each (two cultivars; for each cultivar three pots was the experimental unit). A factorial nested design was used. Between haulm pulling and harvest, both glasshouses were darkened and temperature was constant at 18 °C.

Cultivation and observations. Tubers of 30 g (Expt 4) or 12-14 g (Expt 5) and optimum physiological age were pre-sprouted and desprouted to leave two (Expt 4) or one (Expt 5) sprouts per tuber. One (Expt 4) or two (Expt 5) tubers were planted in each pot. Nutrient solution was provided at frequent intervals. In Expt 4, the following total amounts of nutrients were applied per pot: 2.4 g N, 0.6 g P, 3.6 g K, 0.5 g Ca, 0.3 Mg and 8 ml of a trace element solution (Van Ittersum & Scholte, 1992b) and in Expt 5: 3.7 g N, 0.9 g P, 5.4 g K, 0.7 g Ca and 0.4 g Mg and 12 ml of the trace element solution were given per pot.

Tuber initiation was followed on some extra plants. In Expt 4, tuber initiation started about 31 (cv. Désirée) or 33 (cv. Diamant) DAP and in Expt 5 it started 26 (cv. Désirée) or 30 (cv. Diamant) DAP. The photoperiod treatments started 41 DAP (Expt 4) or 42 DAP (Expt 5). In Expt 4, haulms were pulled 83 DAP and tubers were harvested 92 DAP. In Expt 5, haulm pulling and harvest took place 70 and 81 DAP respectively.

Plant height and haulm fresh and dry weights were determined at haulm pulling. At harvest, individual tuber weights were recorded. In Expt 4, the ten heaviest (generally ≥25 g) tubers per pot and in Expt 5 all tubers heavier than 25 g (about 30 tubers per three pots) were stored for observations on dormancy (Van Ittersum, 1992b).

The sprouts (≥2 mm) were counted about 7 (Diamant) or 5 (Désirée) weeks after the end of dormancy in Expt 4, and about 6 (Diamant) or 3 (Désirée) weeks after the end of dormancy in Expt 5.

Results

Light intensity

Experiment 1. Shading clearly affected haulm development: stems were more elongated and leaves were darker green in colour. At haulm pulling, these effects were most obvious for the late and long shading treatments.

There was no interaction in yield and dormancy parameters between cultivar and shading. Data are therefore averaged over both cultivars. Shading markedly decreased tuber yield (Table 3). No differences were found between early and late shading, and long shading had the largest effect. The dry-matter concentration in the tubers was also lower, especially after early and long shading.

Table 3. Effect of shading during tuber bulking on some tuber parameters, averaged over two cultivars. Expt 1.

	Shading treatment				LSD P=0.05
	Control	Early	Late	Long	
Fresh weight (g/m²)	3660	3170	3190	2650	150
Dry-matter concentration (g/kg)	192	179	188	181	4.3
Duration of dormancy (DAT[a])					
cv. Diamant	124	126	120	117	
cv. Désirée	197	197	192	191	
Mean[b]	161	161	156	154	2.8
Spread in dormancy (days)	23	25	22	21	ns

[a]DAT=days after tuber initiation.
[b]The interaction between cultivar and shading was not significant.

Table 4. Effects of shading during tuber bulking on crop parameters, averaged over two cultivars. Expt 2.

	Shading treatment				LSD P=0.05
	Control	Early	Late	Long	
Haulm					
Dry weight (g/m²)	287	306	286	261	16.6
Tuber					
Fresh weight (g/m²)	3190	3020	3070	2740	104
Dry-matter concentration (g/kg)	209	203	203	201	3.0
Duration of dormancy (DAT[a])					
cv. Diamant	111	114	111	112	
cv. Désirée	196	198	194	194	
Mean	154	156	153	153	1.6
Spread in dormancy (days)	20	21	19	19	ns

[a]DAT=days after tuber initiation.

Table 5. Effect of shading during tuber bulking on crop parameters, averaged over two cultivars (except for spread in duration of dormancy where interaction was statistically significant at $P<0.05$). Expt 3.

	Shading treatment			
	0 %	50 %	75 %	
Haulm				
Dry weight (g/m²)	340	305	274	***
Tuber				
Fresh weight (g/m²)	2390	1740	1260	***
Dry-matter concentration (g/kg)	184	174	168	***
Duration of dormancy (DAT[a])				
cv. Diamant	135	130	128	
cv. Désirée	192	187	184	
Mean	163	158	156	***
Spread in dormancy (days)				
cv. Diamant	11	15	25	***
cv. Désirée	13	16	17	
Number of sprouts per tuber	1.5	1.5	1.7	

***Indicates a statistically significant effect of shading at $P<0.001$.
[a]DAT=days after tuber initiation.

Averaged over both cultivars, dormancy was shortened significantly by the late shading period (5 days) and the long shading period (7 days). There were no effects of shading on the spread in duration of dormancy (time lapse between 10 % and 90 % sprouting). The number of sprouts per tuber of cv. Diamant was not affected by shading (mean: 1.0 sprouts per tuber).

Experiment 2. The effects of shading on haulm development were comparable to those in Expt 1, but were less pronounced. Haulm dry weights were slightly higher after early shading, but significantly lower after long shading (Table 4). Shading slightly decreased the yield and dry-matter concentration of the tubers. Shading the crop hardly affected the dormancy of progeny tubers (Table 4) and no effects were found on the spread in duration of dormancy.

Experiment 3. Haulm dry weight was reduced by about 20 % and tuber yield by 47 % after 75 % shading (Table 5). Shading also decreased the dry-matter concentrations in the tubers.

Dormancy of the tubers was shortened by shading the crop, whereas the spread in duration of dormancy increased, especially for cv. Diamant. The number of sprouts per tuber was not affected by the shading treatments.

Photoperiod

Experiment 4. Haulm and tuber weight and tuber number were higher after a photoperiod of 18 h (P18) (Table 6). At haulm pulling, plant height was not influenced by the photoperiod (data not shown). The mean weight of tubers in the dormancy samples did not differ between P12 and P18.

The interaction between cultivar and photoperiod was statistically significant for the duration of dormancy. The dormancy of cv. Diamant was not influenced by the photoperiod, whereas that of cv. Désirée was prolonged by a longer photoperiod. The spread in dormancy was slightly larger for P18. The photoperiod had no effect on the number of sprouts per tuber after dormancy was over.

Experiment 5. The photoperiod had no effect on haulm and tuber growth, or on the number of tubers per pot (Table 6).

In both cultivars, the duration of dormancy was significantly shorter (about 1 week) after the long photoperiod. The spread in duration of dormancy was lower after the long photoperiod. For cv. Diamant the number of sprouts per tuber was highest in P18, whereas that of cv. Désirée was not affected by the photoperiod.

Table 6. Effect of photoperiod treatments after tuber initiation on various haulm and tuber parameters, averaged over two cultivars. Expts 4 and 5.

Parameter	Photoperiod (hours)		
	12	18	
Experiment 4			
Haulm dry weight (g/pot)	28.7	30.2	**
Tuber fresh weight (g/pot)	649	716	***
Number of tubers > 2.5 g per pot	14.6	16.9	***
Mean tuber weight in sample (g/tuber)	61.0	62.5	
Duration of dormancy (DAT[a])[b]			
cv. Diamant	130	128	
cv. Désirée	191	200	***
Spread in duration of dormancy (days)	17	20	*
Number of sprouts per tuber	1.7	1.8	
Experiment 5			
Haulm dry weight (g/pot)	30.7	31.0	
Tuber fresh weight (g/pot)	902	873	
Number of tubers >2.5 g per pot	19.6	19.4	
Mean tuber weight >25 g (g/tuber)	67.4	69.7	
Duration of dormancy (DAT[a])			
cv. Diamant	125	119	
cv. Désirée	174	167	
Mean	149	143	***
Spread in duration of dormancy (days)	20	16	**
Number of sprouts per tuber[b]			
cv. Diamant	1.7	2.5	***
cv. Désirée	1.2	1.2	

*, **, ***Indicate statistically significant effects of the photoperiod treatment at $P<0.05$, $P<0.01$ and $P<0.001$, respectively.

[a]DAT=days after tuber initiation.

[b]The interaction between cultivar and photoperiod was statistically significant.

Discussion

Light intensity. The effects of shading on haulm and tuber weights and dry-matter concentrations in the tubers clearly showed a relation with the type of weather during the shading periods and the degree of light reduction by the nets. In Expt 1 (1988) the cloudy weather and the 70 % light reduction of the nets resulted in serious yield losses and low dry-matter concentrations in the

tubers after shading the crop. In Expt 2 (1989) the effects were less pronounced because of very sunny weather, drier conditions and nets with only 50 % light reduction. Although the long period of shading in Expt 2 resulted in similar levels of irradiance as those in the 50 %-shading of Expt 3 (1990), the yield losses were less serious in Expt 2, perhaps because of the drier conditions in this experiment. In Expt 3, the absolute effects of 75 %-shading on tuber parameters were similar to those in Expt 1.

The dormancy of the tubers was shortened by up to 7 days after a late or long shading period in Expts 1 and 3. There were no shortening effects of shading on dormancy in Expt 2, perhaps because dormancy is only affected by very low light intensities shortly before haulm pulling, causing also a severe reduction in yield. Light intensity may be one of the factors causing variation in tuber dormancy between different tuber batches, e.g. when comparing batches from autumn and spring crops. However, it is unlikely that light intensity plays a major role in variation in tuber dormancy between years, since in my experiments the levels of irradiance in the shaded plots were very low, and yet dormancy was only shortened by up to 7 days.

It is unlikely that shading affected crop growth and dormancy through its effect on temperature. Temperature effects in the crop were small, and almost absent in the soil; larger differences in temperature during plant growth did not shorten the dormancy of the progeny tubers (Van Ittersum & Scholte, 1992b).

No negative relation was found between the duration of dormancy and the growth of axillary buds of the haulm (and consequently haulm weight). The early shading treatment of Expt 2 was the only treatment giving a significantly higher haulm weight, but this treatment gave a slightly prolonged dormancy. There was also no relationship between dormancy and dry-matter concentration in the tubers. In Expt 1, the early shading period resulted in a very low dry-matter concentration, but this treatment had no effect on dormancy.

In Expts 1 and 3, shading considerably reduced tuber yields and consequently affected the tuber size distribution. Thus tubers in the dormancy samples from the shaded plots were relatively larger than those in the samples from the unshaded plots. Although the relationship certainly does not always hold, larger tubers tend to be initiated earlier (cf. Struik et al., 1991) and therefore may end dormancy earlier (Van Ittersum & Struik, 1992). However, this cannot be the reason why dormancy was shortened after late or long shading. In Expt 1, early shading gave reductions in tuber yield similar to late shading, whereas dormancy was not shortened after the early shading.

Photoperiod. Tuber yields per pot were higher in Expt 5 than in Expt 4 because there were fewer pots per unit area and probably also because of higher rates of nitrogen in Expt 5. In Expt 4, the slightly higher haulm weight after the long photoperiod also resulted in higher tuber yields per pot, because the foliage did not cover the glasshouse floor completely. Generally, however, both haulm and tuber growth were hardly affected by the photoperiod treatments after tuber initiation. Struik et al. (1988) also found that short periods (about 2 weeks) of long days just after tuber

initiation hardly affected haulm and tuber growth, whereas, in contrast, brief or longer periods of long days at an earlier stage clearly increased haulm height and weight.

Photoperiod treatments had rather limited and inconsistent effects on the duration of dormancy. The direct effect of the photoperiod during growth on the duration of dormancy seems of no practical importance. However, short photoperiod conditions directly after planting promote tuber initiation and enhance maturation of the crop and may therefore lead to an earlier calendar date for the end of dormancy, especially when tubers are harvested when mature (cf. Emilsson, 1949).

General discussion on the relationship between growth conditions and dormancy of progeny tubers. The effects of the growth conditions on the duration of dormancy of seed tubers harvested immature were limited (Van Ittersum, 1992b; Van Ittersum & Scholte, 1992b). High rates of nitrogen after tuber initiation, as well as low light intensities during the last weeks of tuber bulking, shortened dormancy by up to 1 week. High temperatures during growth had a cultivar-dependent effect. In cv. Diamant, compared with the regime 18/12 °C (day 12 h/night) only very high temperatures (ca 30-32 °C) shortened dormancy by a maximum of 2-3 weeks. Compared with the regime 18/12 °C no regime with higher temperatures shortened dormancy of cv. Désirée, whereas some regimes even prolonged dormancy. The photoperiod had inconsistent effects on dormancy.

Generally, the variation in duration of dormancy was small *between* the different experiments reported in this series of papers, although there were some striking differences between experiments. For instance, the dormancy of cv. Diamant was rather long in 1990 (compare Tables 3-5). For cv. Désirée, the difference in dormancy between Expts 4 and 5 (Table 6) was large. These differences are hard to explain.

It has been suggested in a working hypothesis (Van Ittersum, 1992b) that a high nitrogen rate, high temperature, low light intensity and a long photoperiod may shorten dormancy because of their retarding effects on tuber initiation, or stimulating influence on second growth or haulm growth. High temperature, long photoperiod and, to a minor extent, nitrogen, delay tuber initiation, but they did not affect the duration of dormancy in a similar way. If dormancy starts at tuber initiation and its induction is associated with factors inducing tuber initiation, then the duration of dormancy is not unambiguously affected by factors which lower the tuberization stimulus.

A very high temperature during growth was the only treatment that caused second growth (heat sprouting). Second growth can be considered the result of an interruption in the stimulus to tuberize, and perhaps an interruption of dormancy of the tubers (Ewing & Struik, 1992). In one experiment, heat-sprouted tubers ended dormancy earlier than tubers grown at the same temperature without heat sprouts. However, the total tuber sample, containing a certain proportion of heat-sprouted tubers, did not always have a shorter dormancy than samples without heat-sprouted tubers (Van Ittersum & Scholte, 1992b). Conditions inducing second growth do not

necessarily shorten the dormancy period of the whole tuber batch.

For nitrogen treatments there was a negative correlation between haulm growth and the duration of dormancy. For treatments regarding temperature, light intensity and photoperiod this negative correlation was not found. I did not observe a close negative correlation between the growth of axillary buds on the haulm and the growth of apical buds on the tubers, although they are both second-order buds of stems (Krijthe, 1946; Van Ittersum, 1992b).

Dormancy is related to a balance of growth-inhibiting (abscisic acid) and growth-promoting hormones (gibberellins and cytokinins), although it is still uncertain whether this relation is causal (Van der Plas, 1987). A high nitrogen rate, high temperature, low light intensity and long photoperiod are all assumed to have, directly or indirectly via growth rates, a stimulating effect on the activity of gibberellins (Ewing & Struik, 1992). This could support the hypothesis that they all shorten the dormancy period. However, the results of my experiments only confirmed this for nitrogen and light intensity. Hormonal regulation of plant growth and development not only depends on the concentration of hormones, but also on the sensitivity of the organs to the hormones (Firn, 1986). Furthermore, the genetic difference in duration of dormancy between the two cultivars may be caused by differences in endogenous hormones. This could imply that the cultivars will be affected differently by environmental conditions. To clarify this, more research is necessary about the relation between plant hormones, environmental conditions and the duration of dormancy in different cultivars.

Burton (1968) stated that the effect of weather conditions, especially high temperatures, on the duration of dormancy might be exerted in two ways: on the environment of the tubers, as during storage, and indirectly via the foliage. My results suggest that as long as tubers are attached to the green foliage, the influence of the environmental conditions on the duration of dormancy is limited. The experiments with temperature during growth indicate that there is a kind of controlling influence of the foliage on the dormancy of the tubers.

In the present experiments, all factors were varied after tuber initiation and no re-initiation occurred because of second growth. However, when varied before tuber initiation, it might be expected that factors delaying tuber initiation (e.g. high temperature and long photoperiod) postpone the dormancy period and consequently the calendar date of the end of dormancy.

CHAPTER 5

SHORTENING DORMANCY AND ADVANCING GROWTH VIGOUR OF SEED POTATOES

SECTION 5.1

SHORTENING DORMANCY OF SEED POTATOES BY STORAGE TEMPERATURE REGIMES

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Summary

Four experiments (three with four cultivars, one with 20 cultivars) investigated the effect of different storage temperature regimes on the duration of dormancy of seed potatoes harvested immature. Regimes included constant temperatures (18 and 28 °C), hot pre-treatments (20 days at 28 °C and subsequently 18 °C) and cold pre-treatments (20 days at 2 °C and subsequently 18 °C).

Compared with 18 °C, storage at 28 °C slightly prolonged dormancy of some cultivars with a genetically short dormancy and shortened dormancy by up to 45 days in cultivars with a long dormancy. Some tubers of one cultivar lost their ability to sprout after storage at 28 °C for 90 days.

A hot pre-treatment shortened dormancy by 2-3 weeks on average, for all cultivars examined. A cold pre-treatment shortened dormancy by 2 weeks on average in some cultivars with a short dormancy and in all cultivars with a long dormancy.

Introduction

Dormancy of a potato tuber is defined as the physiological state in which autonomous sprout growth will not occur, even when the tuber is placed under ideal conditions for sprout growth (Reust, 1986). Dormancy ends when sprout growth can start, but for practical reasons in this paper, the presence of at least one sprout per tuber 2 mm long was taken as the indication that dormancy has ended.

Dormancy is desirable in ware potatoes that have to be stored for a long period. However, for seed tubers that have to be planted soon after their harvest, it is necessary to shorten or break dormancy. Numerous chemicals have been tested for their dormancy breaking potential, but generally, only a few (some very dangerous) have shown acceptable results (Burton, 1989). Storage in a controlled atmosphere with a low oxygen concentration or cutting of the seed, possibly in combination with dipping in dormancy-breaking chemicals, may be other ways to

shorten the dormancy period (Burton, 1989).

The storage temperature also markedly influences the duration of dormancy. Generally, it was found that the period after harvest until sprouting was shorter with increasing constant storage temperatures over the range of about 3-22 °C (Wright & Peacock, 1934; Schippers, 1956b; Burton, 1989). Data on the effects of high (≥25 °C) temperatures are very scarce. Hogetop (1930) investigated the effect of storage temperatures over the range 4.5-33 °C. However, his experiments started at least 4 months after harvest (storage at 2-4 °C) and thus, dormancy had already ended at the start of the experiments. Krijthe (1962b) and Davidson (1958) reported that for some cultivars, temperatures as high as 25 °C and 27 °C, respectively, reduced the dormancy period even more than did storage at 20 °C. However, only Davidson (1958) presented (one year's) data. Snell (1932) and Schippers (1955) found that storage regimes with short periods at 30-32 °C in combination with short periods at 1-2 °C may shorten the dormancy.

Many researchers reported that dormancy can be shortened by a short period (several weeks) of low temperatures (0-5 °C), followed by storage at temperatures favourable for sprout growth (Koltermann, 1927; Tedin, 1938; Emilsson, 1949; Schippers, 1956b; Krijthe, 1962c; Allen et al., 1978; Hutchinson, 1978b; Harkett, 1981; Van Loon, 1983; Turnbull & Hanke, 1985a). However, the differences in effects between cultivars or years are still poorly understood (Burton, 1989; Burton et al., 1992).

The essence of the current study was to investigate effects of short or long storage periods at high temperatures on dormancy, to compare these effects with those of cold pre-treatments, and to find relationships between the genetically determined duration of dormancy and the response to temperature regimes. The effects of the different storage regimes on the growth vigour of the tubers are presented in another paper (Van Ittersum, 1993).

Materials and methods

General procedure. In 1988-90, four experiments (Expts 1-4) were carried out with seed tubers produced on the experimental farm Ir. A.P. Minderhoudhoeve in the East Flevoland polder (52 °N lat.) on a calcareous marine clay soil. Pre-sprouted basic seed was used for the production of these tubers and agronomic and experimental details on their production and on the experiments are given in Table 1.

Haulm was removed by hand (1988 and 1990) or mechanically (1989) at a date depending on tuber size and aphid pressure. The seed tubers were lifted by machine and tubers between 35-50 mm in size and free from damage, disease, greening or deformations were collected and taken to the laboratory. They were stored in darkness at 18 °C and 80 % RH, until the start of the storage treatments. In 1989, tubers were disinfected against *Helminthosporium solani* and *Fusarium solani* with imazalil/thiabendazol (Lirotect Super 375 SC, Ligtermoet Chemie BV, Roosendaal, NL, 125/250 g/l a.i.); tubers were sprayed with 12 ml of the trade product per 100 kg tubers. In 1990,

Table 1. Details of the experiments.

Descriptor	Expt 1	Expt 2	Expt 3	Expt 4
Year	1989	1988	1989	1990
Planting date	May 3	April 21	May 3	April 10
Total available nitrogen (kg N/ha)	145	150	145	120
Tuber initiation (DAP[a])[b]	36-42	46-55	36-42	38-50
Haulm removal (DAP)[c]	68	82-89	69-75	72-87
Harvest (DAP)	96	104	93	93-101
Mean soil temperature at -5 cm (°C) between haulm removal and harvest	20.6	17.9	20.6	18.6
Start of the storage experiment				
Days after planting (DAP)	104	110	98	108
Days after haulm removal (DAH)	36	28-21	29-24	36-21

[a]DAP=days after planting.
[b]The range of dates includes the range for the different cultivars.
[c]The haulm of early maturing cultivars was usually removed earlier.

all tubers were disinfected against *Helminthosporium solani* with imazalil (Fungazalil 10L, Luxan, Elst, NL, 10 % a.i.); the seed was immersed for 2 sec in a 1 % solution of the trade product.

Samples comprised 30 tubers with a narrow range in weight and chosen so that the range in the total weight of individual samples did not exceed 1.5 % within a cultivar. After randomizing the samples over the treatments, they were stored in dark controlled environments with a relative humidity of 80 %. In the chambers with a temperature of 4 °C or lower, the humidity was mostly higher (about 90 %).

The number of sprouted tubers was recorded three times a week. The duration of dormancy of a sample was defined as the period in days from haulm removal until the moment that 80 % of the tubers (Reust, 1986) showed at least one sprout 2 mm long. The spread in duration of dormancy of a sample was defined as the time lapse between 10 % and 90 % sprouting (Van Ittersum, 1992a).

When the effects of different storage temperature regimes on dormancy are compared and a sprout length of 2 mm is the criterion for the end of the dormancy, the effects of temperature on dormancy and initial sprout growth are confounded. The optimum temperature for sprout growth is 15-20 °C (e.g. Burton, 1958; McGee et al., 1984), although when measured over a short period the optimum may be higher (Sadler, 1961). In the current research, the temperature during sprouting was always 18 °C, except when the effect of higher constant storage temperatures was investigated. These higher temperatures during sprouting could be supra-optimal for sprout growth and therefore the effects on dormancy of treatments with a high constant storage temperature may be somewhat underestimated.

Table 2. Survey of the storage temperature regimes applied in Expts 1-4.

Storage temperature regime	Expt 1	Expt 2	Expt 3	Expt 4
Constant temperatures				
18 °C	x	x	x	x
23 °C	x			
28 °C	x	x	x	x
32 °C	x			
Hot pre-treatments				
10 days 28 °C, subsequently 18 °C		x		
20 days 28 °C, subsequently 18 °C		x		x
Cold pre-treatments				
20 days 0 °C, subsequently 18 °C			x	
10 days 2 °C, subsequently 18 °C		x	x	
20 days 2 °C, subsequently 18 °C		x	x	x
30 days 2 °C, subsequently 18 °C			x	
20 days 4 °C, subsequently 18 °C			x	
Combined cold and hot pre-treatment				
10 days 0 °C, 10 days 28 °C, subsequently 18 °C			x	

Storage temperature treatments. The storage temperature treatments of Expts 1-4 are listed in Table 2. In all experiments, treatment at 18 °C was used as reference, since storage at 18 °C is about optimum for sprout growth. Moreover, in August and September a temperature of about 18 °C is common in uncontrolled storage rooms in Western Europe.

The objective of Expt 1 was to find the optimum constant storage temperature for shortening the duration of dormancy. Four cultivars (Désirée, Diamant, Draga and Jaerla) and three samples per treatment were used. The range of individual tuber weights was 20-50 g.

In Expt 2, the effects on dormancy of a high storage temperature, hot pre-treatments and cold pre-treatments were studied. The same cultivars as in Expt 1 and again three samples per treatment were used. The range of individual tuber weights in the samples was 40-80 g (cv. Jaerla 50-100 g).

