ON FLOWERING AND BOTANICAL SEED PRODUCTION

IN POTATO (SOLANUM TUBEROSUM L.)

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ABSTRACT

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The use of true potato seed (TPS) as a propagule for potato tuber (*Solanum tuberosum* L.) production is a viable alternative to the use of seed tubers. For this technology to be successful, efficient production of high-quality botanical seed is crucial. The objectives of the research reported in this thesis were to define production practices that maximise quantity and quality of botanical seed produced, and to contribute to the understanding of above-ground development in potato.

The first part of the study describes experiments on seed production under field conditions in three contrasting agro-ecological zones in Peru. Seed production is described as a function of number of flowers produced, berry set and number of seeds produced per berry. Hundred-seed weight is used as seed-quality parameter. In the second part of the thesis, flower production is analysed as a function of inflorescence production, number of flower primordia initiated per inflorescence and flower primordia survival.

The results of the field experiments indicated that generally, later-produced inflorescences on a shoot or in a field, and later-produced flowers in an inflorescence have a lower berry set and produce fewer and smaller seeds per flower. The effect of the position of the flower in the inflorescence does not affect seed size in all cultivars. Hundred-seed weight of production from primary inflorescences was increased when later-produced inflorescences were not used for seed production, but this could not compensate for the reduction of seed yield. Increasing plant density reduced the number of inflorescences per shoot and the number of flowers per inflorescence. Flower production per m^2 increased with plant density in two of the three cultivars used. Berry set, number of seeds per berry and 100-seed weight were reduced when comparing flowers at similar positions on the shoot. However, because increasing plant density shifted the flower production from later- to earlier- formed flowers, the effect on average berry set, number of seeds per berry and seed size of the total seed production was relatively small. The effect of plant density on seed production was largely determined by the effect on flower production. Artificial extension of the photoperiod and interruption of the night with incandescent light increased the flower production under warm tropical conditions. This effect was principally a result of an increased inflorescence production. Photoperiod treatments did not affect the seed production per flower.

Experiments in controlled conditions showed that increasing photoperiod and temperature increased the production of inflorescence positions per shoot, number of flower primordia per inflorescence and flower primordia survival in the temperature range of 15-25°C (24-h average). Shoot development and flowering in potato were quantified as functions of rates and durations of leaf and flower primordia initiation, and of stem production. Effects of increasing temperature and photoperiods on shoot development and flowering were a result of increasing thermal durations of stem production, and leaf and flower primordia production of individual stems. The effects on individual stems were, however, small compared to the effects on stem and inflorescence production.

Conclusions from the study for practical TPS production are that the last produced flowers in a field have a strongly reduced potential for seed production and that seed production can be best increased by increasing flower production through longer photoperiods and higher temperatures.

Keywords: *Solanum tuberosum* L., flowering, flower position, inflorescence position, photoperiod, shoot development, stem production, temperature, TPS production.

References to chapters 2-8 should be made citing the original publications.

CONTENTS

PREFACE

This thesis is a product of my work on potato between 1983 and 1995. When I started in 1983 on the experimental station in Huancayo, definition of field practices of TPS production was urgently needed. Because little was known about TPS production, the first field experiments were most of all meant as orientations. However, these orientations produced some interesting results, also thanks to the input of Dr. Siert Wiersema. Siert, I am grateful for the fact that you informally picked up the role as my tutor-supervisor in these years; this has been tremendously important to my work on the right track. Moreover, your well-planned and systematic way of working has been a very instructive example.

As I remember, the idea of using some of the results for a PhD thesis first emerged in a discussion of the TPS-work with dr. Ludwine Dellaert when she visited CIP. Ludwine, finally a thesis is there; I can now thank you for having read the very first drafts in the cold nights of Huancayo and sowing the seed of this thesis.

When in 1987 professor dr. Struik accepted the idea of a thesis, field work in Huancayo was already concluded and I was planning my move from Huancayo to San Ramon for the research project I had prepared on TPS production in the warm tropics. This work enabled me to collect more data for a thesis.