In Expt 3, emphasis was given to different kinds of cold pre-treatments. Both the temperature during the cold period and its duration were varied. In addition, there was also one regime with a combined cold and hot pre-treatment (10 days at 0 °C, 10 days at 28 °C and subsequently 18 °C). In the cold pre-treatment at 0 °C, care was taken that the temperature was $\geq$ 0 °C. The same cultivars as in Expts 1 and 2 were used. Each treatment was applied to three samples of

tubers with an individual tuber weight of 40-80 g.

The objective of Expt 4 was to find possible trends in the response to storage regimes for cultivars differing in their duration of dormancy. The effects of three temperature regimes were compared with storage at 18 °C for the 20 cultivars listed in Table 6. Three samples per treatment were used and the range of individual tuber weights was 40-80 g (cv. Eigenheimer: 30-70 g).

Experimental set-up. The temperatures in the storage chambers could be maintained very well at the adjusted level (±0.5 °C; mean temperature ±0.1 °C). There was one storage chamber for each storage temperature. Each chamber was divided into three subunits (blocks), within which the tuber samples were stored in egg trays (one sample per tray). The treatment factors were storage temperature regimes and cultivars. Storage temperatures were randomized over the storage chambers and for each replication (block), the cultivars (and storage regimes if there were more storage treatments in one chamber, e.g. T28/18 and T2/18 after the period at 28 or 2 °C, respectively) were randomized over trays within a subunit. The experimental design was factorial nested.

Results

General cultivar and temperature effects. The duration of dormancy in the 18 °C treatment of cvs Diamant, Jaerla, Désirée and Draga was very consistent over the four experiments. Dormancy of cv. Diamant was much shorter than that of the other cultivars, whereas dormancy of cv. Draga was longest.

Since in all experiments the interaction between storage regimes and cultivars was highly significant ($P < 0.001$) for the dormancy parameters, the differences between temperature regimes are presented per cultivar.

Generally, the initial growth rate of sprouts of tubers stored at 28 °C continuously was very low. Sprouts grown at higher temperatures were shorter and thicker and showed more calcium-deficiency than those grown at 18 °C.

Experiment 1. The optimum constant storage temperature for shortening the duration of dormancy was about 28 °C for all cultivars (Table 3). In cv. Diamant the differences were very small between storage at 18, 23 and 28 °C, whereas in cvs Jaerla, Désirée and Draga dormancy of the 28 °C treatment was 50, 32 and 35 days shorter, respectively, compared with the 18 °C treatment. Storage at 32 °C was detrimental for cvs Diamant, Désirée and Draga; fewer than 80 % of tubers had sprouted by 186 days after haulm pulling (DAH). After about 100 DAH hardly any newly sprouted tubers were observed. The transfer of the samples from 32 °C to 18 °C, 186 DAH, did not change the percentage sprouted tubers. The buds of many tubers were dead (dark brown), but the tubers were still turgid.

Table 3. The duration of dormancy and the spread in duration of dormancy after constant storage temperatures, for four cultivars. Expt 1.

Storage temperature	Cultivar			
	Diamant	Jaerla	Désirée	Draga
Duration of dormancy (DAH[a])[b]				
18 °C	95	134	143	169
23 °C	97	110	124	147
28 °C	89	84	111	134
32 °C	- (6%)[c]	94	- (14%)[c]	- (38%)[c]
Spread in duration of dormancy (days)[d]				
18 °C	17	30	27	23
23 °C	20	21	19	14
28 °C	11	16	18	19
32 °C[e]	-	-	-	-

[a]DAH=days after haulm removal.
[b]LSD=4.6 (P=0.05) for comparison within cultivars between the temperatures 18, 23 and 28 °C.
[c]The total percentage sprouted tubers, 186 DAH.
[d]LSD=6.6 (P=0.05) for comparison within cultivars between the temperatures 18, 23 and 28 °C.
[e]At 186 DAH, the percentage of sprouted tubers was lower than 90 % for all cultivars.

Table 4. The duration of dormancy and the spread in duration of dormancy after different storage temperature regimes, for four cultivars. Expt 2.

Storage temperature regime	Cultivar			
	Diamant	Jaerla	Désirée	Draga
Duration of dormancy (DAH[a])[b]				
18 °C	86	125	136	157
28 °C	73	74	87	109
10 days 28 °C, subsequently 18 °C	62	118	132	148
20 days 28 °C, subsequently 18 °C	57	110	122	139
10 days 2 °C, subsequently 18 °C	68	106	117	144
20 days 2 °C, subsequently 18 °C	70	100	110	138
Spread in duration of dormancy (days)[c]				
18 °C	19	10	20	12
28 °C	13	9	17	13
10 days 28 °C, subsequently 18 °C	19	11	21	12
20 days 28 °C, subsequently 18 °C	11	11	24	12
10 days 2 °C, subsequently 18 °C	16	12	21	15
20 days 2 °C, subsequently 18 °C	12	15	27	16

[a]DAH=days after haulm removal.
[b]LSD=3.5 (P=0.05) for comparisons within a cultivar.
[c]LSD=5.1 (P=0.05) for comparisons within a cultivar.

Table 5. The duration of dormancy and the spread in duration of dormancy after different storage temperature regimes, for four cultivars. Expt 3.

Storage temperature regime	Cultivar			
	Diamant	Jaerla	Désirée	Draga
Duration of dormancy (DAH[a])[b]				
18 °C	78	121	140	159
28 °C	72	75	89	124
20 days 0 °C, subsequently 18 °C	68	110	123	142
10 days 2 °C, subsequently 18 °C	63	96	123	145
20 days 2 °C, subsequently 18 °C	68	101	122	143
30 days 2 °C, subsequently 18 °C	70	97	119	138
20 days 4 °C, subsequently 18 °C	69	110	119	140
10 days 0 °C, 10 days 28 °C, subsequently 18 °C	49	108	115	143
Spread in duration of dormancy (days)[c]				
18 °C	14	15	13	18
28 °C	25	9	14	23
20 days 0 °C, subsequently 18 °C	14	29	17	21
10 days 2 °C, subsequently 18 °C	19	26	14	18
20 days 2 °C, subsequently 18 °C	15	28	13	20
30 days 2 °C, subsequently 18 °C	7	21	18	25
20 days 4 °C, subsequently 18 °C	8	23	14	14
10 days 0 °C, 10 days 28 °C, subsequently 18 °C	4	34	70	15

[a]DAH=days after haulm removal.
[b]LSD=3.8 (P=0.05) for comparisons within a cultivar.
[c]LSD=6.2 (P=0.05) for comparisons within a cultivar.

In cv. Diamant the spread in duration of dormancy was smallest for storage at 28 °C. In the other cultivars the spread was smallest for the storage temperatures 23 and 28 °C.

Experiment 2. For cv. Diamant, dormancy was curtailed by 13 days (28 °C), 29 days (hot pre-treatment of 20 days) or 18 days (cold pre-treatment of 10 days) compared with storage at 18 °C (Table 4). For cvs Jaerla, Désirée and Draga, storage at 28 °C shortened dormancy by 51, 49 and 48 days, a hot pre-treatment of 20 days shortened dormancy by 15, 14 and 18 days, and a cold pre-treatment of 20 days shortened dormancy by 25, 26 and 19 days, respectively. In all cultivars, hot and cold pre-treatments of 20 days gave as much as or significantly more effect than pre-

treatments of 10 days.

The spread in duration of dormancy of cv. Diamant was smaller in the 28 °C treatment, hot pre-treatment of 20 days, and cold pre-treatment of 20 days than in the 18 °C treatment (Table 4). For cvs Jaerla, Désirée and Draga, the spread tended to be larger in the long cold pre-treatment than in the other regimes.

Experiment 3. In cv. Diamant, the 28 °C treatment showed a dormancy period 6 days shorter than the 18 °C treatment (Table 5). The cold pre-treatment of 10 days gave significantly more effect than the longer ones. The temperature during the cold pre-treatment did not have an effect. The combined cold/hot pre-treatment was very effective in this cultivar.

In cvs Jaerla, Désirée and Draga, storage at 28 °C curtailed dormancy by 46, 51 and 35 days (Table 5). For cv. Jaerla the cold pre-treatments at 2 °C had a larger effect than those at 0 or 4 °C. In cvs Désirée and Draga the effect of a longer cold period was slightly larger than the effect of a short cold period. The effect of the combined cold/hot pre-treatment was similar to that of the cold pre-treatments in cvs Jaerla, Désirée and Draga.

Compared with storage at 18 °C, the spread in duration of dormancy of cv. Diamant was larger in the 28 °C treatment and smaller in the cold pre-treatment of 30 days at 2 °C or that of 20 days at 4 °C (Table 5). The combined cold/hot pre-treatment resulted in an extremely small spread.

For cv. Jaerla, the spread was smaller in 28 °C and larger in the cold pre-treatments than in the 18 °C treatment (Table 5). The combined cold/hot pre-treatment resulted in an extremely large spread for cvs Jaerla and, particularly, Désirée. After moving the samples to 18 °C in this treatment, some tubers started to sprout almost immediately, some grew a sprout shorter than 2 mm which did not continue growth for many weeks, and others started to sprout about 2 months later. In cv. Draga the storage treatments had a smaller effect on the spread in duration of dormancy.

Experiment 4. The results for the four temperature treatments and 20 cultivars are listed in Table 6. The trends in the response of the cultivars are visualized by splitting the cultivars into three classes according to their dormancy at 18 °C: short dormancy period (<95 DAH), intermediate dormancy period (95-115 DAH) and long dormancy period (>115 DAH). At 122 DAH, the percentage of sprouted tubers of cv. Vivaks stored at 28 °C was 63 % and had hardly increased for the last 20 days of the treatment. At this date the samples were moved from 28 °C to 18 °C. Subsequently, some unsprouted tubers started sprouting, but the sprouts were unusually thin and elongated. The results of cv. Vivaks were not included in the means of Table 6.

In cultivars with a short dormancy, dormancy was not shortened on average by storage at 28 °C, but cultivars differed in their response (Table 6). A hot pre-treatment curtailed dormancy by 18 days on average, whereas a cold pre-treatment had a shortening effect of 5 days, but again cultivars differed in their response. In cultivars with an intermediate dormancy period, the average

Table 6. The effect of four storage temperature regimes on the duration of dormancy and the spread in duration of dormancy of cultivars with short, intermediate or long dormancy at 18 °C. Expt 4.

Cultivar	Duration (DAH[a])[b]				Spread (days)[c]			
	T18	T28	T28/18	T2/18	T18	T28	T28/18	T2/18[d]
Short dormancy at 18 °C								
Eigenheimer	62	79	55	65	12	21	9	10
Procura	70	74	52	69	21	11	6	10
Saskia	74	74	64	81	15	15	9	15
Diamant	86	80	57	69	23	15	6	15
Sirtema	91	70	67	77	27	13	16	7
Mean	77	76	59	72	20	15	9	12
Intermediate dormancy at 18 °C								
Nicola	98	100	78	94	12	14	17	15
Sirco	98	91	80	95	13	10	12	8
Mansour	101	85	86	100	17	15	17	15
Saturna	101	90	86	95	23	12	27	17
Prevalent	102	96	85	94	13	10	15	11
Irene	105	85	86	92	15	13	23	25
Bintje	109	99	94	84	16	10	28	13
Mean	102	92	85	94	16	12	20	15
Long dormancy at 18 °C								
Vivaks	118	-[e]	103	90	14	-[e]	23	23
Morene	118	87	105	103	12	9	19	16
Bildtstar	119	108	105	106	13	8	15	14
Marfona	119	98	98	105	20	22	32	18
Astarte	121	99	102	112	15	12	18	13
Jaerla	122	80	111	88	14	10	18	17
Désirée	134	91	118	114	16	9	38	28
Draga	153	116	138	145	16	13	16	35
Mean[f]	127	97	111	111	15	12	22	20

[a]DAH=days after haulm removal.
[b]LSD=4.5 (P=0.05) for comparisons within a cultivar.
[c]LSD=8.1 (P=0.05) for comparisons within a cultivar.
[d]T18=18 °C constant; T28=28 °C constant; T28/18=20 days 28 °C and subsequently 18 °C; T2/18=20 days 2 °C and subsequently 18 °C.
[e]At 122 DAH, the percentage of sprouted tubers was 63 % and did not increase at 28 °C.
[f]Excluding cv. Vivaks.

shortening effect of storage at 28 °C was 10 days (much variation between cultivars), whereas the hot pre-treatment shortened dormancy by 17 days (very consistent for the different cultivars). On average, dormancy was shortened by 8 days by a cold pre-treatment (more shortening for cultivars with a longer dormancy period). For cultivars with a long dormancy, storage at 28 °C curtailed the dormancy by 30 days on average, whereas hot or cold pre-treatments shortened dormancy by 16 days.

The correlation coefficients between the dormancy-shortening effect of a storage regime compared with storage at 18 °C on the one hand and the duration of dormancy at 18 °C on the other hand (for all samples) were 0.85 (n=57; $P<0.001$), -0.07 (n=60; ns) and 0.55 (n=60; $P<0.001$), for the regimes 28 °C, hot pre-treatment and cold pre-treatment, respectively.

For cultivars with a short dormancy period, the spread in duration of dormancy was very small in the hot pre-treatment, whereas on average cultivars with an intermediate and long dormancy period showed the largest spread in this treatment (Table 6). Cultivars with a long dormancy period tended to show a smaller spread in the 28 °C treatment and a larger one in the hot or cold pre-treatments.

The correlation coefficients between the duration of dormancy at 18 °C and the spread in duration of dormancy were smaller than 0.4 for all regimes, except for the hot pre-treatment (r=0.51; n=60; $P<0.001$).

Discussion

For each of the cultivars Diamant, Jaerla, Désirée and Draga, the storage regimes which had Expts 1-4 in common had very consistent effects on the duration of dormancy over these experiments. This justifies ascribing the differences in duration of dormancy between storage chambers to the storage regimes. The results for the spread in duration of dormancy were not very consistent over the different experiments. These results will be discussed only briefly.

Compared with storage at 18 °C, there are great possibilities of shortening tuber dormancy by storage regimes with high temperatures. For cultivars with a long dormancy, dormancy was shortened greatly (up to 45 days) by continuous storage at 28 °C. Storage with a hot pre-treatment (20 days 28 °C, followed by 18 °C) shortened dormancy by 2-3 weeks on average, in all cultivars examined. A cold pre-treatment (20 days 2 °C, followed by 18 °C) shortened dormancy by 2 weeks on average in cultivars with a long dormancy and in some cultivars with a short dormancy.

The dormancy-shortening effect of storage at 28 °C compared with storage at 18 °C was highly correlated with the duration of dormancy of the cultivar at 18 °C (Expt 4). Dormancy of cultivars with a short dormancy was hardly affected or was even prolonged, but in cultivars with a longer dormancy 28 °C was about the optimum constant temperature to shorten the time until sprouting (Expts 1 and 4). A constant storage temperature of 32 °C is too high for most cultivars, as was 28 °C for cv. Vivaks. In these cases, after about 2 months the buds and the tuber tissue around the

buds were dead, whereas the tuber was still turgid. Hogetop (1930) found 31 °C to be the maximum temperature for sprouting of (non-dormant) tubers. Higher temperatures caused 'black heart', probably due to lack of oxygen. However, there is some evidence that storage for short periods at 30-32 °C may shorten dormancy (Schippers, 1955).

In contrast with a constant temperature of 28 °C, the hot pre-treatment shortened dormancy by 2-3 weeks on average, in *all* cultivars. In Expt 2, a period of 20 days at 28 °C gave significantly more effect than a period of 10 days. In an extensive experiment with different periods of storage at 28 °C followed by storage at 18 °C, cvs Diamant and Désirée showed an optimum in the storage duration at 28 °C for shortening dormancy (Van Ittersum & Scholte, 1993). This strongly suggests that 28 °C is a favourable temperature for releasing dormancy, but supra-optimum for the subsequent sprout growth.

The very small spread in duration of dormancy in the hot pre-treatments for cultivars with a short dormancy also supports the idea of different temperature optima for releasing dormancy and for sprout growth. When moving the samples from 28 to 18 °C, no sprouts were seen but within 12 days of the transfer, 80 % of the tubers had at least one sprout 2 mm long. Storage at 28 °C seemed to work as a barrier for sprout growth.

Storage with a cold pre-treatment had less effect on dormancy of cultivars with a short dormancy (cvs Diamant and Sirtema excluded), whereas dormancy of cultivars with a longer dormancy was shortened by 2-3 weeks. This is in agreement with the findings of Allen et al. (1978) and Van Loon (1983).

The temperature during the period with low temperature did not seem to be critical in the range 0-4 °C. The results of Schippers (1956b) suggest that for some cultivars, the temperature during the cold period was not very critical over the range 1-10 °C. Increasing the storage duration at low temperatures from 10 days to 20 or 30 days (Expt 3) gave significantly more effect in cultivars with a long dormancy (excluding cv. Jaerla, Expt 3), whereas a period of 10 days tended to shorten dormancy most in cv. Diamant. This suggests that the optimum duration of the period with low temperatures is shorter, the shorter the dormancy of a cultivar. Van Loon (1983) found more effect of a 20-day cold pre-treatment than a 10-day pre-treatment for cultivars with a long dormancy. Generally, periods of low temperatures longer than 30-40 days had no extra effect or may prolong dormancy (Schippers, 1956b; Hutchinson, 1978b). Again, like 28 °C, a low temperature (0-5 °C) seems to be more favourable for releasing dormancy than 18 °C, but is clearly not so for sprout growth. Thus, temperature has not a linear effect on dormancy.

The effect of cold pre-treatments on dormancy may be mediated by changes in activity of plant growth regulators as there is evidence that compared with storage at 10-15 °C, a cold pre-treatment or storage at 2 °C decreases the activity of growth inhibitors (Thomas & Wurr, 1976) and increases the activity or concentration of growth-stimulating hormones such as of gibberellins (Thomas & Wurr, 1976) and cytokinins (Turnbull & Hanke, 1985b).

Krijthe (1962c) and Harkett (1981) stated that the timing of the cold pre-treatment is crucial for

the effect on dormancy. A late start, near the natural end of dormancy (thus, an temperature unfavourable for sprout growth), had less effect or even prolonged dormancy. This was confirmed in one of our own experiments (Van Ittersum & Scholte, unpublished results) for both a cold and hot pre-treatment. Therefore, it seems likely that the effects of storage temperature treatments on dormancy will be greater in tubers that are harvested before maturity. We believe that differences in the timing of the cold pre-treatments (shortly or long before the end of dormancy) between year or cultivars (partly) explain differences in effects of these treatments between years and cultivars.

In Expt 3, the combined cold and hot pre-treatment (10 days at 0 °C, 10 days at 28 °C, followed by storage at 18 °C) showed very specific effects on dormancy. Besides the very short dormancy in cv. Diamant, the very low spread for this cultivar and the extremely high spread for cv. Désirée were remarkable. Buds on some tubers of cv. Désirée reached the threshold length of 2 mm within one week of the transfer to 18 °C, whereas others showed initial sprout growth (about 1 mm) that did not continue. Goodwin (1966) observed similar symptoms: the growth of buds with a length of 0.7-3.2 mm stopped when he moved tubers from wet to dry conditions.

Van Ittersum & Scholte (1992b) showed that the influence of high temperatures during the growth of seed tubers on the duration of dormancy depends on the cultivar, but generally, this influence is limited. In contrast the current results showed that the effects of storage regimes immediately after harvest are large. It may be expected that high temperatures in the soil between haulm killing and harvest also shorten the dormancy (cf. Schippers, 1955).

Conclusions

1. Compared with storage at 18 °C, there is good potential for using other temperature regimes, especially ones with high (28 °C) temperatures, of shortening the dormancy of seed tubers harvested immature. The large effects of high storage temperatures on dormancy are also important for storage of potatoes in the tropics and subtropics.
2. There is a strong statistical correlation between the shortening effect of storage at 28 °C and the duration of dormancy of a cultivar at 18 °C.
3. Dormancy of all cultivars investigated was shortened by 2-3 weeks on average by hot pre-treatments (storage for 20 days at 28 °C and subsequently 18 °C).
4. Dormancy of cultivars with a relatively long dormancy, and of some cultivars with a short dormancy, was shortened by 2 weeks on average by cold pre-treatments (storage for 20 days at 2 °C and subsequently 18 °C).
5. Releasing dormancy and sprout growth probably have different optimum temperatures.

SECTION 5.2

ADVANCING GROWTH VIGOUR OF SEED POTATOES BY STORAGE TEMPERATURE REGIMES

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Summary

The advancing effect of four storage temperature regimes on the growth vigour of seed tubers harvested immature was investigated in a field experiment and two glasshouse experiments, using up to nine cultivars. The storage regimes were: 18 °C; 28 °C; 20 days 28 °C and subsequently 18 °C (hot pre-treatment); and 20 days 2 °C and subsequently 18 °C (cold pre-treatment).

The effects on dormancy were cultivar-dependent. However, at early planting (up to about 120 days after haulm removal=DAH) in all cultivars examined except one, tubers stored at 28 °C were superior in growth vigour to those stored at the other regimes. Generally, hot or cold pre-treatments also significantly improved the growth vigour compared with storage at 18 °C. At later planting (up to 180 DAH), the differences between the regimes diminished.

Storage at 28 °C advanced the growth vigour most, even in cultivars in which dormancy was ended earlier by other storage regimes.

Introduction

In many areas in the world, potatoes are grown more than once a year. In these areas, locally grown or imported seed often has to be planted soon after its harvest. This will give rise to a considerably delayed and irregular emergence and poor initial growth, because at planting the tubers are still in the phase of dormancy or poor growth vigour (Pushkarnath, 1976).

In a previous paper (Van Ittersum & Scholte, 1992a) it was shown that, compared with storage at 18 °C, dormancy can be shortened markedly by certain storage temperature regimes, especially by those with high temperatures. The effects on dormancy depended on the cultivar, but they were associated with the duration of dormancy of a cultivar at 18 °C. Storage at 28 °C slightly prolonged dormancy of cultivars with a very short dormancy and greatly shortened that of cultivars with a long dormancy. A hot pre-treatment (20 days at 28 °C, followed by storage at 18 °C) shortened dormancy of all cultivars investigated. Storage with a cold pre-treatment (20 days at 2 °C, followed by storage at 18 °C) shortened dormancy of some cultivars with a short dormancy

and of all cultivars with a long dormancy.

After dormancy, the performance of the seed tuber depends mainly on its growth vigour, which is the potential to produce a well-developed plant within a relatively short period of time. The effect of the growth vigour is particularly clear in the first phases of plant growth, thereafter, the influence of the prevailing environmental conditions becomes dominant. After dormancy, the growth vigour of a seed tuber gradually increases to a maximum, after which it decreases again (Krijthe, 1962b; Van der Zaag & Van Loon, 1987). The corresponding physiological state of the tuber is denoted by physiological age (Reust, 1986). The time scale of change in vigour is affected by the cultivar and storage temperature (Krijthe, 1962b).

The current research focused on the possibility of manipulating the seed tubers with storage temperature regimes in such a way, that a high growth vigour is obtained as soon as possible after the harvest of the seed. In this paper, the growth vigour of the seed tuber soon after its harvest is called the *early* growth vigour.

Materials and methods

General procedure. One field experiment in Israel (Expt 1) and two glasshouse experiments in Wageningen (Expts 2 and 3) were carried out. The experiments were partly continuations of the experiments described in Van Ittersum & Scholte (1992a) and were conducted with tubers produced in the East Flevoland polder (52 °N lat.). These tubers were harvested while immature (haulm removal at 70-90 days after planting) and were stored at different temperature regimes. Storage took place in dark controlled environments with 80 % RH.

Dormancy parameters were assessed as described in Van Ittersum & Scholte (1992a). The end of dormancy of a sample was defined as the moment that 80 % of the tubers showed at least one sprout 2 mm long.

Experiment 1. The origin and treatment of the tubers of cvs Diamant and Désirée until the start of storage were described in Van Ittersum & Scholte (1992a - Expt 1). The haulm of the seed crop was removed at 10 July 1989 and tubers were harvested 7 August (=28 days after haulm removal, 28 DAH). At 31 DAH, four storage temperature regimes were started: 18 °C (T18), 28 °C (T28), 20 days 28 °C and subsequently 18 °C (T28/18) and 20 days 2 °C and subsequently 18 °C (T2/18). Four samples (24 tubers of 30-50 g each) per treatment were used. At 79 DAH the T28 samples were transferred to 18 °C. At 87 DAH all tubers were desprouted (if sprouts were present), packed and 5 days later they were transported to Israel by air.

At 106 DAH (24 October 1989), the samples were planted in the Negev (31 °N lat.) on a poor sandy soil with 0.5 % organic matter. The experimental design was split-plot, with four blocks, cultivars as the main factor and storage temperature regimes as the split factor. Twenty-four tubers per plot were planted by hand, in a 20x92 cm arrangement. The plots were irrigated every

4-5 days with a total amount of 300 mm until haulm killing. Nitrogen was injected into the irrigation water, totalling 315 kg N/ha. The usual cultural practices were carried out. At 93 days after planting (DAP) the haulm was killed by a night frost. The experiment was harvested 125 DAP.

The start of the emergence of each plot was recorded. At 43, 54 and 68 DAP, the number of plants and the number of stems per plant was determined and a visual crop stand score was given. The score (0-10) represented the relative haulm development (0=no emerged plants, 10=best plot per cultivar and block). At harvest, total tuber fresh yields were determined, tubers were counted and they were graded (<35 mm, 35-60 mm, >60 mm, and misshapen tubers).

Experiment 2. This experiment was the continuation of an experiment described in Van Ittersum & Scholte (1992a - Expt 3). The haulm of the seed crop was removed at 11 July (cvs Draga and Jaerla) or 17 July (cvs Désirée and Diamant) 1989. The tubers for the experiment were harvested at 4 August. For all cultivars, the growth vigour of seed tubers following four temperature regimes was compared: 18 °C constant (T18), 28 °C constant (T28), 20 days 2°C and subsequently 18 °C (T2/18) and 10 days 0 °C, 10 days 28 °C and subsequently 18 °C (T0/28/18). Three samples (six 40-80 g tubers each) per treatment were used.

The assessment of the growth vigour started at the same date for all treatments of the one cultivar, i.e. once all T18-samples of that cultivar showed at least 90 % sprouting. Therefore, the planting dates for the tests were rather late compared with those in Expts 1 and 3, i.e.: 23 October 1989 (98 DAH - cv. Diamant), 29 November (141 DAH - cv. Jaerla), 22 December (158 DAH - cv. Désirée) and 8 January 1990 (181 DAH - cv. Draga). For each cultivar a randomized complete block design with three blocks was used. Twelve days before the planting of a test, the tubers were desprouted and pre-sprouted again in darkness at 18 °C and 80 % RH. Tubers were planted in a plastic tray (LxWxH=30x23x10 cm) filled with enriched peat soil. Trays were placed in a glasshouse at 18/12 °C (day 12 h/night); artificial light (35 W/m²; 400-700 nm) was given in addition to daylight for the whole day period. The test ended 28 DAP (cvs Diamant and Jaerla) or 35 DAP (cvs Désirée and Draga).

At harvest, the number of plants (=seed tubers that produced green plant parts) and the number of main stems was recorded. The haulm was cut at soil level and weighed both fresh and dry. The number of stems was expressed per plant and the haulm weight was expressed per planted tuber.

Experiment 3. Expt 3 was the continuation of an experiment already described in Van Ittersum & Scholte (1992a - Expt 4). Three groups of three cultivars, each differing in duration of dormancy at 18 °C, were chosen from the 20 cultivars of that experiment (Table 1). The haulm of the seed crop of the different cultivars was removed between 26 June and 6 July 1990. Tubers were harvested at 20 July. Four temperature regimes started at 27 July: 18 °C constant (T18), 28 °C constant (T28), 20 days 28 °C and subsequently 18 °C (T28/18) and 20 days 2 °C and subse-

Table 1. Planting dates (calendar date and in parentheses days after haulm pulling = 1 July 1990) and the growth period of the first and second growth vigour test (Test 1 and 2), for cultivars with short, intermediate or long dormancy at 18 °C. Expt 3.

Descriptor	Duration of dormancy of cultivars at 18 °C		
	Short[a]	Intermediate[b]	Long[c]
Test 1			
Planting date	17 September (79)	12 October (104)	29 October (121)
Growth period (days)	28	28	28
Test 2			
Planting date	19 October (111)	12 November (135)	10 December (163)
Growth period (days)	28	23	24

[a]cvs Diamant, Eigenheimer and Sirtema.
[b]cvs Nicola, Saturna and Sirco.
[c]cvs Désirée, Draga and Marfona.

quently 18 °C (T2/18). Three samples of 20 tubers of 40-80 g each were used per treatment (30-70 g in cv. Eigenheimer).

The tubers for T28 were transferred to 18 °C, one week after the moment that all the T28-samples of a cultivar showed at least 90 % sprouting to create uniform storage conditions in all treatments after the end of dormancy. At the time these samples were moved to 18 °C, they had been stored at 28 °C for 52 (cv. Sirtema) to 98 (cv. Draga) days.

The growth vigour of each group of cultivars was assessed two times (Tests 1 and 2). The planting dates were the same for all cultivars of each group (Table 1). For each test, the experimental design was split-plot with three blocks, cultivars as the main factor and storage regimes as the split factor; an experimental unit consisted of a sample of ten tubers. Test 1 took place when dormancy had ended for the samples of about two out of the four storage treatments. Test 2 started when all treatments of a group of cultivars had reached 100 % sprouting. The tubers were desprouted and pre-sprouted again in darkness at 18 °C and 80 % RH for 10 days. The tubers were planted as in Expt 2, in a plastic tray (LxWxH=45x30x10 cm). Trays were placed in a glasshouse at 18/12 °C (day 12 h/night). Artificial light (35 W/m²; 400-700 nm) was given from 08.00 till 20.00 h and in addition plants were exposed to natural light from 10.00 till 14.00 h to prevent malformations of the leaves. Test 1 ended 28 DAP. In Test 2 the growth period for the cultivars with an intermediate or long dormancy was ended before 28 DAP to avoid strong mutual competition for light among the plants within trays (Table 1).

The same observations were conducted as in Expt 2. The start of emergence in a tray was defined as the moment with the first visible green plant parts. In Test 2, for some cultivars tuber initiation had started at harvest. In these cases tuber weights were also determined. After 75 days

Table 2. The effect of four storage temperature regimes on the early growth vigour and tuber yields (after the haulm was killed by a night frost at 93 days after planting) of cvs Diamant and Désirée, in a field experiment in Israel. Expt 1.

Parameter	Storage temperature regime[a]				LSD P=0.05
	T18	T28	T28/18	T2/18	
cv. Diamant					
Duration of dormancy (DAH[b])	87	79	61	70	2.3
Start of emergence (DAP[c])	17	12	15	20	3.5
Emergence (%), 43 DAP	99	99	96	99	
Number of stems/plant, 43 DAP	1.3	2.4	2.0	1.5	0.27
Crop stand score[d], 43 DAP	6	10	8-9	7	1-2 [e]
Crop stand score, 68 DAP	9-10	8-9	8-9	9	ns
Tuber yield (kg/m²)	3.18	3.19	3.13	3.18	0.39
Number of tubers per m²	27	32	29	28	3.5
cv. Désirée					
Start of emergence (DAP)	35	17	22	20	3.5
Emergence (%), 43 DAP[f]	24 a	99 c	79 b	97 c	
Number of stems/plant, 43 DAP	1.1	1.4	1.0	1.0	
Crop stand score, 43 DAP	0-1	10	4	6-7	1-2 [e]
Crop stand score, 68 DAP	2-3	9-10	6	8	1-2 [e]
Tuber yield (kg/m²)	0.84	2.69	1.82	2.27	0.39
Number of tubers per m²	13	25	18	23	3.5

[a]T18=18°C constant; T28=storage at 28 °C for 48 days; T28/18=20 days 28 °C and subsequently 18 °C; T2/18=20 days 2 °C and subsequently 18 °C.
[b]DAH=days after haulm killing.
[c]DAP=days after planting.
[d]0=no emergence; 10=best relative haulm development per cultivar.
[e]The LSD should be used as an indication for significant differences. The LSD is smaller for scores near 0 or 10 than for scores around 5-6.
[f]The data were analysed after a logit transformation. Means followed by the same letter were not significantly different at $P \leq 0.05$ (*t*-test).

of storage, the weights of the tuber samples (including sprouts) stored at 18 and 28 °C were determined to assess weight losses due to evaporation and respiration after storage at high temperatures.

Results

The interaction between cultivars and storage treatments was statistically significant for all parameters in all experiments.

Experiment 1

In cv. Diamant the treatments had ended dormancy before the transport to Israel (92 DAH). T28/18 resulted in the shortest dormancy (Table 2).

The emergence of T28 was a little earlier than that of the other treatments. The final percentage of emergence hardly differed between the different treatments (Table 2). At 43 DAP, the number of stems per plant was highest for T28, the stem number of T28/18 was also significantly higher than that of T18. At the same date, the crop stand score was highest for T28 and lowest for T18. However, 25 days later there was a tendency for the reverse, although differences between the treatments were not significant.

Tuber yields did not differ between the storage treatments. The number of tubers per m^2 was 10-15 % higher for T28 than for the other treatments and the proportion by weight of tubers larger than 60 mm was slightly lower for T28 than for the other treatments (data not presented).

For cv. Désirée only T28 had ended dormancy (87 DAH), before the tubers were transported to Israel.

The emergence of T28 was slightly earlier than that of T2/18 and T28/18 and much earlier than that of T18 (Table 2). At 43 DAP the emergence of T28 and T2/18 was almost complete, whereas the percentage of emergence of T28/18 and T18 was only 79 and 24 % respectively. At 68 DAP, the percentage of emergence of T28/18 and T18 was 80 and 56 respectively (not tabled). The number of stems per plant of T28 was slightly higher than that of the other treatments. At 43 DAP the crop stand of T28 was superior to that of the other treatments and the crop stand of T2/18 and T28/18 was much better than that of T18. At 68 DAP the differences were slightly smaller, but still obvious.

Tuber yield of T28 was much higher than that of the other treatments (Table 2). T2/18 yielded 84 % of T28, T28/18 68 % and T18 31 %. The number of tubers per m^2 was also highest for T28 and lowest for T18. For T28, and to a lesser extent, T28/18 and T2/18, the percentage of tubers larger than 60 mm was higher than that of T18 (data not presented).

Experiment 2

The effects of the storage regimes on dormancy were described in Van Ittersum & Scholte (1992a - Table 5).

In the growth vigour test (carried out when dormancy of all treatments of a certain cultivar had ended), T28 resulted in the highest haulm dry weights for cvs Diamant and Jaerla and in the lowest dry weight for cvs Désirée and Draga (Table 3). In T28 of cv. Draga, only 45 % of the

Table 3. The effect of four storage temperature regimes on the early growth vigour of four cultivars in a glasshouse test. Plants were harvested 28 (cvs Diamant and Jaerla) or 35 (cvs Désirée and Draga) days after planting (for planting dates see Materials and methods). Expt 2.

Cultivar	Storage temperature regimes[a]				LSD P=0.05
	T18	T28	T2/18	T0/28/18	
Haulm dry weight (g/planted tuber)					
Diamant	0.67	2.32	1.52	1.28	0.36
Jaerla	1.53	2.08	1.17	1.81	0.46
Désirée	1.74	1.30	1.92	2.02	0.36
Draga	2.60	0.28	2.74	2.78	0.32
Number of stems per plant					
Diamant	1.1	3.3	1.2	1.4	0.41
Jaerla	1.7	3.0	1.3	2.0	0.42
Désirée	1.7	3.0	2.3	2.1	0.56
Draga	1.8	2.4	2.3	3.1	0.82

[a]T18=18°C constant; T28=28 °C constant; T2/18=20 days 2 °C and subsequently 18 °C; T0/28/18=10 days 0 °C, 10 days 28 °C and subsequently 18 °C.

tubers produced a plant and the haulm dry weight was very low. For cv. Diamant, T2/18 and T0/28/18 resulted in a significantly larger haulm dry weight than T18.

The number of stems per plant was much higher for T28 than for the other treatments of cvs Diamant, Jaerla and Désirée. In cv. Draga, only the difference in number of stems per plant between T0/28/18 and T18 was significant.

Experiment 3

The effects of the different storage regimes on the dormancy parameters were presented in Van Ittersum & Scholte (1992a - Table 6). After 75 days of storage, the tuber weight losses, averaged over nine cultivars, were about 8 and 11 % after storage at 18 and 28 °C respectively.

Test 1. The trends in the effects of the storage regimes on the start of emergence (in days after planting) were similar for the different cultivars. On average, the emergence of T28 started 12 DAP, whereas that of T28/18, T2/18 and T18 started 18, 19 and 21 DAP, respectively. Treatment T18 of cv. Draga was the only treatment that showed no emergence within the time lapse of the test. In T28 of all cultivars, the final percentage of emergence was (almost) 100, whereas in the other treatments of cvs Diamant, Saturna, Désirée and Draga, the final emergence was lower than 100% (especially T18).

T28 gave the highest haulm dry weight for all cultivars (Table 4; Fig. 1). Differences with the other regimes were very large, except for cv. Draga. The growth of T28 of this cultivar was

Table 4. The effect of four storage temperature regimes on the early growth vigour of nine cultivars. Plants were harvested 28 days after planting (for planting dates see Table 1). Expt 3 - Test 1.

Cultivar	Storage temperature regimes[a]			
	T18	T28	T28/18	T2/18
Haulm dry weight (g/planted tuber)[bc]				
Diamant	0.01 a	1.36 c	0.35 b	0.07 a
Eigenheimer	0.12 a	1.60 c	0.77 b	0.56 b
Sirtema	0.16 a	2.56 c	0.76 b	0.24 a
Nicola	0.37 a	1.88 d	1.27 c	0.68 b
Saturna	0.03 a	1.83 c	0.19 b	0.09 ab
Sirco	0.32 a	1.72 c	0.69 b	0.22 a
Désirée	0.72 a	1.79 c	1.35 b	1.16 b
Draga	0	0.30 b	0.19 ab	0.06 a
Marfona	0.45 a	2.62 b	0.34 a	0.45 a
Mean	0.24	1.74	0.66	0.40
Number of stems per plant[c]				
Diamant	1.1 a	1.5 b	1.2 a	1.1 a
Eigenheimer	1.2 a	1.9 b	1.8 b	1.7 b
Sirtema	1.1 a	2.5 c	1.4 b	1.1 a
Nicola	1.3 a	3.1 c	1.9 b	1.5 a
Saturna	1.0 a	2.4 b	1.1 a	1.0 a
Sirco	1.1 a	1.9 c	1.5 b	1.2 a
Désirée	1.4 a	2.2 b	2.0 b	1.6 a
Draga	0	3.7 b	1.2 a	1.0 a
Marfona	1.4 a	3.8 c	2.0 b	1.6 a
Mean	1.2	2.5	1.6	1.3

[a]T18=18°C constant; T28=28 °C constant; T28/18=20 days 28 °C and subsequently 28 °C; T2/18=20 days 2 °C and subsequently 18 °C.
[b]The analysis of variance was carried out per group of cultivars, after a $\log(x+1)$-transformation. Values of treatment T18 of cv. Draga were not used in the analysis of variance.
[c]For each cultivar: different letters indicate that differences between storage regimes are significant at $P \leq 0.05$ (*t*-test).

poor. For eight cultivars the treatment with the second highest haulm dry weight was T28/18. T2/18 gave a higher haulm dry weight than T18 in most cases, but differences were not always significant. T18 hardly produced any haulm dry weight for some cultivars.

For all cultivars the number of stems per plant was highest for T28 (Table 4). T28/18 also gave a higher stem number than T18, whereas T2/18 and T18 gave hardly more than one stem per plant.

Table 5. The effect of four storage temperature regimes on the early growth vigour of nine cultivars. The plants were harvested 23-28 (Table 1) days after planting (for planting dates see Table 1). Expt 3 - Test 2.

Cultivar	Storage temperature regime[a]				LSD P=0.05
	T18	T28	T28/18	T2/18	
Haulm dry weight (g/planted tuber)					
Diamant	1.19	1.95 (0.1)[b]	1.77	1.67	0.22
Eigenheimer	1.61	2.10 (0.4)	1.88 (0.2)	1.90 (0.3)	0.22
Sirtema	1.35	1.73 (0.3)	1.62	1.32	0.22
Nicola	1.16	2.15	1.68	1.87	0.29
Saturna	0.45	3.11	1.02	0.89	0.29
Sirco	1.11	1.87	1.47	1.15	0.29
Désirée	1.17	1.41	1.28	1.58	0.39
Draga	0.91	0.26	1.44	1.22	0.39
Marfona	1.18	1.91	1.14	1.12	0.39
Mean	1.12	1.83	1.48	1.41	
Number of stems per plant					
Diamant	1.3	2.6	1.9	1.6	0.39
Eigenheimer	2.9	3.9	2.7	3.0	0.39
Sirtema	1.4	2.8	2.0	1.2	0.39
Nicola	2.6	3.2	2.5	2.7	0.50
Saturna	1.7	4.1	2.4	2.0	0.50
Sirco	2.1	2.5	2.3	2.4	0.50
Désirée	2.3	2.7	2.8	3.0	0.62
Draga	2.9	3.5	3.3	2.6	0.62
Marfona	3.0	3.3	3.1	2.6	0.62
Mean	2.2	3.2	2.5	2.3	

[a]For explanation: see Table 4.
[b]In parentheses, tuber dry weight per tuber planted.

Test 2. On average, the emergence of T28, T28/18, T2/18 and T18 started 9, 11, 11 and 12 DAP, respectively. There was 100 % of emergence by the end of the test in all cases, except for T28 of cv. Draga, in which only 93 % of the tubers produced a plant (two tubers only produced small sprouts).

T28 gave the highest haulm dry weight for seven out of nine cultivars, but the differences with the other regimes were not always significant (Table 5). For cv. Désirée differences between the regimes were small, whereas for cv. Draga T28 gave a much lower haulm dry weight than the other regimes. Generally, the differences between T28/18 and T2/18 were small, whereas both tended to produce a higher haulm dry weight than T18. For cvs Diamant, Eigenheimer and Sirtema tubers had been formed, especially in T28.

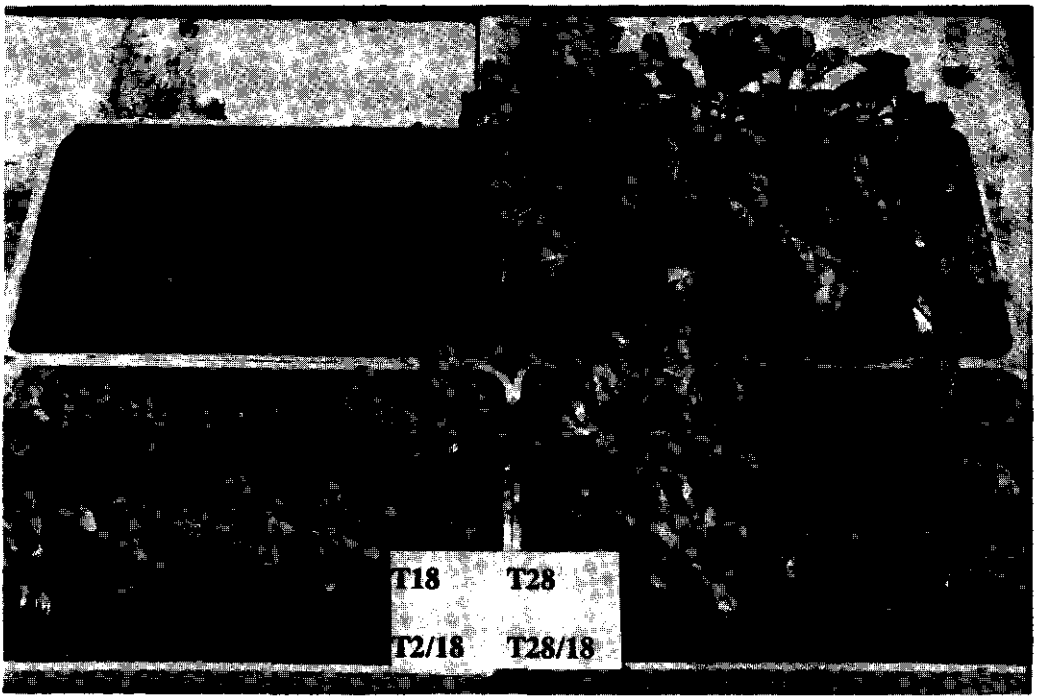

Fig. 1. The effect of storage temperature regimes on the growth vigour of seed tubers of cv. Eigenheimer, planted 17 September 1990 (79 days after haulm pulling) and photographed at harvest (28 days after planting). Test 1 - Expt 3. For codes and data, see Table 4.

T28 produced the highest number of stems per plant, except for cv. Désirée (Table 5). For some cultivars, the number of stems of T28/18 or T2/18 was slightly higher than that of T18.

Discussion

Effects on early growth vigour. Shortly after dormancy, an increasing physiological age of the seed tubers (provided that the tubers are not very aged and the growth vigour decreases again) results in an earlier emergence, more stems per tuber, faster initial growth, and earlier tuber initiation (Madec & Perennec, 1955; O'Brien et al., 1983; Bodlaender & Marinus, 1987). This higher growth vigour is particularly reflected in a higher haulm weight soon after planting. Therefore, haulm weight is a good parameter for measuring growth vigour.

The effects of the different storage temperature regimes on the growth vigour of seed tubers, planted 80-120 DAH (≡ during or soon after the end of dormancy; Expt 1 and Expt 3 - Test 1), were very clear and similar for the different cultivars. For all cultivars, except for Draga, the highest growth vigour was obtained after storage at 28 °C. T28/18 also had a very positive effect

on the early growth vigour, generally more than T2/18, although in Expt 1 the growth vigour of T2/18 of cv. Désirée was remarkably high. The differences in growth vigour between the treatments diminished when planting was postponed, but for most cultivars T28 still resulted in the highest growth vigour (Test 2 - Expt 3). Thus, storage at 28 °C until the end of dormancy of the tubers was most favourable to advance growth vigour. However, it can be unfavourable for cultivars with a long dormancy period and a relatively fast rate of physiological ageing (Van Ittersum et al., 1990) as the results of cv. Draga showed. For this type of cultivars, the period of storage at 28 °C should be shorter. This explains why treatment T28/18 was more favourable for cv. Draga.

Desprouting the sprouted tubers before planting probably increased the number of stems per plant since it broke apical dominance. Besides, high storage temperatures also had a positive influence on the number of stems per plant.

Absolute data of Test 1 are difficult to compare with those of Test 2 (Expt 3), since in Test 2 the light intensity in the glasshouses (4 h daylight per day, in autumn) was somewhat lower, and for cultivars with an intermediate or long dormancy the growth period was shorter (Table 1). Therefore, a decrease in haulm weight may have had several causes, but an increase in haulm weight is a very strong indication for an increase in growth vigour between Test 1 and Test 2. The haulm weights in Test 2 were always as high as or much higher than those in Test 1, except in T28 of some cultivars. Therefore, it can be concluded that the growth vigour of most treatments increased between Test 1 and 2 despite the high storage temperatures.

It could be expected that tuber weight losses due to transpiration and respiration are high at 28 °C. However, in my experiments storage of young tubers at 28 °C and 80 % RH only resulted in limited extra losses compared with storage at 18 °C.

Data in the literature on the effect of storage temperature regimes on the growth vigour of tubers soon after their harvest are scarce. Rosa (1928) compared storage temperatures ranging from 4 to 30 °C. After 4 weeks of storage the tubers were cut and planted. He found that storage at 30 °C gave the earliest emergence. When planting took place after about 2 months storage, differences between the treatments disappeared. Various researchers reported a higher total sprout length per tuber and, for some cultivars, slightly more sprouts per tuber, after a cold pre-treatment (Wurr & Allen, 1976; Allen et al., 1978; Susnoschi, 1981b; Van Loon, 1983).

Dormancy and early growth vigour. More than the effects of the regimes on early growth vigour, the effects on dormancy were very cultivar-dependent (Van Ittersum & Scholte, 1992a). T28 resulted in the highest growth vigour at early plantings, whereas dormancy of this treatment was not always shortest. For example, in cv. Diamant T28/18 resulted in a much shorter dormancy than T28 (Table 2 and Van Ittersum & Scholte, 1992a - Table 6), and in cv. Eigenheimer T28 gave a longer dormancy period than all other treatments (Van Ittersum & Scholte, 1992a -

Table 6). In Expt 3, after all T28-tubers of a cultivar had ended dormancy, the T28-samples were transferred to 18 °C. Therefore, for example for cvs Diamant and Eigenheimer the accumulated day-degrees since the onset of sprouting was lower in T28 than in other treatments. Nevertheless, T28 was superior in growth vigour. O'Brien et al. (1983) suggested that the physiological age of tubers is characterized by the temperature sum experienced since the start of sprouting. However, my experiments show that the temperature until the formation of a 2 mm sprout, is also important.

Van Ittersum & Scholte (1992a) discussed that 28 °C is a temperature favourable for releasing dormancy, but too high a temperature for subsequent sprout growth. The current experiments show, that high temperatures (such as 28 °C) also enhance physiological ageing. This also explains why T28/18 resulted in a higher early growth vigour than T18, but in a lower vigour than T28.

Effects on tuber yield. Generally, plants from physiologically older seed tubers ultimately develop less foliage and show earlier senescence. However, the effects of the age of the seed on tuber yields are hard to predict, because of possible interactions with environmental conditions during growth in the field (Perennec & Madec, 1980; Van der Zaag & Van Loon, 1987). Several researchers (Allen et al., 1979; Reust, 1982; O'Brien et al., 1983) suggested or found, that at early harvest the yield of physiologically older seed is higher than that of younger seed, whereas the reverse is more true at later harvest.

The results of cv. Diamant in Expt 1 showed that the seed of T28 emerged earlier, produced more stems, and had a rapid initial growth, but 68 DAP the haulm of T28 looked slightly more senescent already than that of the other treatments (Table 2). After the haulm was killed by a night frost 93 DAP, the tuber yields did not differ between the regimes and it cannot be excluded that, in case of a mature harvest, tuber yields of T28 would have been lower than those of the other treatments. For cv. Désirée, the advancing effects of T28 (and to a lesser extent of T2/18 and T28/18) were so large and the final emergence of T18 was so low, that the tuber yields differed greatly and it is unlikely that the differences would have been disappeared at mature harvest.

Conclusions

1. There is much potential for using storage temperature regimes to advance the growth vigour of seed potatoes harvested immature.
2. Compared with storage at 18 °C, storing seed tubers at 28 °C until the end of dormancy has the greatest advancing effect on the growth vigour. However, this treatment can be disastrous for cultivars with a long dormancy period and a rapid rate of physiological ageing.
3. Storage with a hot pre-treatment (20 days at 28 °C and subsequently 18 °C) also improves the early growth vigour compared with storage at 18 °C.

4. Generally, storage with a cold pre-treatment (20 days at 2 °C and subsequently 18 °C) advances growth vigour slightly more than storage at 18 °C.
5. The regime that results in the shortest dormancy does not always result in the greatest advancing effect on growth vigour.

SECTION 5.3

SHORTENING DORMANCY OF SEED POTATOES BY A HAULM APPLICATION OF GIBBERELLIC ACID AND STORAGE TEMPERATURE REGIMES

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Summary

In three experiments with cvs Diamant (short dormancy) and Désirée (long dormancy), the effect of a haulm application of gibberellic acid (GA) on the dormancy of seed potatoes harvested immature was investigated. Several storage temperature regimes were imposed to examine the interaction between GA and storage temperature. The storage regimes included 18 and 28 °C continuously, hot pre-treatments of different duration (different periods at 28 °C and subsequently 18 °C) and a cold pre-treatment (20 days at 2 °C and subsequently 18 °C).

A foliar spray of 375-750 g GA/ha 3-6 days before haulm killing shortened dormancy, and minimally induced sprouting before harvest. The magnitude of the GA effect depended on the cultivar and storage temperature regime. Compared with untreated tubers stored at 18 °C, dormancy was shortened by about 40 days by a GA application and storage at 18 °C (Diamant), or by about 90 days by a GA application and storage at 28 °C (Désirée).

Introduction

Since the beginning of this century, researchers have been searching for possibilities to shorten the dormancy period of seed potatoes in order to be able to plant the tubers as soon as possible after their harvest. Numerous chemical methods have been examined, but only a few proved to be useful (Denny, 1926; Burton, 1989). Since the 1950's, the dormancy-shortening effect of gibberellic acid (GA) has been known. It was also shown that the end of tuber dormancy of potatoes coincided with an increase in the activity of endogeneous gibberellins (Smith & Rappaport, 1961; Białek & Bielińska-Czarnecka, 1975).

Dipping or soaking cut tubers in GA appears to shorten dormancy, but the effects of GA on intact tubers are variable (Timm et al., 1960; Slomnicki & Rylski, 1964; Bruinsma et al., 1967). Tubers treated with GA may produce abnormally elongated sprouts and morphologically deviating plants (Rappaport et al., 1957; Timm et al., 1960; Choudhuri & Ghose, 1963), and dipping has also phytosanitary disadvantages. There are a few reports in the literature about efforts to shorten

tuber dormancy by means of a haulm application of GA at tuber initiation (Goburdhun, 1978) or 1-4 week(s) prior to harvest (Lippert et al., 1958; Tsukamoto et al., 1960). Such treatments seemed to offer promise, but have not been investigated in further detail.

Van Ittersum & Scholte (1992a) showed that there are large possibilities to shorten dormancy by means of some storage temperature regimes applied immediately after harvest.

In the present research, we investigated the effect of a haulm application of GA (3-14 days prior to haulm killing) on dormancy of seed tubers harvested immature, as well as its interaction with storage temperature regimes. The effects of GA and storage regimes on the growth vigour of seed tubers will be reported in another paper (Van Ittersum et al., 1993).

Materials and methods

General procedure

In 1988-90, three experiments (Expts 1-3) were carried out with cvs Diamant (short dormancy period) and Désirée (long dormancy period). Expts 1 and 3 were conducted on the experimental farm Ir. A.P. Minderhoudhoeve in the East Flevoland polder (52 °N lat.), on a calcareous marine clay soil. Expt 2 was carried out near Wageningen on a sandy soil. Agronomic and experimental details are given in Table 1.

The date of spraying the GA was chosen based on the size of the tubers, aphid pressure, and the weather forecast (calm and dry weather was preferred). 'Berelex' powder (ICI, Rotterdam, the Netherlands, 92 % gibberellin A_3) was dissolved in a small amount of ethanol. It is not sure whether the active compound in our experiments was indeed GA_3, or a possible impurity (e.g. GA_1, personal communication, E. Knegt, Wageningen Agricultural University). The GA solution was sprayed on the foliage in 1000 l water per ha, using a knapsack sprayer. The control treatments were sprayed with a mixture of water and the same amount of ethanol as used for the GA treatments, and all treatments were applied before noon.

The haulms were removed by pulling, except in Expt 1, where the haulms were killed chemically with dinoseb (DNPB in oil, Luxan, Elst, NL, 250 g/l a.i.). Twenty l/ha and 10 l/ha of the trade product were sprayed 96 and 114 days after planting, respectively. Tubers were left in the soil for 2-3 weeks after which they were harvested. Subsequently, tubers ranging in size from 35-50 mm, free from damage, greening, or diseases were taken to the laboratory. If present, the sprouts on tubers from plants treated with GA were removed, unless otherwise mentioned. In Expt 3, tubers were disinfected against *Helminthosporium solani* with imazalil (Fungazalil 10L, Luxan, Elst, NL, 10 % a.i.). The seed was immersed for 2 sec in a 1 % solution of the trade product. Tubers were stored in darkness at 18 °C and 80 % RH until the start of the storage regimes.

Dormancy parameters were assessed by regular (2-3 times a week) observations on tuber samples (30 tubers each; the range in the weight of individual samples did not exceed 1.5 % within cultivars). Dormancy of each stored tuber was deemed to have ended when at least one

vigorous sprout 2 mm long was present. Some (about 15 %) of the tubers from GA-treated plants produced very thin and elongated sprouts, without a thickened base. These sprouts often showed necroses and did not continue growth. Therefore, such tubers were not considered to have ended dormancy. Generally, not long after the formation of these sprouts, the tubers produced vigorous sprouts.

The duration of dormancy of a sample was defined as the period in days from haulm destruction until the moment that 80 % of the tubers had ended dormancy (Reust, 1986). The spread in duration of dormancy for a sample was characterized by the time lapse between 10 % and 90 % sprouting (Van Ittersum, 1992a).

In all experiments, a constant storage temperature of 18±0.5 °C was considered as the standard. In Expts 2 and 3, effects of other temperature regimes were related to this standard. Storage took place in dark controlled environments with 80 % RH.

Treatments and observations

Experiment 1. The experimental design of this experiment was a split-plot with four blocks, cultivars as main factor and GA treatments as split factor. Besides the control, the treatments were 70 or 375 g GA/ha 7 or 14 days before chemical haulm killing (DBH).

One 30-tuber sample (individual tubers 35-50 mm and 50-90 g) per plot was taken. All samples were stored at 18 °C.

Table 1. Experimental details of the Experiments 1-3.

Descriptor	Expt 1	Expt 2	Expt 3
Year	1988	1989	1990
Planting date	April 21	April 20	April 10
Plant spacing (cm)	25x75	25x75	25x75
Gross plot dimensions (m)	7x3	4.5x4.5	35x3
Net plot dimensions (m)	5x1.5	2.5x3	30x1.5
Total available nitrogen (kg N/ha)	150	175	120
Tuber initiation (DAP[a])[b]	49-55	38-48	40-44
Haulm destruction (DAP)	96	84	83
Harvest (DAP)	118	97	104
Mean soil temperature at -5 cm (°C) between haulm removal and harvest	19.8	21.5	19.0
Start of storage regimes:			
-Days after planting (DAP)	123	103	108
-Days after haulm destruction (DAH)	27	19	25

[a]DAP=days after planting.
[b]The first date indicates the date for Désirée and the second that for Diamant.

From the GA-treated plants a number of tubers that sprouted in the soil were harvested carefully and stored without desprouting. The dry-matter concentration in the tubers was determined by drying a sample of ca 400 g in an oven at 105 °C for 16 h.

The number of sprouts (≥2 mm) per tuber was recorded 99 (Diamant) or 150 (Désirée) days after haulm destruction (DAH).

Experiment 2. The experimental design of the field experiment was the same as in Expt 1. Besides the control, the treatments were 375 or 750 g GA/ha 3, 6, 9 days before haulm pulling (DBH).

Three 30-tuber samples (individual tuber weight 40-80 g) per plot were taken and stored at: 18 °C (T18), 28 °C (T28) or 20 days at 2 °C and subsequently 18 °C (T2/18).

At haulm pulling, haulm fresh and dry weights were recorded for the control and the sprays at 9 DBH. Tuber yields at harvest of all treatments were determined, and the dry-matter concentration in the tubers was assessed.

Experiment 3. Two GA haulm treatments (0 and 750 g GA/ha at 6 DBH) were applied in two replications, for both cultivars. Tuber samples were taken, comprising 30 tubers (15 tubers from each of the two replications; individual tuber weight 40-80 g), and stored for 0, 2, 4, 6, 8, 10, or 12 weeks at 28 °C before transfer to 18 °C (hot pre-treatments of different duration). Three samples per treatment were used.

Possible differences in the GA effect in relation to tuber weight were investigated by also storing 60 small (15-30 g) tubers per cultivar and GA treatment at 18 °C.

The number of sprouts ≥2 mm per tuber was recorded 3 weeks after the end of dormancy of each treatment.

Experimental set-up during the storage periods

There was one controlled environment (chamber) for each storage temperature, and storage temperatures were randomized over the chambers. Tubers were stored in egg trays (one sample per tray).

In Expts 1 and 2, the samples were ranked according to their plot number of the field experiment. In Expt 3, each chamber was divided into three units (blocks) and these units were subdivided in two subunits. The treatment factors were storage temperature regimes, cultivars and GA treatments. For each replication (block), the cultivars were randomized over the subunits and the GA treatments (and storage regimes if there were more storage treatments in one chamber, e.g. hot pre-treatments of different duration after they were transferred to 18 °C) were randomized over the egg trays within the subunits. The experimental design was a factorial nested design.

Results

General effects of GA. Foliar GA spray (especially the higher concentrations) resulted in foliage elongation and in a light-green leaf colour, first visible about 3 days after spraying. Approximately 8-10 days after the relatively early (7 to 14 DBH) sprays, some tubers of Diamant started to sprout in the soil. At harvest, many tubers from plants sprayed relatively early showed one or more elongated sprouts and occasionally (375 g GA/ha at 14 DBH, Expt 1) even secondary tubers. Diamant showed more sprouted tubers than Désirée. Tubers from later sprayed plants showed less (6 DBH) or no (3 DBH) sprouting at harvest. However, the slightly elongated buds which sometimes developed on tubers receiving these treatments were damaged at harvest.

During storage, the tubers from GA-treated plants frequently started to sprout from a lateral or basal eye, whereas tubers from untreated plants generally showed apical sprouts. Sprouts on tubers from treated plants initially lengthened rapidly. The sprouts were slightly more elongated than usual, but showed an ordinary thickened base with root primordia.

In all experiments, the interactions among cultivar, GA treatment, and storage regimes (Expts 2 and 3) were highly significant ($P < 0.001$) for dormancy parameters and the number of sprouts per tuber.

Experiment 1. Haulm killing was incomplete after the first spray with dinoseb. At harvest, most tubers from the GA-treated plants showed sprouts up to several centimetres long. These sprouts did not resume their growth during storage until the time that desprouted tubers also resumed sprouting.

Tuber dry-matter concentrations were significantly lowered by GA, up to 1.7 % by the earliest spray and the highest concentration (data not shown).

Dormancy was clearly shortened by a spray of 375 g GA/ha at 7 or 14 DBH (Table 2). For Désirée, the application at 7 DBH was more effective than the one at 14 DBH. The low GA concentration only gave a significant shortening for Diamant when applied 7 DBH.

For plants sprayed with 375 g GA/ha at 7 or 14 DBH, 1 and 3 %, respectively of the tubers of Désirée did not produce sprouts during storage.

The effects of GA on the spread in duration of dormancy (time lapse between 10 % and 90 % sprouting) were small, except for Désirée (Table 2). For this cultivar, the spread increased noticeably when the 375 g GA/ha concentration was applied.

Sprout number of tubers from plants sprayed with a high GA concentration was significantly ($P < 0.05$) higher than that of tubers from control plants (Diamant: 1.7 vs 1.2 sprouts per tuber and Désirée: 1.8 vs 1.5 sprouts per tuber). Sprouts on tubers from plants sprayed with 375 g GA/ha showed slightly more calcium deficiency than other treatments.

Table 2. The effect of different haulm applications of gibberellic acid (GA) on duration of tuber dormancy (days to 80 % sprouted) and the spread in duration of tuber dormancy (days between 10 and 90 % sprouted), for Diamant and Désirée.

Treatment	Duration (DAH[a])[b]		Spread (days)[c]	
	'Diamant'	'Désirée'	'Diamant'	'Désirée'
Control	79	142	23	17
70 g GA/ha at 14 DBH [a]	76	139	27	20
375 g GA/ha at 14 DBH	58	122	23	37
70 g GA/ha at 7 DBH	65	142	26	21
375 g GA/ha at 7 DBH	57	115	17	29

[a]DAH=days after haulm destruction; DBH=days before haulm destruction.
[b]LSD=4.5 (P=0.05), for comparisons within a cultivar.
[c]LSD=7.2 (P=0.05), for comparisons within a cultivar.

Table 3. The effect of a foliar spray with gibberellic acid (375 or 750 g GA/ha) at 3 or 9 days before haulm pulling (3 or 9 DBH) on the haulm, tuber and total weights, averaged over two potato cultivars (Diamant and Désirée).

Parameter	Control	GA application				LSD[a] P=0.05
		3 DBH		9 DBH		
		375	750	375	750	
Tuber fresh weight (g/m²)	3246	3335	3246	3331	3221	ns
Dry matter conc. tuber (g/kg)	204	202	194	191	187	6.7
Tuber dry weight (g/m²)	658	671	644	632	600	51
Haulm dry weight (g/m²)	476	-[b]	-[b]	504	551	55
Total dry weight (g/m²)	1134	-[b]	-[b]	1136	1151	ns

[a]ns=not significant.
[b]Not recorded.

Experiment 2. Within 20 h after the sprays at 6 DBH, 13 mm precipitation was measured. Consequently, these GA applications were quite ineffective and results are not presented.

For both cultivars, tuber fresh weights were not significantly affected, but tuber dry-matter concentrations were significantly lowered by high concentrations or early sprays of GA (Table 3). The tuber dry weight yield of plants treated with 750 g GA/ha at 9 DBH was significantly lower (ca 9 %) than that of the control, whereas the haulm dry weight of this treatment was significantly greater. Total dry weights were not affected by GA.

The 750 g GA/ha treatment tended to shorten dormancy more than the 375 g/ha GA treatment, but this was not clear after cold pre-treatments (Table 4). Differences between the sprays at 3 and

Table 4. The effect of different haulm applications of gibberellic acid (GA) on duration of tuber dormancy and the spread in duration of tuber dormancy at various storage temperature regimes, for Diamant and Désirée.

	cv. Diamant			cv. Désirée		
GA treatment/Storage regimes[a]	T18	T28	T2/18	T18	T28	T2/18
Duration of dormancy (DAH[b])[c]						
Control	95	83	70	152	86	131
375 g GA/ha at 9 DBH[b]	60	65	66	133	60	122
750 g GA/ha at 9 DBH	51	61	65	125	50	121
375 g GA/ha at 3 DBH	50	69	64	134	60	124
750 g GA/ha at 3 DBH	46	63	63	131	50	121
Spread in duration of dormancy (days)[d]						
Control	30	22	14	27	24	26
375 g GA/ha at 9 DBH	33	32	11	40	36	44
750 g GA/ha at 9 DBH	23	35	10	44	36	52
375 g GA/ha at 3 DBH	27	41	11	32	37	32
750 g GA/ha at 3 DBH	21	37	9	36	34	43

[a]T18=18 °C; T28=28 °C; T2/18=20 days at 2 °C and subsequently 18 °C.
[b]DAH=days after haulm pulling; DBH=days before haulm pulling.
[c]LSD=7.1 (P=0.05), for comparisons between GA treatments within a cultivar and storage regime combination, and 10.3 for all comparisons within a cultivar.
[d]LSD=8.7 (P=0.05), for comparisons between GA treatments within a cultivar and storage regime combination, and 10.5 for all comparisons within a cultivar.

9 DBH were small. For Diamant, GA had the greatest effect on dormancy duration (up to 49 days), when storage took place at 18 °C; many tubers started sprouting almost immediately after harvest. For Désirée, the largest effect (up to 36 days) was obtained after storage at 28 °C. The treatments 750 g GA/ha at 3 or 9 DBH plus storage at 28 °C shortened dormancy of Désirée by more than 100 days compared with the control treatment stored at 18 °C. For both cultivars GA only had a small extra shortening effect (10 days or less), when a cold pre-treatment (T2/18) was applied during storage.

Storage at 28 °C itself had a much larger effect on dormancy of Désirée than that of Diamant, whereas the effect of the cold pre-treatment was similar for both cultivars.

One percent of the Désirée tubers from treated plants and stored at 28 °C did not sprout during storage.

For T28 of Diamant, and all regimes of Désirée, the GA treatments resulted in a much larger spread in duration of dormancy than the control treatment (Table 4).

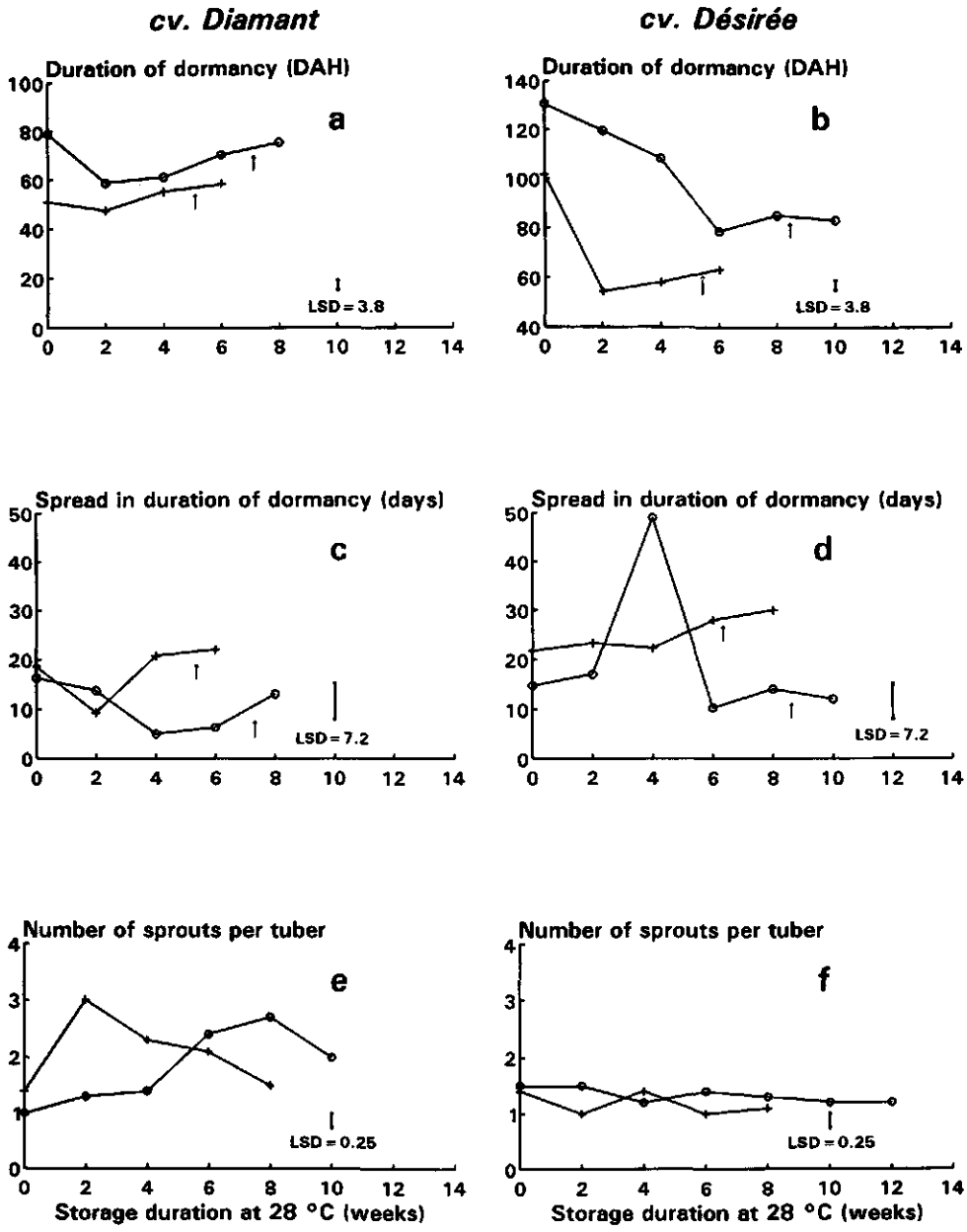

Fig. 1. The effect of a foliar spray of gibberellic acid (750 g GA/ha at 6 days before haulm pulling) and different storage periods at 28 °C before transfer to 18 °C on the duration of dormancy (a and b; DAH=days after haulm pulling), the spread in duration of dormancy (c and d) and the number of sprouts (≥2 mm) per tuber 3 weeks after the end of dormancy (e and f), for Diamant and Désirée. The vertical bars denote the LSD (P=0.05) for comparisons between treatments. The arrows indicate the date that 80 % (Fig. a,b) or 90 % (Fig. c,d) of the tubers were sprouted at 28 °C. o=no GA; + = +GA.

Experiment 3. For Diamant, GA had a shortening effect of 28 days when storage took place at 18 °C (Fig. 1a, 0 weeks), whereas the effects were smaller after hot pre-treatments of 2 or more weeks. For Désirée, the shortening effect of GA was 29 days at 18 °C, but the effect increased up to 66 days after hot pre-treatments of 2-4 weeks (Fig. 1b). For both cultivars, the treatments with the shortest dormancy showed sprouted tubers very soon after the start of storage (25 DAH).

All cultivar and GA treatment combinations showed a minimum duration of dormancy, but after different storage durations at 28 °C (Fig. 1a,b). The storage duration at 28 °C resulting in this minimum duration of dormancy was shorter for tubers from GA-treated plants, and shorter for Diamant than for Désirée.

Two percent of the Diamant tubers from treated plants and stored for 6 weeks at 28 °C did not sprout at all. For Désirée, this percentage varied from 1 to 6 % for tubers from GA-treated plants and stored for 0-6 weeks at 28 °C.

There was no significant difference in the dormancy-shortening effect of GA on large tubers and small tubers, when storage took place at 18 °C (data not shown).

The spread in duration of dormancy increased by GA, when sprouting took place at 28 °C (Fig. 1c,d). For Diamant, hot pre-treatments slightly longer than the ones resulting in the shortest dormancy resulted in very small spreads. Tubers from untreated plants of Désirée and stored for 4 weeks at 28 °C showed an extremely large spread.

In Diamant, GA increased the number of sprouts per tuber after storage at 18 °C or after short hot pre-treatments, whereas the opposite was true after storage with longer periods at 28 °C (Fig. 1e). Without a GA application the sprout number increased the longer the tubers were stored at 28 °C, but it decreased again after a maximum number was reached for 8 weeks storage at 28 °C. This maximum sprout number followed by a decrease occurred in a treatment with a much shorter storage duration at 28 °C for tubers from treated plants. The GA application and storage regimes had little effect on the sprout number with Désirée (Fig. 1f).

Discussion

Effect of GA. A haulm application of GA, shortly before haulm killing, has a tuber dormancy-shortening effect of many weeks. Over the range of 3 to 14 days before haulm killing, the moment of application did not seem to be of great importance. It seems that exogenous GA is transported readily in the entire conductive vascular system of a plant (Moore, 1989). A late application (3-6 DBH) has several advantages. It resulted in minimal sprouting before harvest and therefore is more favourable from a phytosanitary point of view since at harvest sprouts will break and cause tuber injuries (Lippert et al., 1958). Moreover, a late application did not cause second growth phenomena and had no negative effects on tuber yields (cf. Fischnich et al., 1959; Struik et al., 1989b). The effect of the concentration of the application seemed to be fairly limited over the range of 375-750 g GA/ha, whereas low concentrations are clearly less effective (Rappaport et

al., 1958). It is important that the GA is taken up before significant rainfall occurs.

The shape and morphology of the sprouts on tubers from GA-treated plants differed only slightly from those on tubers from untreated plants, in contrast to sprouts on *tubers* treated with GA (Rappaport et al., 1957; Hartmans & Van Es, 1979). A small disadvantage of the haulm treatment with GA may be that a few (1-6 %) of the tubers (especially of Désirée) lost their sprouting capacity. This was more clear if tubers were stored at 28 °C.

Sprouts that were formed when the tubers were still attached to the mother plant did not continue their growth after harvest (or perhaps not after haulm killing). This shows resemblance to the findings of Fischnich et al. (1959) and Madec & Perennec (1969), and to the behaviour of heat sprouts formed on tubers when plants were exposed to high temperatures (Van Ittersum & Scholte, unpublished results). Madec & Perennec (1969) treated cuttings with GA and the tubers on the cuttings started sprouting subsequently (or regrowing according to their terminology). The sprouts did not continue to grow after harvest, whereas during storage sprouting of tubers from treated cuttings was advanced by several weeks compared with tubers from untreated cuttings. They suggested that absence of bud growth before and after harvest is not controlled by the same factors. Sprouting of tubers when they are still attached to the plant is due to a temporary interruption of the inhibition of the buds by the plant.

In most cases, a haulm application of GA resulted in a larger spread in duration of dormancy within the tuber samples. There is no reason to assume that this larger spread is due to a different GA effect on dormancy of tubers of different sizes (Expt 3).

Generally, the number of sprouts produced by tubers from GA-treated plants was only slightly higher than that produced by tubers from untreated plants, despite the fact that sprouts grown before harvest were removed and some buds may have been damaged at harvest.

Interaction between GA and storage temperature regimes. For Diamant, the effect of a GA application on dormancy was smaller after hot pre-treatments than after storage at 18 °C, whereas for Désirée the effect of GA was larger after short hot pre-treatments than after storage at 18 °C (Expt 3). This seems plausible if both high GA concentrations in the tuber and storage at 28 °C are effective in releasing dormancy, but that 28 °C is a supra-optimum temperature for sprout growth (Van Ittersum & Scholte, 1992a). Apparently for Diamant (genetically short dormancy), the spray with GA almost suffices to release dormancy, and subsequent storage at 28 °C delays sprout growth. For Désirée (genetically long dormancy), the tubers still respond to storage at 28 °C after a GA treatment. In this reasoning, it is also not surprising that the duration of storage at 28 °C resulting in the shortest dormancy was greater for both cultivars when the foliage was not sprayed with GA, and greatest for Désirée (Fig. 1a,b). Besides the concentration of plant hormones, the sensitivity of the plant tissue to these substances is important (Trewavas, 1981). It might be surmised that storage at 28 °C increases the sensitivity to GA, because for Désirée the effect of GA was much greater after hot pre-treatments of 2-4 weeks than after continuous storage

at 18 °C.

The very small spread in duration of dormancy after hot pre-treatments slightly longer than the ones resulting in the shortest dormancy of Diamant (4-6 weeks at 28 °C without a GA spray, and 2 weeks at 28 °C with a GA spray) supports the assumption that 28 °C is favourable to release dormancy, but supra-optimum for subsequent sprout growth. At the end of the 28 °C-periods, all tubers are ready for sprouting and buds will grow rapidly when the temperature for sprout growth is optimum (15-20 °C; Burton, 1989). For Désirée, these trends were not evident. It is remarkable that for tubers from untreated Désirée plants, a hot pre-treatment of 4 weeks (slightly shorter than the one resulting in the shortest dormancy) was enough to break dormancy of only some of the tubers, whereas dormancy of other tubers from the same harvest was hardly shortened, giving rise to a very large spread (Fig. 1b). In other experiments we also found that storage treatments with short periods of high or low temperatures may result in a very large spread in duration of dormancy (Van Ittersum & Scholte, 1992a).

It is not surprising that a cold pre-treatment had minimal shortening effect on tuber dormancy for Diamant plants sprayed with GA (Table 4), as some tubers from plants sprayed with GA started sprouting almost immediately after harvest. For Désirée, the effect of GA was also small after a cold pre-treatment. An interaction between the effect of GA and a cold pre-treatment is conceivable if a cold pre-treatment results in a higher GA activity (Thomas & Wurr, 1976). This possibly implies smaller effects of GA after cold pre-treatments.

Conclusions

Dormancy of seed tubers harvested immature can be shortened markedly by a foliar spray of GA 3-6 days before haulm killing, with minimal pre-harvest sprouting or negative effects on sprout morphology. The effect of GA on dormancy depends highly on the cultivar and storage temperature regime. The duration of dormancy of Diamant and Désirée was reduced by 30-50 or 80-100 days, respectively, with a foliar spray of GA and storage at an appropriate temperature regime. Part of the interaction among cultivar, GA, and storage temperature regime can be explained by the assumption that both GA and storage at 28 °C are effective in releasing dormancy, whereas 28 °C is too high a temperature for sprout growth.

SECTION 5.4

ADVANCING GROWTH VIGOUR OF SEED POTATOES BY A HAULM APPLICATION OF GIBBERELLIC ACID AND STORAGE TEMPERATURE REGIMES

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Summary

Seed tubers that are planted soon after their harvest give low yields because of dormancy and low growth vigour. In the research reported in this paper, we investigated the advancing effect of a haulm application of gibberellic acid (750 g GA/ha) 6 days before haulm pulling and its interaction with storage temperature regimes on the growth vigour of immaturely harvested seed tubers of three cultivars. The effects on tuber yield were also examined in one experiment. The storage regimes were: 18 °C continuously, hot pre-treatments of different duration (different periods at 28 °C and subsequently 18 °C) and a cold pre-treatment (20 days at 2 °C and subsequently 18 °C).

Both a foliar spray with GA and storage at 28 °C enhanced physiological ageing of the tubers and greatly advanced the growth vigour, without negative effects on the morphology of the plants. There was a clear interaction between the GA treatment and the storage temperature regime.

At early planting, the effect of the treatments on tuber yield were small for Diamant (short dormancy), but strongly positive for Désirée and Draga (long dormancy).

Introduction

In countries where two crops of potatoes are grown in succession within one year, often dormant seed tubers from the previous crop or young imported seed tubers are used. Consequently, plant emergence is slow and erratic, resulting in an uneven plant stand and moreover, many plants are singly stemmed. Hence, actual yields are much lower than potential yields (Sikka, 1982).

Breaking or shortening the dormancy of the seed tubers could improve their performance. However, after dormancy the physiological state (physiological age) of the tuber may still be sub-optimal for optimal crop growth. The physiological age of the tuber is particularly reflected in its growth vigour, which is defined as the potential to produce a well-developed plant within a

relatively short period of time. After the end of dormancy, the growth vigour increases gradually until a maximum, whereupon the vigour decreases again (Van der Zaag & Van Loon, 1987). The relation between the growth vigour and the chronological age of the tuber depends on several factors, especially the cultivar and the storage temperature (Krijthe, 1962b; Van der Zaag & Van Loon, 1987; Van Ittersum et al., 1990). The physiological age of the tubers also affects the growth pattern of the plants produced by the tubers, but this also depends on the environmental conditions. Physiologically older seed tubers may result in earlier senescence of the plants, relatively high tuber yields at early harvest and lower yields at mature harvest (O'Brien et al., 1983; Van der Zaag & Van Loon, 1987).

In a previous paper, we showed that dormancy of seed tubers harvested immature can be shortened by many weeks, by means of a foliar spray of gibberellic acid (GA) on the seed crop, shortly before haulm killing, and by different storage temperature regimes (Van Ittersum & Scholte, 1993).

In the current paper, research on the advancing effects of a haulm application of GA and its interaction with storage temperature regimes on the growth vigour of seed tubers harvested immature is presented. In one experiment, the effects on tuber yields were also examined.

Materials and methods

General procedure. Several preliminary experiments were carried out, which led to the design of the experiments described in this paper. The results of the preliminary experiments supported those of the experiments reported here.

A greenhouse experiment carried out in Wageningen (Expt 1) and a field experiment conducted in Israel (Expt 2) will be presented. The first part of these experiments (production of the seed tubers) was carried out in the East Flevoland polder (52 °N lat.). The foliage of the seed crops was sprayed with 0 or 750 g gibberellin A_3 ('Berelex' powder, ICI, Rotterdam, NL, 92 % gibberellin A_3) per ha, 6 days prior to haulm pulling. The tubers of these crops were harvested immaturely (haulm pulling took place at ca 85 days after planting) and stored at different storage temperature regimes in dark controlled environments with 80 % RH.

Dormancy was deemed to have ended when 80 % of the tubers showed at least one vigorous sprout 2 mm long.

Experiment 1. The first part of this experiment with cvs Diamant and Désirée was described in Van Ittersum & Scholte (1993 - Expt 3). The GA was applied at 26 June 1990; 6 days later the haulms were removed and the tubers were harvested 23 July. At 27 July (25 days after haulm pulling=DAH), hot pre-treatments (HT) of different duration started: 0, 2, 4, .., 16 weeks storage at 28 °C, before transfer to 18 °C (HT0, HT2, HT4,...., HT16; the GA treatments are coded with GAHT0, GAHT2, etc.). The duration of dormancy was assessed on three tuber

samples (30 tubers of 40-80 g each). Extra tubers of similar weight were stored for the growth vigour tests.

Growth vigour was assessed three times (Tests 1-3). The planting dates of the tests were: 79, 120 and 148 DAH. For each test, the experimental design was a split-plot with three replications (blocks), cultivars as the main factor and GA treatments and storage regimes as split factors; an experimental unit consisted of a tuber sample of ten tubers. In Test 1, hot pre-treatments of 0, 2, 4 and 6 weeks (for both cultivars and GA treatments) were compared, in Test 2, hot pre-treatments of 0, 2, 4, 6, 8 and 12 weeks, and in Test 3, hot pre-treatments of 0, 2, 4, 6, 8, 12 and 16 weeks. Eleven days before the planting of a test, ten tubers per treatment and replication were desprouted and pre-sprouted in darkness at 18 °C and 80 % RH. Tubers were planted in a plastic tray (LxWxH=45x30x10 cm) filled with enriched peat soil and placed in a greenhouse at 18/12 °C (day 12 h/night). Artificial light (35 W/m²; 400-700 nm) was given from 0800 to 2000 HR and in addition, plants were exposed to natural light from 1000 to 1400 HR to prevent malformations of the leaves due to only artificial light. For Désirée, all tests ended 28 days after planting (DAP). For Diamant, Test 1 ended 28 DAP, but Tests 2 and 3 ended 22 DAP to avoid strong mutual competition for light among plants within a tray.

The start of emergence of a tray was defined as the moment with the first visible green plant parts. At harvest, the number of plants (=tubers that produced green plant parts) and the number of stems were recorded. The haulms were cut at soil level and weighed both fresh and dry. The number of stems was expressed per plant and the haulm weight was expressed per tuber planted. If tubers did not produce a plant within the time lapse of the test, they were examined for the production of non-emerged sprouts that might form stems later.

Experiment 2. In the first part of this experiment the foliage of the seed crop (for details see Van Ittersum & Scholte, 1993: Table 1: Expt 3) of three cultivars (Diamant, Désirée and Draga) was sprayed with 0 or 750 g GA/ha at 6 days before haulm pulling. The experimental design of this part of the experiment was a randomized complete block design, with four blocks and cultivars and GA treatments as factors. The haulms were removed at 2 July 1990 and the tubers were harvested at 23 July and stored in darkness at 18 °C. At 1 August (30 DAH), four storage temperature regimes started: 18 °C (T18 or GAT18), 28 °C (T28 or GAT28), 20 days at 28 °C and subsequently 18 °C (T28/18 or GAT28/18) and 20 days at 2 °C and subsequently 18 °C (T2/18 or GAT2/18). Two tuber samples (30 tubers of 40-80 g each) per treatment and replication were stored. At 79 DAH, the T28 samples were also transferred to 18 °C.

At 85 DAH, one sample per treatment and replication was disinfected with pencycuron (Monceren, Bayer Nederland BV, Arnhem, NL, 250 g/l a.i.; tubers were immersed in a 3 % solution of the trade product), desprouted (if sprouts were present) and packed. At 92 DAH, the samples were transported to Israel by air. Dormancy was assessed in Wageningen on the remainder of the tuber samples. For Draga, samples of only three treatments (T18, T28, GAT28)

were transported to Israel.

At 111 DAH (21 October 1990), the samples were planted on a poor sandy soil (90 % sand, 6 % clay; 0.5 % organic matter; pH=6.9), in the Negev (31 °N lat.). The experimental design was split-plot, with four blocks, cultivars (Diamant and Désirée) as the main factor, and GA treatments and storage regimes as split factors. The samples of Draga were planted in a separate randomized complete block design (four blocks and a treatment factor with three levels). Twenty-four tubers per plot were planted by hand, in a 20x92 cm arrangement. The experiment was irrigated every 4-5 days with a total amount of 370 mm. Nitrogen was injected into the irrigation water, totalling 337 kg N/ha. Disease control was provided by six applications of 2.5 kg/ha mancozeb (Manzidan) each. The haulms died because of natural senescence and infection by *Alternaria solani*. The experiment was harvested 122 DAP.

At 19, 30, 45, 51, 75 and 94 DAP, the numbers of plants and stems were recorded and a visual crop stand score was allocated. For 19, 30, 45 and 51 DAP, the score (1-10) represented the relative haulm development (1=no emerged plants, 10=best plot per cultivar and block) and for 75 and 94 DAP, the senescence and dying off due to *Alternaria solani* was also taken into account (1=completely senesced or many leaf necroses, 10=best plot per cultivar and block: minimal ($\leq$10 %) senescence or necroses). At harvest, tuber fresh yields were determined, and tubers were counted and graded (<35 mm, 35-60 mm, >60 mm, and misshapen tubers).

Results

Experiment 1

Dormancy. The effects of a foliar GA spray and the storage duration at 28 °C on the dormancy parameters were presented in Van Ittersum & Scholte (1993 - Fig. 1).

Emergence. In Test 1 (planting date 79 DAH), both a foliar spray with GA and storage at 28 °C advanced the emergence. For Diamant, the emergence of the control treatment (HT0) started 24 DAP, whereas the emergence of GAHT6 started 12 DAP. For Désirée, the control treatment and HT2 did not show any emergence within the time lapse of the test, whereas the emergence of GAHT6 started 15 DAP. At later plantings (120 and 148 DAH), the differences in emergence between treatments diminished for both Diamant and Désirée (data not shown).

Haulm dry weight. In all growth vigour tests, the plants produced by tubers from GA treatments did not show any morphological abnormalities.

Both cultivars showed similar responses to GA and the storage duration at 28 °C. In Test 1, Diamant (short dormancy) showed much greater haulm dry weights than Désirée (long dormancy), but GA and increasing storage duration at 28 °C had a very positive influence on the haulm dry weight for both cultivars (Fig. 1a,b).

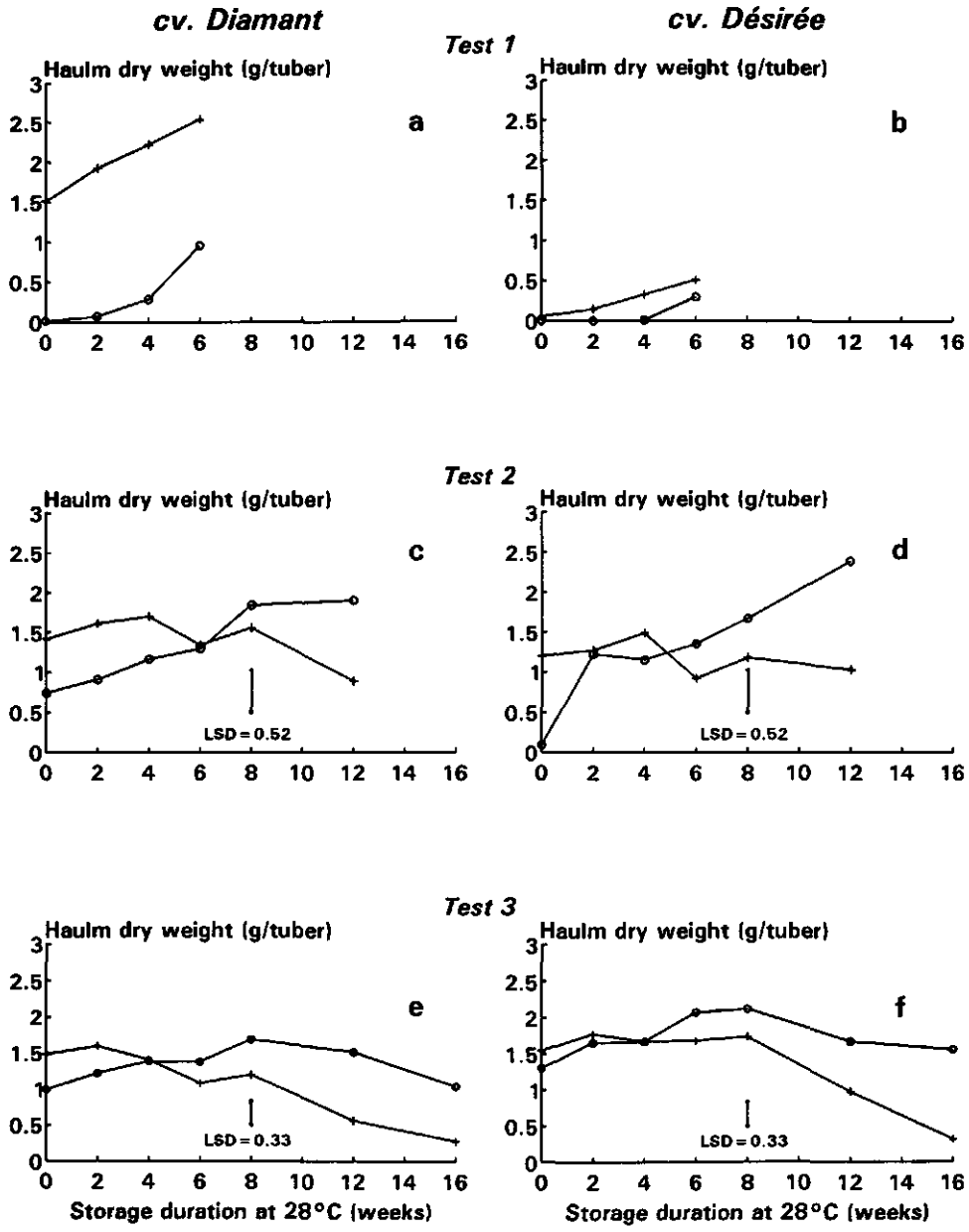

Fig. 1. The effect of a haulm application of 750 g gibberellic acid/ha 6 days before haulm pulling and the duration of storage at 28 °C before transfer to 18 °C on the haulm dry weight produced by seed tubers of cvs Diamant and Désirée. Planting took place at 79 days after haulm pulling (79 DAH; Test 1), 120 DAH (Test 2) or 148 DAH (Test 3). Plants were harvested 22-28 (see text) days after planting. The data of Diamant Test 1 were analysed after a log(x+1)-transformation; both the differences between the GA treatments and the (linear) effect of the duration of storage at 28 °C were highly significant ($P<0.001$). The vertical bars represent the LSD ($P=0.05$). o=no GA; +=+GA.

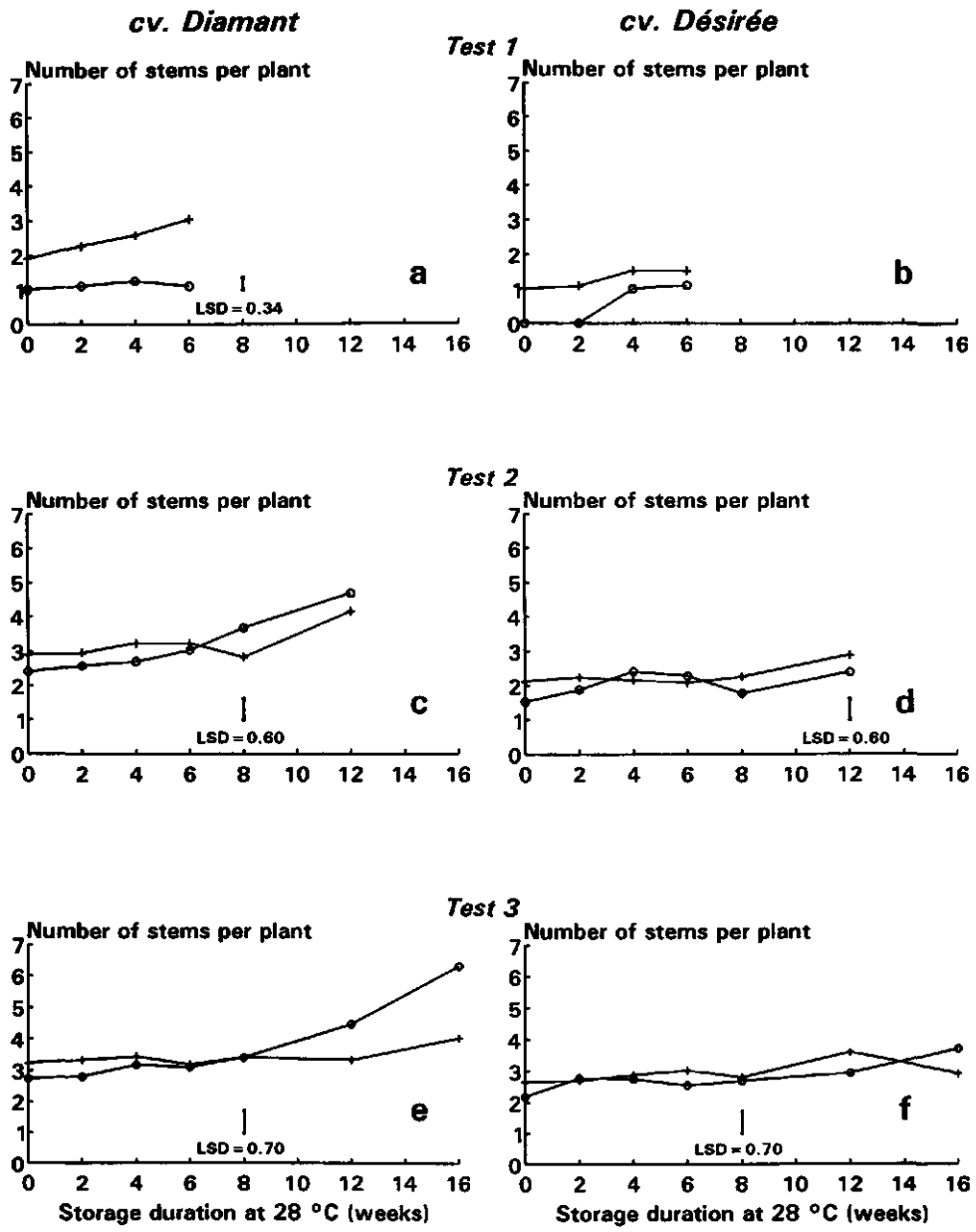

Fig. 2. The effect of a haulm application of 750 g gibberellic acid/ha 6 days before haulm pulling and the duration of storage at 28 °C before transfer to 18 °C on the number of stems produced by seed tubers of cvs Diamant and Désirée. Planting took place at 79 days after haulm pulling (79 DAH; Test 1), 120 DAH (Test 2) or 148 DAH (Test 3). Plants were harvested at 22-28 (see text) days after planting. The interaction between GA and the duration of storage at 28 °C was significant ($P<0.01$) for Diamant in Test 1. In Tests 2 and 3, the three factor interaction between cultivar, GA and duration of storage at 28 °C was significant ($P<0.01$). The vertical bars represent the LSD ($P=0.05$). o=no GA; + = +GA.

In Tests 2 and 3, no significant interaction with cultivars occurred. In both tests, GA only had a positive effect on the haulm dry weight after short or no hot pre-treatments (Fig. 1c-f). After long hot pre-treatments, the tubers from untreated plants produced the greatest haulm weights. In Test 2, tubers from plants sprayed with GA showed the highest growth vigour after relatively short hot pre-treatments (about 4 weeks), whereas tubers from untreated plants showed a greater haulm dry weight with increasing (up to 12 weeks) storage duration at 28 °C (Fig. 1c,d). In Test 3, the highest growth vigour was obtained after hot pre-treatments of about 2 weeks for tubers from GA plants and about 8 weeks for tubers from untreated plants (Fig. 1e,f).

Plant number. In Tests 2 and 3, not all tubers from plants sprayed with GA produced a plant within the time lapse of the test, especially when stored with long hot pre-treatments. In Test 2, 23 % of the Diamant tubers of treatment GAHT12 only produced non-emerged sprouts of several centimetres. For Désirée, 13 % of the tubers of treatments GAHT6 and GAHT8 did not produce sprouts at all, whereas 40 % of the tubers of GAHT12 only produced non-emerged sprouts (values not tabulated).

In Test 3, 3-10 % of the tubers from Diamant plants sprayed with GA and stored for 8-16 weeks at 28 °C did not produce any sprouts. Almost 50 % of the tubers of GAHT16 only produced non-emerged sprouts. For the other treatments, this percentage was 0-7 %. For Désirée, 7-20 % of the tubers from plants sprayed with GA and stored at 28 °C for 6-16 weeks did not produce any sprouts, whereas 50 % of the tubers of GAHT16 only produced non-emerged sprouts. For the other treatments, this percentage was 0-10 % (values not tabulated).

Stem number. For Diamant in Test 1, the number of stems per tuber was increased by GA and by the combination of GA and storage at 28 °C (Fig. 2a). If plants of Désirée were produced, the effects of GA and storage at 28 °C on the number of stems were rather small (Fig. 2b).

In Tests 2 and 3 the differences between the two GA treatments were not significant (Fig. 2c-f), except for Diamant when hot pre-treatments of at least 12 weeks were applied (Fig. 2e). For Diamant, longer hot pre-treatments increased the number of stems per plant for tubers from untreated plants. This trend was not observed for the GA treatment or either treatment (GA, hot pre-treatments) of Désirée (Fig. 2e,f).

Experiment 2

The interactions among cultivars, GA treatments and storage regimes were statistically significant ($P < 0.05$) for dormancy as well as yield parameters. The plants produced by tubers from GA treatments did not show any morphological abnormalities.

Table 1. The effect of a haulm application of gibberellic acid (GA) and different storage temperature regimes on the duration of dormancy, growth vigour and tuber yields of seed tubers of Diamant.

Parameter	GA[a]	Storage temperature treatment[b]				LSD P=0.05
		T18	T28	T28/18	T2/18	
Duration of dormancy (DAH[c])	-	84	79	58	70	4.8
	+	51	59	56	67	
Emergence (%), 19 DAP[cd]	-	1 a	66 d	14 b	3 a	
	+	57 c	93 f	74 e	54 c	
Emergence (%), 30 DAP[d]	-	50 a	100 e	93 c	85 b	
	+	99 de	97 d	99 de	100 e	
Emergence (%), 51 DAP	-	99	100	100	100	
	+	100	98	100	100	
Number of stems/plant, 51 DAP	-	1.2	2.2	1.7	1.5	0.26
	+	2.0	2.8	2.3	1.9	
Crop stand score[e], 30 DAP	-	1	7	4	2-3	1-2[f]
	+	7	10	8	7	
Crop stand score, 51 DAP	-	5	10	8	6-7	1-2[f]
	+	9-10	9	10	9	
Crop stand score, 94 DAP	-	9-10	6	8	10	1-2[f]
	+	7	5	6	6	
Tuber yield (kg/m²)	-	3.45	4.04	3.84	3.78	0.40
	+	3.76	3.58	3.35	3.59	
Number of tubers per m²	-	27	31	30	30	4.1
	+	31	31	27	30	

[a] -=control; +=750 g GA/ha 6 days before haulm pulling.
[b] T18=18 °C constant; T28=49 days 28 °C and subsequently 18 °C; T28/18=20 days 28 °C and subsequently 18 °C; T2/18=20 days 2 °C and subsequently 18 °C.
[c] DAH=days after haulm pulling; DAP=days after planting.
[d] The data were analysed after a logit transformation. Means followed by the same letter were not significantly different at $P \leq 0.05$ (t-test).
[e] 1=no emerged plants; 10=treatment with the best haulm development.
[f] The LSD should be used as an indication for significant differences. The LSD is smaller for scores near 1 or 10 than for scores around 5-6.

cv. Diamant. Dormancy was shortened most by GA if storage took place at 18 °C (Table 1). The effect of GA was not significant after a hot or cold pre-treatment. Tubers of all treatments had ended dormancy and were desprouted (85 DAH) before they were transported to Israel.

Emergence was advanced by GA after all storage regimes (Table 1). Moreover, T28 also had a positive effect on the rate of emergence. At 30 DAP, T18 was the only treatment with less than 80 % emergence. The final percentage of emerged plants was nearly 100 % for all treatments.

For all storage regimes, the seed tubers from plants sprayed with GA produced significantly more stems per plant. For tubers from untreated plants, T2/18, T28/18 and especially T28 also resulted in a higher number of stems than T18 (Table 1).

Tubers from plants sprayed with GA produced a significantly greater crop stand score at 30 DAP for all regimes. The treatment with the highest score was GAT28. Moreover, for tubers from untreated plants T2/18, T28/18, and especially T28 scored higher than T18. At 51 DAP, the differences between the treatments were smaller, but treatment T18 still had the lowest score. At 94 DAP, the score was lower (=plants looked more senesced) for the GA treatments and for T28 than for the other treatments (Table 1).

Differences in tuber yield and number of tubers per unit area were not very large, and significant only in a few cases. GAT18 did not yield significantly more than T18, whereas for the other regimes the yield of the GA treatment was either significantly lower (T28 and T28/18) or not (T2/18). For tubers from untreated plants, T28 gave a higher yield than T18 (Table 1). GA did not affect the percentage of misshapen tubers (data not shown).

cv. Désirée. Dormancy was shortened by GA after all storage regimes and the GA effect was greatest after a hot pre-treatment (Table 2). At planting (111 DAH), the tubers of T18 had not ended dormancy.

The emergence was advanced by GA for all storage regimes except T28 (Table 2). T28 emerged earlier than the other regimes, whereas T18 emerged very slowly. The final (51 DAP) percentage of emerged plants of GAT28 and GAT28/18 was only 89 and 95, respectively. Some of the tubers that did not produce plants had decayed at 51 DAP, whereas others still looked normal but had not produced any sprouts.

The number of stems per plant increased significantly with GA except for T28. This storage regime had a very positive effect on stem number by itself (Table 2).

At 30 DAP, GA had a very positive effect on the crop stand score when the storage regimes T18, T28/18 and T2/18 were applied. The treatments GAT2/18 and T28 showed the highest and second highest scores. Three weeks later, these treatments still showed the highest scores, but differences with most other treatments were smaller. T18 still showed very poor development (Fig. 3). At 94 DAP this treatment showed the least senesced foliage. For T18, T28/18 and T2/18, crops from tubers from GA plants were more senesced than those from tubers from untreated plants (Table 2).

Table 2. The effect of a haulm application of gibberellic acid (GA) and different storage temperature regimes on the duration of dormancy, growth vigour and tuber yields of seed tubers of Désirée.

Parameter	GA[a]	Storage temperature treatment[b]				LSD P=0.05
		T18	T28	T28/18	T2/18	
Duration of dormancy (DAH[c])	-	134	87	115	112	4.8
	+	103	71	62	97	
Emergence (%), 19 DAP[cd]	-	0 a	62 d	1 a	2 a	
	+	23 b	59 d	31 c	85 e	
Emergence (%), 30 DAP[d]	-	0 a	98 e	91 c	94 cd	
	+	85 b	82 b	85 b	97 de	
Emergence (%), 51 DAP	-	100	99	100	100	
	+	99	89	95	98	
Number of stems/plant, 51 DAP	-	1.0	2.3	1.3	1.1	0.26
	+	1.9	2.3	2.1	2.2	
Crop stand score[e], 30 DAP	-	1	8	3	4	1-2[f]
	+	5	7	6	10	
Crop stand score, 51 DAP	-	2	9	7	6	1-2[f]
	+	8	8	8	10	
Crop stand score, 94 DAP	-	10	6	8	8	1-2[f]
	+	6-7	6	6-7	6	
Tuber yield (kg/m²)	-	2.41	3.70	3.45	3.22	0.40
	+	3.10	3.36	3.35	3.78	
Number of tubers per m²	-	26	32	29	26	4.1
	+	30	31	32	36	

[a,b,c,d,e,f]For explanation, see Table 1.

Compared with the control (T18), all treatments showed higher tuber yields, with T28 and GAT2/18 being the highest yielding treatments (ca 155 % of the T18-yield).

The number of tubers per m² of GAT2/18 was higher than that of the other treatments, but the tuber-size distribution based on weights (<35, 35-60, and >60 mm) was affected only slightly by the treatments. GA again had no influence on the percentage of misshapen tubers (data not shown).

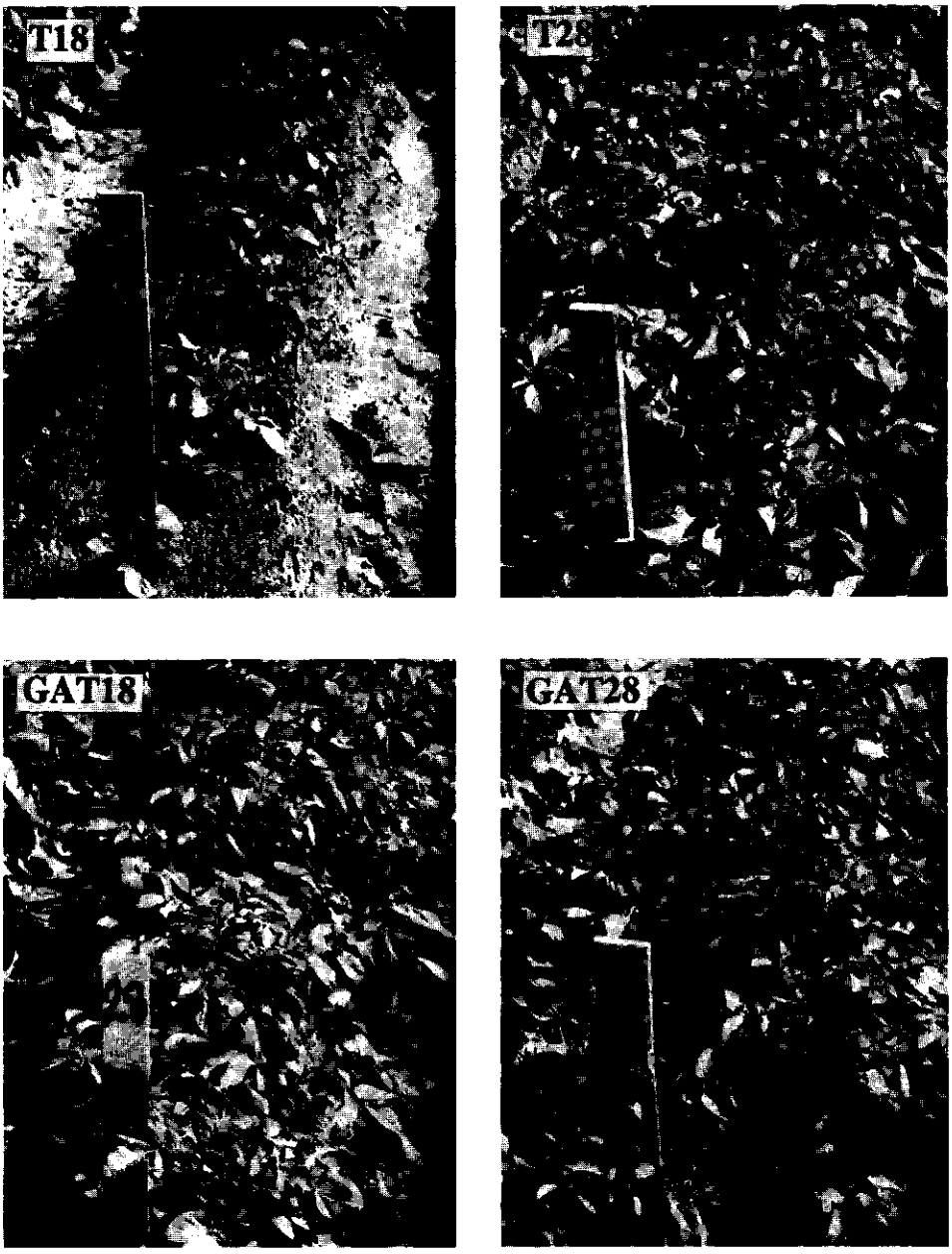

Fig. 3. The effect of a haulm application of GA (750 g/ha 6 days before haulm pulling) and storage at 18 or 28 °C on the growth vigour of seed tubers of cv. Désirée, planted 111 days after haulm pulling (21 October 1990) in the Negev in Israel, and photographed 51 days after planting. For codes and data, see Table 2.

Table 3. The effect of a haulm application of gibberellic acid (GA) and different storage temperature regimes on the duration of dormancy, growth vigour and tuber yields of seed tubers of Draga.

Parameter	Treatment[ab]			LSD P=0.05
	T18	T28	GA+T28	
Duration of dormancy (DAH[c])	152	109	74	7.0
Emergence (%), 19 DAP[cd]	0 a	1 a	24 b	
Emergence (%), 30 DAP[d]	0 a	42 b	72 c	
Emergence (%), 51 DAP[d]	23 a	93 c	80 b	
Emergence (%), 75 DAP[d]	71 a	93 c	80 b	
Number of stems/plant, 51 DAP	1.2	1.5	2.8	0.32
Crop stand score[e], 30 DAP	1	4	10	1-2[f]
Crop stand score, 51 DAP	1	6	10	1-2[f]
Crop stand score, 94 DAP	10	8	6	1[f]
Tuber yield (kg/m²)	1.05	2.64	2.95	0.51
Number of tubers per m²	19	25	30	5.3

[a,b,c,d,e,f]For explanation, see Table 1.

cv. Draga. Dormancy was shortened by 78 days after a foliar spray of GA and storage at 28 °C (Table 3).

The emergence of T28 and especially GAT28 was greatly advanced compared to T18 (Table 3). At 75 DAP, the percentage of emergence of T18 was 71 %, whereas that of the other treatments had not increased. Among the tubers that did not produce plants, were both decayed and normal tubers.

At 51 DAP, the number of stems per plant of GAT28 was significantly higher than that of T18 and T28 (Table 3). In the first part of the growing season, the crop stand scores of T28, and especially GAT28, were much higher than that of T18, but later the reverse was true. At harvest, T18 was the only treatment that still showed some green foliage.

Tuber yields of T28 and GAT28 were almost three-fold of that of T18 and their number of tubers per unit area also were much higher (Table 3). Tubers from T18 were much smaller than those from the other treatments (data not shown).

Discussion

Effects on growth vigour. In contrast to tubers directly treated with GA (Choudhuri & Ghose, 1963), tubers from plants sprayed with GA did not produce morphologically abnormal plants.

The growth vigour of seed tubers is particularly reflected in the haulm production shortly ($\leq$2 months) after planting (Van der Zaag & Van Loon, 1987; Van Ittersum et al., 1990). A foliar GA spray advanced the growth vigour of the seed tubers. This was particularly clear at early plantings; at later plantings differences diminished. At early plantings, GA also increased the number of stems per plant.

Storage of seed potatoes at 28 °C was very favourable for inducing a high growth vigour relatively soon after harvest and enhanced physiological ageing, as shown before (Van Ittersum et al., 1990; Van Ittersum, 1993). Storage of seed potatoes for limited periods ($\leq$75 days) at this high temperature (and 80 % RH) only resulted in small extra weight losses compared with storage at 18 °C (Van Ittersum, 1993). The interaction between GA and the storage regime was very clear in Expt 1. At early plantings the combination of GA and storage at 28 °C improved the growth vigour, whereas at later plantings storage at 28 °C reduced the growth vigour of tubers from plants sprayed with GA (Fig. 1c-f), and a considerable number of tubers did not produce plants. The optimum storage duration at 28 °C was shorter for tubers from plants sprayed with GA than for tubers from untreated plants. Obviously, a foliar GA spray enhances physiological ageing of the tubers.

Both experiments showed that a foliar GA spray and prolonged storage at 28 °C may result in excessive seed ageing. Some tubers from GA-treated plants were unable to produce plants after prolonged storage at 28 °C. This illustrates that this combination of treatments should only be applied for very early plantings (thus, when only short storage periods are available). For later plantings, application of one treatment (GA or storage at 28 °C) suffices to advance the growth vigour.

The occurrence of excessive ageing also depends on the rate of physiological ageing of the cultivar. In earlier experiments (Van Ittersum, 1993) it was shown that the growth vigour of cv. Draga (very long dormancy and relatively rapid rate of ageing) was very poor after storage at 28 °C throughout the dormant period (98 days). However, in Expt 2 tubers were stored at 28 °C for only 49 days and the growth vigour was much higher than after storage at 18 °C. This supports the suggestion that for cultivars with a rapid rate of physiological ageing, the storage period at 28 °C should be more limited (Van Ittersum, 1993).

Dormancy and growth vigour. Expt 2 had several treatments with a similar or longer duration of dormancy than other treatments, but a higher growth vigour (e.g. compare GAT28/18-T28/18, GAT2/18-T2/18, T28-T28/18 in Table 1). At planting, these treatments with the highest growth vigour accumulated similar or lower numbers of day-degrees since the onset of sprouting than

those with the lowest growth vigour. Comparison of Fig. 1 of the current paper with Fig. 1 in Van Ittersum & Scholte (1993) also shows that treatments resulting in the shortest dormancy not necessarily result in the highest growth vigour: the optimum storage duration at 28 °C to shorten dormancy was shorter than the optimum storage duration at 28 °C to advance the growth vigour. This supports an earlier point that the temperature sum from the start of sprouting does not account completely for the physiological age of the tubers, as O'Brien et al. (1983) suggested, but that treatments during growth of the tubers, and the storage temperature until the start of sprouting are also important (Van Ittersum, 1993).

Effects on tuber yield. Tubers from treatments resulting in the highest physiological age (T28 and all GA treatments - Expt 2) gave the earliest emergence and the highest crop stand scores at 30 DAP, but also the earliest senescence (crop stand score at 94 DAP). This agrees with the findings of other researchers (Van der Zaag & Van Loon, 1987). For Diamant (short dormancy), the differences in crop stand between the control treatment and the other treatments were smaller during the first part of the season and diminished faster than for Désirée and Draga (long dormancy cultivars). Consequently, differences in final tuber yields were smaller for Diamant than for Désirée and Draga. For Diamant, seed treatments resulting in the lowest (T18) or highest (GAT28, GAT28/18 and GAT2/18) physiological age tended to give the lowest yields. For Désirée and Draga, the control seed tubers were physiologically so young that they yielded much less than all other treatments. For Désirée, a hot or cold pre-treatment alone greatly improved tuber yields. The results illustrate that after longer growing periods, the yields of crops grown from physiologically younger seed may approach, equal, or exceed those of crops grown from older seed (O'Brien et al., 1983).

Conclusions

A foliar GA spray 6 days prior to haulm pulling greatly advanced the growth vigour of seed tubers harvested immature, without causing negative effects on the morphology of the plants produced by these tubers. There was a clear interaction between the effects of a foliar GA spray and the storage temperature regime on the growth vigour. Both a foliar GA spray and storage at 28 °C enhanced physiological ageing of the tubers. At early plantings, these treatments were highly favourable for the growth vigour of seed potatoes, but at later plantings they may be unfavourable.

In these studies, treatments resulting in the shortest dormancy did not necessarily result in the highest growth vigour, when seed tubers were planted soon after their harvest.

The effects of GA and storage treatments on tuber yield depend on the cultivar, the time between haulm killing of the seed crop and planting of the next crop, and on the length of the growing season.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

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Dormancy and its determination

Dormancy before haulm removal. During storage between haulm removal and the onset of sprouting, under conditions ideal for sprout growth, the physiological state of the tuber does not allow autonomous sprout growth (Reust, 1986). It is not clear whether this physiological state of the tuber is similar to that during its growth. Madec & Perennec (1969) suggested that absence of bud growth is not controlled by the same factors before and after harvest. *Autonomous* sprout growth also seems impossible during tuber growth. The formation of leaf primordia by the apical bud of the tuber does not continue after the haulm has been removed. Heat sprouting or sprout growth induced by a foliar spray with gibberellic acid (GA) is only temporary and is mediated by the foliage or the roots. No heat sprouting occurs when the tuber is separated from the plant before the heat treatment (Lugt et al., 1964; Madec & Perennec, 1969) and sprouting does not continue when the connections with foliage and roots are severed (Madec & Perennec, 1969; Van Ittersum & Scholte, 1992b; 1993). During tuber growth the tuber buds seem to be partly controlled by the plant. The plant controls dormancy and shields dormancy from influences of environmental conditions (Van Ittersum, 1992c).

The base date for measuring duration of dormancy. In experiments with different planting dates Perennec & Madec (1960) and Cho et al. (1983) demonstrated that tubers initiated first were also the first to sprout. In my study it was shown that there is a positive correlation between the duration of dormancy (in days after haulm pulling) and the date of tuber initiation, even in tubers from the same plant or crop (Van Ittersum & Struik, 1992). Various researchers found a poor relation between the end of dormancy (calendar date) and the harvest date (Burton, 1963; Bottini et al., 1982). These findings support Burton's suggestion (1963) that tuber dormancy should be measured from the date of tuber initiation. Since specific efforts need to be made to determine the date of tuber initiation, it is much more convenient to express the duration of dormancy in days after planting or in days after haulm removal. However, information about the time of tuber initiation is essential for comparing the duration of dormancy of different batches of tubers that have different dates of tuber initiation.

Morphological and physiological changes during dormancy. After haulm pulling at an immature stage, no changes occurred in the length of the axis and in the number of leaf primordia of tuber buds of cvs Diamant and Désirée for at least 60 and 95 days, respectively (Van Ittersum et al., 1992). Differences in duration of dormancy between the two cultivars (according to the 2 mm-criterion) seem to be mainly due to differences in the periods with absence of bud growth; the initial rates of sprout growth were similar (Van Ittersum et al., 1992). The tubers used for these

morphological measurements were from the same batches as those used for measuring the response to a dormancy-breaking treatment with growth substances (bio-assay; Section 2.2). During the period in which the morphological characteristics did not change the response to the bio-assay increased. This means that the endogenous hormone concentrations or the sensitivity to growth substances changed long before any morphological changes were measured. If the increase in response to the assay shows a characteristic pattern for various cultivars, growth conditions and storage conditions, then dormancy could be quantified. This would offer prospects of measuring the effects of growth or storage conditions and of predicting the end of dormancy instead of waiting until sprouts appear. However, more research will be necessary to clarify whether the bio-assay can be used for this purpose (Section 2.2).

The criterion for the end of dormancy. In the current study dormancy was deemed as having ended when a tuber showed at least one sprout 2 mm long. When the duration of dormancy was assessed at conditions optimally suited for sprout growth (about 18 °C), then about 20 days were needed to obtain sprouts 2 mm long from the moment that sprout growth started (Van Ittersum et al., 1992). However, in some of the storage regimes the temperature during sprouting was much lower or higher than the optimum for sprout growth (Chapter 5). In these cases, probably more than 20 days were needed to obtain sprouts 2 mm long. Consequently, the dormancy-shortening effect of these treatments was somewhat greater than measured.

In this thesis, the duration of dormancy of tubers within a batch was characterized by two parameters, i.e. a location parameter and a dispersion parameter. The moment of 80 % sprouting, being the definition of the European Association for Potato Research for the end of dormancy, was used as a location parameter. The spread in the duration of dormancy was characterized by the time lapse between 10 % and 90 % sprouting. Although in the case of a normal distribution the whole frequency distribution of the duration of dormancy of tubers within a seed batch is characterized by these parameters, the two parameters are not very complementary. The moment of 50 % sprouting would be a more obvious location parameter in combination with the time lapse between 10 % and 90 % sprouting as the dispersion parameter. The standard deviation of the duration of dormancy of the individual tubers in a sample could be used as an alternative spread parameter.

Variation in duration of dormancy

Variation in duration of dormancy within a tuber lot is particularly important when young seed tubers are planted. The variation will be reflected in variation in emergence and plant growth. For older tubers which are around the phase of optimum physiological age for planting, the emergence and plant growth will be fast and regular.

Table 1. Relevance of some internal and external factors for the duration of dormancy (in days after haulm removal) of seed tubers harvested immature. 0, ±, +, ++, +++ and ++++ indicate increasing relevance (± indicates inconsistent findings). For cv. Désirée, some internal factors during growth were not investigated.

Factor	cv. Diamant	cv. Désirée
Internal factors during growth		
Date of tuber initiation	+	
Position of the tuber on the plant	+	
Tuber shape	±	
Tuber weight	++	0
External factors during growth		
Nitrogen supply	+	+
Temperature	++	++
Light intensity	+	+
Photoperiod	±	±
Foliar spray with gibberellic acid	++++	++++
External factors during storage		
Temperature	++++	++++

The variation in duration of dormancy within a tuber lot appears to be large. Cultivar Diamant, with the largest variation in duration of dormancy within a tuber lot, showed a clear relation between dormancy and tuber weight. The variation in duration of dormancy within a tuber lot comprising tubers of similar weight did not differ much between cvs Diamant and Désirée. It would be worth investigating whether this is true for more cultivars. The differences in duration of dormancy between tubers of one plant of cv. Diamant were also related to the date of tuber initiation and the position of the tuber on the plant (Table 1).

In many experiments, significant differences of several weeks in the time lapse between 10 % and 90 % sprouting occurred between cultivars or treatments. This shows the relevance of a spread parameter for the characterization of the duration of dormancy of a tuber lot. However, the differences in spread between treatments were not very consistent over the different experiments and were mostly hard to explain.

Besides the factors investigated in my study (Van Ittersum & Struik, 1992), other factors might be important in causing variation in duration of tuber dormancy within a tuber lot. Contradictory results have been reported on the relation between the specific gravity of the tubers and sprout growth (Wurr, 1980; Silva & Andrew, 1983). Tubers which have turned green during their growth because of exposure to sunlight have a shorter dormancy period than unexposed tubers (Gadewar et al., 1980; Van Ittersum, unpublished results). Damaged or cut tubers (Appleman, 1914) and tubers infected with *Phytophthora infestans* (Dóstál, 1942) have a shorter dormancy

period than undamaged and uninfected tubers. Van Ittersum & Scholte (1992b) found that heat sprouted tubers which were desprouted before storage may have a shorter dormancy period than tubers from the same lot without heat sprouts. Most of these factors were not important in my experiments since only tubers free from damage, greening or disease were used in the tuber samples and heat sprouting occurred only incidentally after very high temperatures during tuber growth.

Generally, the variation in duration of dormancy (time lapse to 80 % sprouting) *between* different tuber lots is limited (Section 4.1). Few data are available on the absence of interaction between cultivars and the source of variation (years or origins). The present study showed that environmental conditions such as nitrogen, temperature and light during tuber growth had little effect on the duration of dormancy (Table 1). Some treatments produced very large effects on tuber yields (up to 50 % reduction), but nevertheless the effects on tuber dormancy were almost absent. The small variation in duration of dormancy between tuber lots is also remarkable since there was large variation in duration of dormancy within a lot. Apparently, the plant produces tubers of different dormancies but shields the tubers from the effects of environmental conditions that might affect dormancy.

The field experiments with 19 cultivars showed that the duration of dormancy hardly differed between the 2 experimental years, but that dormancy was shorter in all cultivars produced in Swifterbant compared with those produced in Wageningen (Section 4.1). The soil in Wageningen is low in mineralization potential, contrary to the soil in Swifterbant. This difference (and consequently the greater nitrogen availability in Swifterbant) could explain a small part of the shorter dormancy in Swifterbant. Average solar radiation hardly differs between Swifterbant and Wageningen. The differences in temperatures during tuber bulking between the two locations were very small and cannot be important (cf. Van Ittersum & Scholte, 1992b). It is therefore unlikely that the difference in duration of dormancy between tubers from Swifterbant and Wageningen was caused solely by the factors during growth investigated in this research programme.

In Table 2 the duration of tuber dormancy (in days after tuber initiation and in days after haulm removal) of the control treatments of various experiments described in Chapters 4 and 5 has been listed for cvs Diamant and Désirée. It should be borne in mind that in most cases the date of tuber initiation was assessed only roughly, especially in the phytotron experiments where only a few plants were available to assess this date. Dormancy did not differ much between the various experiments carried out in the phytotron or in Swifterbant. In 1988 and 1989 at Wageningen-Hoog, dormancy of cv. Diamant did not differ from that of tubers from Swifterbant, but in 1990 the dormancy period of Wageningen-Hoog seed was much longer than in 1988 and 1989 and than in Swifterbant. Dormancy of cv. Désirée was about 1-3 weeks longer at Wageningen-Hoog than at Swifterbant, in all years.

These results illustrate that the variation in duration of dormancy between tuber lots is generally rather small. Sometimes, large differences between locations or years may occur, but not necessarily for all cultivars. These differences are hard to explain.

Table 2. End of dormancy (days after tuber initiation or days after haulm removal) of the control treatments of various experiments with cvs Diamant and Désirée as described in Chapters 4 and 5. The tubers were produced in growth chambers or glasshouses at 18/12 °C and 12 h daylength, or in the field at Swifterbant or Wageningen-Hoog.

Origin	Year	Dormancy expressed in days after			
		tuber initiation		haulm removal	
		Diamant	Désirée	Diamant	Désirée
Phytotron					
Growth chamber	1989	125	183	81	133
Glasshouse	1989	130	191	80	139
Glasshouse	1990	125	174	85	130
Glasshouse	1990	124	179	78	129
Mean		126	182	81	133
Field					
Swifterbant	1988	120	177	86	136
Swifterbant	1988	120	189	79	142
Swifterbant	1989	111	177	78	140
Swifterbant	1990	129	171	86	134
Swifterbant	1990	118	174	79	131
Mean		120	178	82	137
Wageningen-Hoog	1988	120	200	79	154
Wageningen-Hoog	1988	124	197	78	145
Wageningen-Hoog	1989	116	200	74	151
Wageningen-Hoog	1989	111	196	69	147
Wageningen-Hoog	1990	136	194	101	150
Wageningen-Hoog	1990	135	192	105	150
Mean		124	197	84	150

Shortening dormancy

The small effects of environmental conditions during tuber growth on the duration of dormancy contrast with the large potential to manipulate dormancy with a foliar spray of gibberellic acid shortly before haulm removal (Table 1). Apparently, the plant cannot control dormancy when large amounts of GA are applied to the haulm shortly before haulm removal. However, one experiment suggested that the plant corrects or counterbalances the high GA concentrations when the GA has been applied longer before haulm removal, because the effect of GA applied 14 days before haulm killing was smaller than the effect of GA when applied 7 days later (Van Ittersum & Scholte, 1993).

The large influence of storage temperature regimes contrasts with the small effect of the temperature during tuber growth (Table 1). Apparently, as soon as the controlling influence of the

plant is removed, or perhaps decreases because of senescence in cases when tubers are harvested when they are more mature, the influence of the temperature on dormancy becomes very evident. In the experiments on the effect of temperature during tuber growth, an increase of 7-12 °C in average daily temperatures during 4 weeks often did not curtail dormancy (Van Ittersum & Scholte, 1992b). During storage, however, an increase of 10 °C in daily temperature during 20 days resulted in a very consistent dormancy-shortening effect of 2-4 weeks (Van Ittersum & Scholte, 1992a; 1993).

To obtain the stage where dormancy ends, i.e. by definition when the tuber shows at least one sprout 2 mm long, two separate processes are needed: dormancy release and sprout growth. Both low and high temperatures seem to be favourable for dormancy release, whereas intermediate temperatures (15-20 °C) are optimum for sprout growth. This (partly) explains why storage at 2 or 28 °C for long periods after harvest seems to be less effective in shortening dormancy than shorter periods with these temperatures, and why long periods of 28 °C either do not affect dormancy or shorten it less in cultivars with a short dormancy compared with cultivars with a long dormancy. It also explains why the duration of a hot pre-treatment resulting in the shortest dormancy was shorter for tubers from plants treated with GA than for tubers from untreated plants.

The dormancy-shortening treatments described in this thesis show promise as good alternatives for tuber treatments with GA, Rindite, carbon disulphide, thiourea or other chemicals (Burton et al., 1992). The effects of the treatments described were very consistent and were associated with the genetically determined duration of dormancy of the cultivars (Van Ittersum & Scholte, 1992a). Dormancy-shortening effects of a single week up to several months can be achieved by choosing the appropriate storage regime and/or a foliar spray with GA. Moreover, the present treatments are much safer than treatments with Rindite or carbon disulphide. Storage regimes with high temperatures are cheap and easy in the tropics and subtropics. Their implementation in practice will depend on economic, logistical and phytosanitary motives. A disadvantage of the foliar spray with GA might be that dormancy of all tubers of the treated crop is shortened, including those not destined to be planted soon after harvest.

Dormancy and plant hormones

My research strongly confirms the literature on the dormancy-shortening effect of exogenous GA (Rappaport & Wolf, 1969; Burton, 1989) and cytokinins (CK) (Hemberg, 1970; Turnbull & Hanke, 1985a). The effect of the foliar GA spray supports the view of Bruinsma & Swart (1970) that GA has a dormancy-breaking potency in addition to its sprout growth-promoting effect. However, it is in contrast to the view of Madec & Perennec (1969), who stated that the GA effect was restricted to an effect on sprout growth. I believe that the effect of a foliar spray with GA is too large to be restricted to initial sprout growth. Buds on untreated tubers stored at 18 °C took about 20 days to grow out to a length of 2 mm (Van Ittersum et al., 1992), whereas the

dormancy-shortening effect of GA was about 30 days at 18 °C (Van Ittersum & Scholte, 1993).

Current literature still supports the hypothesis that dormancy is related to a balance of growth-inhibiting (e.g. abscisic acid, ABA) and growth-stimulating (e.g. GA and CK) substances (Coleman, 1987; Van der Plas, 1987). In the remaining part of this section I shall discuss whether my findings on the effects of the environmental conditions on dormancy agree with the current knowledge about the effect of environmental conditions on hormone concentrations and about the link between dormancy and the balance between growth-inhibiting and growth-stimulating hormones.

Current knowledge about the relation between hormones and tuberization and about the variation in hormonal concentrations within a plant is too limited to explain the variation in date of tuber initiation within a plant or to relate dormancy to the position of the tuber on a plant. Vreugdenhil & Struik (1989) stressed that the hormonal status apparently varies for different sites within a potato plant, since different steps in the process of tuber formation occur simultaneously on different positions in the same stem. The correlation between growth substance concentrations and tuber growth rate indicates that the relation between dormancy and tuber weight might be based on growth substances (Van Ittersum & Struik, 1992).

High nitrogen rates, high temperatures, low light intensities and long photoperiods are all associated with higher levels of gibberellin activity (Ewing & Struik, 1992). In my study high nitrogen levels and low light intensities showed (small) dormancy-shortening effects. However, only some of the high temperature regimes during growth shortened dormancy compared with regimes with lower temperatures, and the photoperiod had inconsistent effects.

Exogenous GA is readily transported in the plant (Moore, 1989) and thus a foliar spray with GA probably increased the GA concentration in the tubers. Both low and high storage temperatures were able to enhance dormancy release. Compared with storage at 10-15 °C, 2 °C decreased the growth inhibitor activity, increased the activity of GA in eye plugs (Thomas & Wurr, 1976) and increased the concentration of CK in the tuber buds (Turnbull & Hanke, 1985b). For cv. Désirée, the effect of GA was small after storage with a cold pre-treatment. Conceivably, this might be because a foliar spray with GA and a cold pre-treatment both increase the GA concentration in the tubers. No research seems to have been done to compare hormone concentrations in tubers stored at a high (28 °C) or at an intermediate (10-20 °C) temperature.

The increase in response to the bio-assay (Section 2.2) may imply that the organ's responsiveness to plant growth substances changes during storage. Several researchers have stressed that in additon to the concentration of hormones, the sensitivity of the tissue to plant hormones, mediated by hormone receptors, is very important for hormonal regulation of growth and development (Trewavas, 1981; Firn, 1986). It may be surmised that storage at 28 °C increases the GA sensitivity. This could explain why a foliar spray with GA had a very large effect on dormancy of cv. Désirée after hot pre-treatments of several weeks (Van Ittersum & Scholte, 1993). The minimum duration of dormancy of a tuber sample was about 40-50 DAH,

because the tubers were harvested about 20 DAH (the storage regimes started about 5 days later) and the buds need some time (about 20 days) to reach the threshold length of 2 mm. For cv. Diamant, a foliar GA spray already sufficed to minimize the duration of dormancy and this could be why a combination of GA and storage at 28 °C did not result in any extra shortening effects (Van Ittersum & Scholte, 1993).

If storage at low (e.g. 2 °C) temperatures increases the GA concentration and storage at high (e.g. 28 °C) temperatures increases the GA sensitivity, a combination of a cold and a hot pre-treatment might be extremely effective in shortening dormancy. In one experiment (Van Ittersum & Scholte, 1992a), a treatment was included in which the tubers were stored for 10 days at 0 °C, followed by 10 days at 28 °C and subsequently they were stored at 18 °C continuously. For cv. Diamant, this treatment resulted in an immediate sprouting of all tubers after the transfer from 28 to 18 °C. In cultivars with a longer dormancy (Jaerla and Désirée), some of the tubers started sprouting immediately after the period at 28 °C, whereas dormancy of other tubers was hardly affected. For cv. Draga (very long dormancy) this treatment had a rather small effect. It would be very interesting to investigate whether combined cold and hot pre-treatments (of longer duration for cultivars with a long dormancy) are more effective in shortening dormancy than cold or hot pre-treatments alone.

In conclusion, some effects of factors on dormancy reported in this thesis seem consistent with the proposition that such effects are mediated by changes in the hormone balance. However, the effects (or absence of effects) of most factors during growth are still especially poorly understood.

Dormancy and physiological ageing

Both a foliar spray with GA and storage at high temperatures greatly favoured the growth vigour of seed tubers planted soon after their harvest. This advancing effect on growth vigour can (partly) be ascribed to the dormancy-shortening effect of these factors, but it might also be caused by an additional effect on physiological ageing. In this thesis a number of examples have been discussed in which dormancy was not shortened, whereas the growth vigour was advanced. For example, in several cultivars storage at 28 °C until the end of dormancy did not shorten dormancy compared with storage at 18 °C, whereas growth vigour of the 28 °C treatment was always largest (Van Ittersum, 1993).

It is less easy to elucidate whether a foliar GA spray has an ageing effect in addition to a dormancy-shortening effect. Generally, the effects of GA on dormancy and physiological ageing are confounded. Van Ittersum et al. (1993) gave two examples (cv. Diamant: T28/18-GAT28/18 and T2/18-GAT2/18) in which the duration of dormancy did not differ between the two treatments within a set, but the growth vigour was advanced in the GA treatments. Moreover, the fact that relatively many tubers from GA-treated plants did not produce a plant when stored for long periods at 28 °C and planted relatively late (Van Ittersum et al., 1993) suggests that GA has an ageing effect in addition to a dormancy-shortening effect. However, more research is necessary to

conclude whether or not these physiologically aged tubers occur at an earlier stage for the GA treatment than could be expected because of the dormancy-shortening effect of GA.

As stated before, a storage temperature of 2 or 28 °C is not the optimum for sprout growth. Therefore, dormancy may have been released relatively earlier than observed in treatments with these sprouting temperatures compared with treatments in which sprouting took place at 18°C. In an experiment with cv. Jaerla (not published) a cold pre-treatment of 20 days at 2 °C and a hot pre-treatment of 20 days at 28 °C were compared. Dormancy ended long after both samples had been transferred to 18 °C. In this cultivar, the dormancy of tubers from the cold pre-treatment was significantly shorter than in those from the hot pre-treatment, whereas the growth vigour of the hot pre-treatment was significantly greater. Thus it is likely that dormancy release and physiological ageing are at least partly two separate processes.

Data on high temperatures during tuber bulking from my experiments and from the literature also seem to illustrate that releasing dormancy and physiological ageing are (partly) two distinct processes. Most of the growth temperature treatments did not shorten dormancy compared with growth at the 18/12 °C regime (Van Ittersum & Scholte, 1992b), but sprouts were more numerous after higher growth temperatures, pointing to a greater physiological age. Data from Went (1959), Bodlaender (1973) and Wurr (1979) also indicate a faster rate of physiological ageing at higher temperatures during tuber bulking.

O'Brien et al. (1983) proposed using the accumulated day-degrees from the moment that sprouts of 3 mm have been formed as a measure of physiological age. This measure may be useful for practical purposes, when storage is under low or moderate, constant temperatures. However, from a theoretical point of view this measure is incomplete. As mentioned earlier, treatments may not differ in the moment that sprouts of 2 or 3 mm are formed, whereas they differ in growth vigour or physiological age. Temperature or other conditions during the growth and dormancy of tubers are also important. In addition, Scholte (1987) showed, that the build-up of the temperature sum is very important. High temperatures during and shortly after dormancy have a smaller ageing effect than high temperatures applied later during storage, long after the end of dormancy.

The results in Chapter 5 indicate that the effects of GA and storage temperature regimes on tuber yields of the next crop depend on the duration of dormancy and on the rate of physiological ageing of the cultivar, the planting date, and the length of the growing season.

General conclusions

During dormancy, the length of the axis and the number of leaf primordia of the buds of tubers harvested immature do not change and thus these morphological characteristics cannot be used to quantify dormancy. After haulm removal, the response of tubers to a dormancy-breaking intervention with growth stimulating substances (bio-assay) increases with time. This response might be used to measure the 'intensity' of dormancy and to predict the end of dormancy, but more research is necessary to develop such an application.

The individual potato plant produces tubers with a rather large variation in the duration of dormancy. This variation may be related to the variation in tuber weight, the date of tuber initiation and to the position of the tuber on the plant during tuber growth. At the level of the entire crop, conditions during tuber growth such as nitrogen, temperature, light intensity and photoperiod have little or zero effect on the duration of dormancy of tubers harvested immature. Generally, the variation in duration of dormancy *between* tuber lots of the same cultivar is small. Fairly large (up to 4 weeks) differences in the duration of dormancy may occasionally occur between tuber lots and they are hard to explain.

Both a foliar GA spray shortly before haulm removal and storage temperature regimes greatly shorten the dormancy and advance the growth vigour of seed potatoes harvested immature. In this study the advancing effects varied from a single week up to several (>3) months depending on whether one or both treatments were used and whether a storage regime with low or high temperatures was opted for. The storage regime interacts with the foliar spray of GA. The effects of GA and storage regimes on dormancy, and growth of the next crop, are greater for cultivars with a long dormancy than for those with a short dormancy. These treatments offer very good prospects for improving the performance of seed potatoes that are planted soon after the harvest.

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SUMMARY

DORMANCY AND GROWTH VIGOUR OF SEED POTATOES

Dormancy and productivity of seed potatoes

Generally, the potato is propagated vegetatively by means of tubers. The physiological properties of a tuber change with time; this is reflected in changes in the sprouting behaviour. Since the time scale of changes in the sprouting behaviour differs between cultivars and is influenced by storage conditions, the term 'physiological age' of tubers is commonly used. After planting, the physiological age is reflected in the growth vigour. The growth vigour of a seed tuber is defined as its potential to produce a well-developed plant within a relatively short (defined) period of time. After the harvest, the potato tuber has a dormancy period during which it shows no sprout growth; the growth vigour is zero. The growth vigour of the tuber increases initially upon termination of dormancy and levels off at a maximum. After some time, the growth vigour gradually declines and ultimately this leads to the inability to produce a new plant. The physiological age of the tuber also affects the growth pattern of the plant. Generally, plants from physiologically young tubers senesce later than plants from physiologically older tubers. At harvests early in the season, the tuber yields produced by plants from older seed tubers will be higher than that produced by plants from young seed tubers, whereas at later dates of harvest the opposite may occur.

The research programme

Tuber dormancy is a favourable factor for tubers that have to be stored for a certain period before consumption or other use, but is disadvantageous for seed tubers that have to be planted soon after the harvest. The duration of dormancy depends on the genotype, but may also be influenced by the conditions during growth and during storage of the tubers. It is important to know the factors affecting dormancy and to be able to predict the duration of dormancy in order to store the tubers appropriately. It would be very helpful if dormancy could be measured long before it ends. The research described in the first part of this thesis (Chapters 2-4) aimed at measuring morphological and physiological changes during dormancy and explaining the variation in duration of dormancy in order to improve the predictability of the duration of dormancy.

Non-dormant seed tubers with a high growth vigour are not always available at planting. Often, seed tubers need to be planted soon after their harvest. In these cases, dormancy and a low growth vigour result in suboptimal crop growth and low tuber yields. Chapter 5 of this thesis discusses ways of curtailing the dormancy of seed potatoes and of advancing their growth vigour.

The research described in Chapters 2-4 was carried out on cvs Diamant (short dormancy) and Désirée (long dormancy). The research described in Chapter 5 was carried out on other cultivars too. The standard storage regime was in darkness, at 18 °C and 80 % relative humidity in well

controlled chambers (conditions ideal for sprout growth). The duration of dormancy was defined as the period from tuber initiation until the moment that a tuber had grown at least one sprout 2 mm long. For practical reasons, the duration of dormancy was often expressed in days after haulm removal. The research focused on tubers harvested while immature, as usual in the Netherlands when growing seed potatoes.

Morphological and physiological changes during dormancy

After haulm pulling at an immature stage, no changes occurred in the length of the axis and in the number of leaf primordia of tuber buds of cvs Diamant and Désirée for at least 60 or 95 days respectively. After this period, tubers of both cultivars grew apical sprouts 2 mm long in about 20 days. Thus, the duration of dormancy of a cultivar cannot be predicted by means of simple morphological characteristics of the tuber buds. The difference in duration of dormancy between the two cultivars according to the 2 mm criterion was mainly caused by the difference in the period without bud growth, and not by differences in initial growth rate of the sprouts until a sprout length of 2 mm has been reached.

Efforts were also made to quantify dormancy by means of a bio-assay in which the response to a dormancy-breaking intervention was measured. In the bio-assay, tuber samples were taken from storage regularly. Lateral eye plugs from these tubers were dipped in a range of concentrations of a dormancy-breaking growth substance (6-benzylaminopurine). After incubation for 7 days, the sprouted eye plugs were counted. Generally, the response to the dormancy-breaking treatment increased the longer the tubers were stored, indicating that the 'intensity' of dormancy is not constant during the dormancy period. Cultivars with a short dormancy responded more strongly to the assay than cultivars with a long dormancy. These trends could be discerned, but there was a large variation in response. The method seemed to be very sensitive to small variations in external conditions during the incubation. If the variation in response is caused by variation in external conditions during the incubation, and if this variation can be reduced, the bio-assay would be a promising way of measuring dormancy and of predicting the remaining dormancy period.

Variation in duration of dormancy within a seed tuber lot

The variation in duration of dormancy between tubers from one plant may amount to many weeks. This variation was much larger in cv. Diamant than in cv. Désirée. In cv. Diamant there was a clear relationship between dormancy and tuber weight; heavier tubers ended dormancy earlier than lighter tubers. In cv. Désirée there was almost no relationship between dormancy and tuber weight.

The frequency distribution of the duration of dormancy of the tubers within one lot (comprising undamaged and healthy tubers with a narrow range in individual weight, and stored at constant temperatures) was well described with a location parameter and a dispersion parameter. In this thesis, the moment of 80 % sprouted tubers, being the definition of the European Association for

Potato Research for the end of dormancy of a tuber sample, was used as the location parameter. The time lapse between 10 % and 90 % sprouting was used to characterize the spread in duration of dormancy within a tuber lot.

The variation in duration of dormancy within plants (and tuber lots) of cv. Diamant was investigated further by means of an experimental set-up which allowed frequent, non-destructive observations on stolon and tuber development. During plant growth, the 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 were observed. Regression analyses were used to select sets of variables that best explained the variation in duration of dormancy.

The duration of dormancy (in days after haulm pulling) was most closely related to tuber weight. The duration of dormancy was also related to the date of tuber initiation (the later the tubers were initiated, the later their dormancy ended) and to the position of the tuber on the plant during its growth, even for tubers of similar weight.

Variation in duration of dormancy between tuber lots

Variation in the duration of dormancy between seed tuber lots refers to variation in the duration of dormancy between tuber lots (from one cultivar and stored under similar conditions) caused by differences between years, seasons or origins. Own experiments confirmed reports in the literature that this variation generally is less than 4 weeks. Only a few cases are known in which there was no interaction between the cultivar and the source of variation.

Differences in the duration of dormancy between years, seasons or origins may have many causes. A number of factors were tested against the hypothesis that dormancy might be shortened by the following conditions during growth: conditions unfavourable for tuber initiation, those which favour the induction of second growth or those which stimulate growth of axillary buds of the haulm. Such conditions are high nitrogen rates, high temperatures, low light intensities and long photoperiods. These factors were varied experimentally during 2-6 weeks after tuber initiation.

Nitrogen top dressings (75-150 kg N/ha) shortened the dormancy by about one week. The effect of high temperatures depended on the cultivar. In cv. Diamant, compared with the standard regime 18/12 °C (day 12 h/night) only very high temperatures (30-32 °C) shortened the dormancy by a maximum of 2-3 weeks. Compared with the standard regime no regime with higher temperatures shortened dormancy in cv. Désirée, whereas some regimes even prolonged dormancy. Reducing the light intensity by 50-75 % shortened the dormancy by up to one week. Dormancy was prolonged or shortened by up to 9 days by extending the photoperiod from 12 to 18 h. Positive and negative effects differed between the cultivars and experiments but not in a systematic way. Generally, the effects on tuber dormancy of the factors investigated were small. Dormancy was not unambiguously affected by factors which lower the tuberization stimulus, those which favour the induction of second growth or those which stimulate growth of axillary buds of

the haulm. A green, active plant seems to have a controlling influence on tuber dormancy, as long as the tubers are attached to it.

Shortening dormancy and advancing growth vigour

Chapter 5 of this thesis discusses the effects on dormancy and growth vigour of several storage temperature regimes and a foliar spray of gibberellin A_3 (GA) 3-6 days prior to haulm removal. Both techniques shortened the dormancy and advanced the growth vigour by many weeks.

The effect of the storage regimes on dormancy was investigated, using up to 20 cultivars. The effects of the regimes (compared with storage at 18 °C) were associated with the genetically determined duration of dormancy of the cultivar at 18 °C. Storage at 28 °C slightly shortened or prolonged dormancy of cultivars with a short dormancy and shortened dormancy of cultivars with a long dormancy by up to 45 days. Some tubers of one cultivar lost their ability to sprout after storage at 28 °C. Storage with a hot pre-treatment (20 days at 28 °C and subsequently 18 °C) shortened dormancy by 2-3 weeks on average in all cultivars examined. A cold pre-treatment (20 days at 2 °C and subsequently 18 °C) shortened dormancy by 2 weeks on average in some cultivars with a short dormancy and in all cultivars with a long dormancy.

The magnitude of the effect of a foliar GA spray on dormancy depended on the cultivar and storage regime. For cv. Diamant (short dormancy), the foliar GA spray had the largest effect (30-50 days) when storage took place at 18 °C. For cv. Désirée (long dormancy), the largest effect of a foliar GA spray was obtained in combination with storage at 28 °C; compared with tubers from untreated plants stored at 18 °C, this combination of treatments shortened dormancy by 80-100 days.

In an experiment with cvs Diamant and Désirée, tubers from untreated and GA-treated plants were stored at 28 °C. Every 2 weeks, tuber samples were transferred to 18 °C. All four cultivar and GA treatment combinations had an optimum duration of storage at 28 °C for the dormancy-shortening effect. The storage duration at 28 °C resulting in the shortest dormancy was shorter for cv. Diamant (short dormancy) than for cv. Désirée (long dormancy) and was shorter after a foliar GA spray. From these results and from the results of the experiment with 20 cultivars, it was concluded that 28 °C is a favourable storage temperature for releasing dormancy, but that 18 °C storage is more favourable for the subsequent sprout growth.

A foliar GA spray and storage at 28 °C enhanced physiological ageing of the tubers. At early plantings, the growth vigour of tubers was greatly enhanced by both treatments. At later plantings, the differences in growth vigour between tubers from the GA treatment and its control as well as between tubers stored at 28 °C and stored at 18 °C diminished. Combinations of both treatments may cause excessive seed ageing and may have negative effects on the growth vigour at later plantings. Tubers from GA-treated plants produced plants without any morphological abnormalities.

The effect of a GA spray and storage regimes on the tuber yield of the next crop depended on

the duration of dormancy of the cultivar. For cultivars with a long dormancy, this effect was very positive.

In the research described in this thesis, several examples were found in which the treatment resulting in the shortest dormancy did not give the highest growth vigour at early planting. These examples suggest that physiological ageing and releasing dormancy are (partly) different processes.

Conclusions

During dormancy, the length of the axis and the number of leaf primordia of the buds of tubers harvested immature do not change and thus, these characteristics cannot be used to quantify dormancy and to predict the duration of dormancy. After haulm removal, the response of tubers to a dormancy-breaking intervention with growth-stimulating substances increased with time. The response to this technique could possibly be used to predict the end of dormancy, but more research is necessary to develop such an application.

The duration of dormancy of tubers from one plant varies greatly. This spread may be related to the spread in tuber weight, the date of tuber initiation and to the position of the tuber on the plant during tuber growth.

The variation in duration of dormancy between different seed tuber lots is generally small. The effects on dormancy of factors during growth, such as nitrogen, temperature and light are rather small, contrary to the effects of a foliar GA spray and the effect of storage temperature regimes. Both a foliar GA spray and storage regimes shorten the dormancy and advance the growth vigour of seed tubers greatly. The effects varied from a single week up to several (>3) months, depending on the cultivar, whether one or both treatments were used, and on whether a storage regime with low or high temperatures was chosen. The treatments offer very good prospects for improving the performance of seed potatoes that are planted soon after the harvest.

SAMENVATTING

KIEMRUST EN GROEIKRACHT VAN AARDAPPELPOOTGOED

De kiemrust en produktiviteit van de pootaardappel

De aardappel wordt meestal vermeerderd via knollen. De fysiologische eigenschappen van een aardappelknol veranderen met de tijd; dit komt tot uitdrukking in het spruitgedrag van de knol. Omdat de tijdschaal van veranderingen in het spruitgedrag verschilt tussen rassen en beïnvloed wordt door de bewaarcondities, is de term 'fysiologische leeftijd' ingevoerd. Na het poten van een knol blijkt deze leeftijd vooral uit de groeikracht. De groeikracht wordt gedefiniëerd als het vermogen van de knol om in relatief korte (vooraf gedefiniëerde) tijd een omvangrijke plant te leveren.

Na de oogst maakt de knol een fase van kiemrust door, waarin ook onder voor spruitgroei ideale omstandigheden geen spruiten worden gevormd; de groeikracht is nul. Na afloop van deze kiemrustperiode neemt de groeikracht langzaam toe tot een maximum. Na enige tijd neemt de groeikracht weer langzaam af totdat de knol uiteindelijk niet meer in staat is een plant te produceren.

De fysiologische leeftijd van de knol is ook van invloed op het groeipatroon van de gevormde plant. Planten uit fysiologisch jong pootgoed verouderen in het algemeen langzamer dan die uit fysiologisch ouder pootgoed. De knolopbrengst geproduceerd door planten uit jong pootgoed zal achterblijven bij die van planten uit oud pootgoed bij relatief vroege oogst, terwijl het tegengestelde het geval kan zijn bij relatief late oogst.

Doelstellingen en opzet van het onderzoek

Kiemrust is voordelig voor knollen die gedurende een zekere periode bewaard moeten worden vóór consumptie of ander gebruik, maar is nadelig voor knollen die kort na de oogst gepoot moeten worden. De kiemrustduur hangt af van het genotype, maar wordt ook beïnvloed door de omstandigheden tijdens de groei en bewaring van de knollen. Het is belangrijk de factoren te kennen die de kiemrust beïnvloeden en het einde van de kiemrustperiode te kunnen voorspellen, zodat het pootgoed op de beste wijze bewaard kan worden afhankelijk van de bestemming van de knollen. Het zou een groot voordeel zijn wanneer de kiemrust gemeten kan worden lang voordat ze eindigt. Het onderzoek dat beschreven wordt in het eerste deel van dit proefschrift (Hoofdstukken 2-4) richtte zich op de meting (kwantificering) van kiemrust en op het onderzoeken van de factoren die de variatie in kiemrustduur veroorzaken, zodat de kiemrustduur beter voorspelbaar wordt.

Uit kiemrust zijnde pootaardappelen met een goede groeikracht zijn niet altijd beschikbaar. Vaak moeten knollen snel na de oogst gepoot worden, bijvoorbeeld in delen van de wereld waar de aardappel meerdere keren per jaar geteeld wordt en knollen van het ene gewas weer gebruikt

worden voor het daaropvolgende gewas. Wanneer pootaardappelen worden geïmporteerd vanuit andere streken of landen moeten ze soms ook snel na de oogst gepoot worden. Kiemrust of een geringe groeikracht leidt dan tot niet-optimale gewasgroei en opbrengstreducties. Het onderzoek dat beschreven wordt in Hoofdstuk 5 van dit proefschrift richtte zich op de mogelijkheden om kiemrust van pootaardappelen te verkorten en de groeikracht van de knollen snel na de oogst te bevorderen.

Het onderzoek beschreven in de Hoofdstukken 2-4 werd uitgevoerd met de rassen Diamant (korte kiemrustduur) en Désirée (lange kiemrustduur). Het onderzoek beschreven in Hoofdstuk 5 werd daarnaast ook uitgevoerd met andere rassen. De standaardbewaring vond plaats in het donker bij 18 °C en 80 % relatieve luchtvochtigheid in goed gecontroleerde bewaarcellen (ideale condities voor spruitgroei). De kiemrustperiode werd gedefiniëerd als de periode vanaf knolaanleg tot het moment dat de knol tenminste één spruit met een lengte van 2 mm gevormd heeft. Om praktische redenen werd de kiemrustduur vaak uitgedrukt in dagen vanaf de loofvernietiging. Het onderzoek richtte zich op onrijp geoogste knollen, zoals in Nederland gebruikelijk is bij de teelt van pootgoed.

Morfologische en fysiologische veranderingen tijdens kiemrust

Na looftrekken in een onrijp gewasstadium traden er gedurende tenminste 60 (Diamant) of 95 (Désirée) dagen geen veranderingen op in het aantal bladprimordia of in de lengte van knolknoppen. Bij beide rassen groeiden de apicale knoppen vanaf het begin van de spruitgroei in ongeveer 20 dagen uit tot een lengte van 2 mm. De kiemrustduur van een ras is derhalve niet voorspelbaar met behulp van eenvoudige morfologische kenmerken. Het verschil in lengte van de kiemrustduur tussen de beide rassen volgens het 2 mm criterium berustte vooral op het verschil in de periode van stilstand in groei en niet op verschillen in initiële groeisnelheid van de spruiten tot een lengte van 2 mm is bereikt.

Er werd ook geprobeerd de kiemrust te kwantificeren met behulp van een biotoets, waarin de respons op een rustbrekende ingreep gemeten werd. In de biotoets werden geregeld knolmonsters uit de bewaring genomen. Laterale oogstukjes uit de knollen werden vervolgens gedompeld in een concentratiereeks van een groeistof met een rustbrekende werking (6-benzylaminopurine). Na 7 dagen incubatie werd het aantal oogstukjes met kiemen geteld. In het algemeen bleek de respons op deze methode toe te nemen, naarmate de knollen langer bewaard waren sinds de loofverwijdering. Dit wijst erop, dat de 'intensiteit' van rust niet constant is gedurende de kiemrustperiode. Rassen met een korte kiemrust toonden meestal een snellere toename in respons dan rassen met een lange rust. Deze trends waren waarneembaar, maar er was sprake van een grote variatie in de respons. De methode leek zeer gevoelig voor kleine veranderingen in uitwendige omstandigheden tijdens de incubatie. Indien deze variatie in respons inderdaad veroorzaakt werd door de variatie in uitwendige omstandigheden tijdens de incubatie en indien het lukt deze te verkleinen, dan zou de biotoets perspectief kunnen bieden om de kiemrust te meten en

de resterende rustduur te schatten.

Variatie in kiemrustduur binnen een partij pootgoed

De variatie in kiemrustduur tussen knollen afkomstig van één plant bleek vele weken te kunnen bedragen. Bij het ras Diamant was deze variatie belangrijk groter dan bij het ras Désirée. Voor Diamant bestond er een duidelijke relatie tussen de kiemrustduur en het knolgewicht; de kiemrust van zwaardere knollen eindigde eerder dan die van lichtere knollen. Voor Désirée was een relatie tussen kiemrust en knolgewicht vrijwel afwezig.

De frequentieverdeling van de kiemrustduur van knollen van een partij (bestaande uit gave en gezonde knollen met een beperkte spreiding in gewicht en bewaard bij constante temperaturen) bleek afdoende gekarakteriseerd te kunnen worden met een plaatsparameter en een spreidingsparameter. Als plaatsparameter werd in dit proefschrift het moment van 80 % kieming gehanteerd, zijnde de definitie voor het einde van de kiemrust van een monster van de Europese Associatie voor Aardappelonderzoek. Als spreidingsparameter werd de tijdsduur tussen 10 % en 90 % kieming gebruikt.

In een proefopstelling die niet-destructieve waarnemingen gedurende de stoloon- en knolgroei mogelijk maakte, werd de variatie in kiemrustduur binnen planten (en partijen) van het ras Diamant nader onderzocht. De waargenomen (verklarende) variabelen waren stoloonaanlegdatum, stoloonlengte, positie van het stoloon aan de plant, knolaanlegdatum, positie van de knol aan het stoloon, knolvorm en knolgewicht. Met behulp van multiple regressie-analyse werd de set van variabelen gezocht die de variatie in kiemrustduur het best kon verklaren.

De kiemrustduur (in dagen vanaf loofvernietiging) bleek het duidelijkst samen te hangen met het knolgewicht. De duur van de kiemrust bleek ook gerelateerd aan de knolaanlegdatum (later aangelegde knollen eindigden hun kiemrust eerder) en aan de positie van de knol aan de plant tijdens de groei, zelfs bij gelijk knolgewicht.

Variatie in kiemrustduur tussen partijen pootgoed

Met variatie in kiemrustduur tussen partijen pootgoed wordt bedoeld die variatie in kiemrustduur tussen partijen (van één ras en bewaard onder gelijke omstandigheden), die ontstaat ten gevolge van jaar-, seizoens- of herkomstverschillen. Op basis van een literatuuronderzoek en op basis van eigen gegevens werd geconcludeerd dat deze variatie doorgaans minder dan 4 weken bedraagt. Slechts weinig gevallen zijn bekend waarbij geen interactie bestond tussen het ras en de externe factoren die de variatie veroorzaakten.

Jaar-, seizoens- of herkomstverschillen in kiemrustduur kunnen vele oorzaken hebben. Een aantal factoren zijn nader onderzocht in het kader van de toetsing van een werkhypothese. Volgens deze hypothese zouden de volgende groeicondities een kiemrustverkortende invloed kunnen hebben: condities die ongunstig zijn voor knolaanleg, die gunstig zijn voor de inductie van doorwas of condities die gunstig zijn voor de uitgroei van okselknoppen van het loof. Dergelijke

condities zijn hoge stikstofgiften, hoge temperaturen, lage lichtintensiteiten en lange fotoperioden. De stikstofgift, temperatuur, lichtintensiteit en fotoperiode werden experimenteel gevariëerd gedurende 2-6 weken na knolaanleg.

Extra stikstof (75-150 kg N/ha) verkortte de kiemrust met ongeveer één week. Het effect van hoge temperaturen ten opzichte van het standaardregime 18 °C overdag en 12 °C 's nachts (12 uur daglengte) was rasafhankelijk. Bij het ras Diamant bleken alleen zeer hoge temperaturen (30-32 °C) de kiemrust te kunnen verkorten, met maximaal 2-3 weken. Bij het ras Désirée verkortte geen enkel temperatuurregime de kiemrust ten opzichte van het standaardregime, terwijl sommige regimes met hoge temperaturen zelfs de rust verlengden. Een verlaging van de lichtintensiteit met 50-75 % verkortte de kiemrust met maximaal één week. Een verlenging van de fotoperiode van 12 tot 18 uur had een kiemrusteffect van maximaal 9 dagen, maar de effecten verschilden in omvang en richting tussen de rassen en experimenten op een niet systematische wijze. Het effect van de onderzochte factoren bleek dus over het algemeen zeer gering te zijn. De kiemrust werd niet éénduidig beïnvloed door factoren die de inductie tot knolaanleg verlagen, factoren die de inductie tot doorwas bevorderen en factoren die de groei van okselknoppen van het loof stimuleren. Een actieve, groene plant lijkt een controlerende invloed uit te oefenen op de kiemrust van haar knollen zolang de verbinding niet is verbroken.

Verkorting van kiemrust en vervroeging van groeikracht

In het onderzoek beschreven in Hoofdstuk 5 werd het effect op de kiemrustduur en groeikracht onderzocht van diverse bewaartemperatuurregimes en een gewasbespuiting met gibberelline A_3 (GA), 3-6 dagen voor de loofverwijdering. Beide technieken verkortten de kiemrust en vervroegden de groeikracht met vele weken.

Het effect van de bewaarregimes op de kiemrust werd onderzocht voor 20 rassen. De effecten van de regimes (t.o.v. bewaring bij 18 °C) op de kiemrust bleken gerelateerd aan de genetisch bepaalde kiemrustduur van het ras bij 18 °C. Bewaring bij 28 °C gaf een geringe verkorting of zelfs een verlenging van de kiemrust bij rassen met een korte kiemrust, terwijl het de kiemrust van rassen met een lange rustduur met maximaal 45 dagen verkortte. Een aantal knollen van één ras verloor de mogelijkheid tot kiemen na bewaring bij 28 °C. Een warmtestoot tijdens de bewaring (20 dagen 28 °C gevolgd door 18 °C) verkortte de kiemrust van *alle* rassen met gemiddeld 2-3 weken. Een koudestoot (20 dagen 2 °C gevolgd door 18 °C) verkortte de kiemrust van sommige rassen met een korte rust en van alle rassen met een lange rust met gemiddeld 2 weken.

De grootte van het effect van een gewasbespuiting met GA op de kiemrust hing af van het ras en het bewaartemperatuurregime. Een GA-bespuiting had bij het ras Diamant (korte kiemrust) het grootste effect (30-50 dagen) indien de knollen bewaard werden bij 18 °C. Bij het ras Désirée (lange kiemrust) was het effect het grootst als de knollen bij 28 °C bewaard werden; ten opzichte van bij 18 °C bewaarde knollen van onbehandelde planten werd op deze manier de kiemrust met

80-100 dagen verkort.

In een experiment met de rassen Diamant en Désirée werden knollen van wel of niet met GA behandelde planten bij 28 °C bewaard, waarbij elke 2 weken monsters werden teruggeplaatst naar 18 °C. Elk van de vier ras- en GA-behandelingscombinaties vertoonden een optimale bewaarduur bij 28 °C ten aanzien van de kiemrustduurverkorting. De bewaarduur bij 28 °C die resulteerde in de kortste rust was korter voor het ras Diamant (korte kiemrust) dan voor het ras Désirée (lange kiemrust) en was korter na een gewasbespuiting met GA. Uit deze resultaten en uit de resultaten van de proef met 20 rassen werd geconcludeerd dat 28 °C een gunstige bewaartemperatuur is voor de opheffing van de kiemrust, maar dat 18 °C een meer optimale bewaartemperatuur is voor de daaropvolgende spruitgroei.

Een gewasbespuiting met GA en bewaring bij 28 °C bevorderden de fysiologische veroudering. Beide behandelingen hadden een zeer positieve invloed op de groeikracht bij relatief vroeg poten. Bij relatief laat poten werden de verschillen in groeikracht tussen knollen van de GA-behandeling en de controle, en die tussen knollen bewaard bij 28 en bij 18 °C geringer. Combinaties van beide behandelingen kunnen tot sterke veroudering van de knollen leiden en de groeikracht verlagen bij relatief laat poten. Knollen afkomstig van met GA bespoten planten produceerden planten zonder morfologische afwijkingen.

Het effect van de GA-bespuiting en de bewaarregimes op de knolopbrengst van het volggewas hing onder meer af van de kiemrustduur van het ras. Bij rassen met een lange kiemrust was dit effect zeer positief.

In het onderzoek, beschreven in dit proefschrift, werden verschillende voorbeelden gevonden, waarin de behandeling die tot de kortste rust leidde niet in de hoogste groeikracht resulteerde. Deze voorbeelden suggereren dat fysiologische veroudering en het opheffen van de kiemrust (gedeeltelijk) twee verschillende processen zijn.

Conclusies

Gedurende de kiemrust veranderen de knoppen van onrijp geoogste knollen niet in aantal bladprimordia en in lengte. Deze morfologische kenmerken kunnen derhalve niet gebruikt worden om de kiemrust van de knol te kwantificeren en het einde van de kiemrust te voorspellen. De respons van de knollen op een rustbrekende ingreep met groeistimulerende stoffen lijkt toe te nemen, naarmate de knollen langer bewaard zijn. Voorspelling van het einde van de kiemrust met behulp van deze techniek zou perspectief kunnen bieden, maar hiervoor is aanvullend onderzoek nodig.

De kiemrustduur van knollen afkomstig van één plant of partij vertoont een aanzienlijke spreiding. Deze spreiding kan een samenhang vertonen met de spreiding in knolgewicht, de knolaanlegdatum en de positie van de knol aan de plant tijdens de groei.

De spreiding in kiemrustduur tussen verschillende partijen blijkt doorgaans gering te zijn. Het effect van de uitwendige omstandigheden tijdens de groei van de knollen op de kiemrustduur is

vrij klein. Dit in tegenstelling tot het effect van een gewasbespuiting met gibberellinezuur, kort voor de loofvernietiging, en dat van bewaartemperatuurregimes onmiddellijk na de oogst. Zowel een gewasbespuiting met GA als bewaarregimes kunnen de kiemrust aanzienlijk verkorten en de groeikracht vervroegen. De effecten variëerden van een enkele week tot meerdere (>3) maanden, afhankelijk van het ras, van het feit of beide behandelingen werden gebruikt en van de keuze van een bewaarregime met lage of hoge temperaturen. De behandelingen bieden grote mogelijkheden om de produktiviteit te verbeteren van pootgoed dat snel na de oogst gepoot wordt.

CURRICULUM VITAE

Martin Klaas van Ittersum werd geboren op 6 januari 1963 te IJsselmuiden. Na het behalen van het VWO-diploma aan de Christelijke Scholengemeenschap te Emmeloord, begon hij in 1981 met de studie Landbouwplantenteelt aan de toenmalige Landbouwhogeschool te Wageningen. In november 1987 behaalde hij het doctoraalexamen (met lof) met als doctoraalvakken landbouwplantenteelt (hoofdvak), wiskundige statistiek, agrarische bedrijfseconomie en bodemvruchtbaarheid en plantenvoeding. Gedurende het laatste jaar van zijn studie gaf hij voor de vakgroep Wiskunde van de Landbouwuniversiteit werkcolleges in de vakken inleiding en voortzetting statistiek. Per januari 1988 trad hij in dienst bij de vakgroep Landbouwplantenteelt en graslandkunde van de LUW als assistent in opleiding en verrichtte het onderzoek dat beschreven is in dit proefschrift. Van januari tot en met september 1992 was hij toegevoegd docent Produktkunde bij de eerder genoemde vakgroep en vanaf oktober 1992 is hij werkzaam als universitair docent bij de vakgroep Theoretische produktie-ecologie van de Landbouwuniversiteit.