Back in Wageningen, still a lot had to be done to finish a thesis. First, I took the opportunity to carry out an experiment in the department of Agronomy which nicely complemented the field work from Peru. And, by that time, most of the processing of the Peru-data and all the writing-up still had to be done. When I took up a job at IVO in 1990, there was not much time to continue writing. However, this job, along with other other activities I undertook over the last few years, served me well to keep the importance of my TPS work in perspective. On the one hand, I was constantly reminded of the distance between the world of scientists working 'on-station' and the farmers, and on the other hand I learned to see the relevance of the small pieces of 'technical' research, such as the work on TPS.

Finishing this thesis would have been less fun and more difficult without the support of many friends and collegues. I herewith want to thank you all; for letting me use your computer, helping me out with a computer programme, providing me with pollen, drawing figures for publications, discussing bee-behaviour and plant morphology, sharing your house with me, taking care of my dogs, for spending your holidays collecting field data for me, and the many other forms of professional and moral support.

I especially want to thank Gary and Karin Atlin, John and Sue Elphinstone, Freddy Payton and Sjaan and Erica Hopmans for the hospitality, for the good times in Huancayo, San Ramon and Lima, and for 'being there', when my motivation needed a stimulus, when the situation in Peru turned grim, and when 'problemitas' had to be solved. I also want to thank the thirteen field-assistents whose support and companionship I enjoyed very much while working in the field. Cesar 'Choclito' Rios, you did a great job in continuing the experiments in Lima in the 85/86 season when I was ill. Elena Madge, thank you for your contribution to the experimental work in the field and behind the computer in Huancayo. Special words of thanks to the people of the CIP car-pool and cafeteria: I have always enjoyed your friendliness and cooperation. Your small gestures often had a significant positive effect on my working-spirit. Also, thanks to Patricio Malagamba, Noel Pallais,

Rolando Cabello and all other CIP-collegues and friends: you made it a great experience to work at CIP. I want to thank CIP as an institution for giving me the opportunity and facilities to work and live in Peru for severaly years.

Ank Bos and Jacob van Dam, your cooperation in the experimental work in Wageningen is very much appreciated. Special thanks to Jan Neuteboom and other collegues from the department of Agronomy and 'The Institute', Piet Stap, Willemien Lommen, The Michielsens, and Roland Friele and Julie Meerveld for lending an ear, and sharing professional and personal brainwaves and anxieties.

Last but not least, I want to thank Paul Struik. Paul, you provided me with the opportunity to work in your department and shared your ideas with me on potatoes and other subjects. I thank you for your patience, time and energy spent on my manuscripts. Working with you was -and still is- a pleasure.

Finally, I sincerely hope that the work presented in this thesis will contribute to the benefit of farmers working the fields with potatoes and the people eating them, especially those who live in Peru.

All in all, the potato is a beautiful crop to grow, an exciting plant to study
and a delightful tuber to eat.....

Conny Almekinders.

NOTE

Chapters 2-7 of this thesis have been published by Potato Research, Scientia Horticulturae or Netherlands Journal of Agricultural Science. Chapter 8 has been submitted for publication by Potato Research. The presentations of the chapters in this thesis differ from the original publications in the following ways:

. The titles and running titles have been adapted.
. The 'References' of the individual papers have been combined into one list.
. Acknowledgements are given in the Preface.
. Minor alterations have been made in the Tables, to standardize the presentation.
. Some minor alterations in the terminology referring to 'shoots' and 'stems' were necessary, since the definition of these plant parts was developed during the study. Within each chapter the terminology is used as defined in the particular chapter.

Chapter 1

GENERAL INTRODUCTION

1 GENERAL INTRODUCTION

1.1. True potato seed (TPS)

Potato can be reproduced vegetatively or sexually. Normally, for potato seed and ware tuber production, potatoes are propagated vegetatively by growing them from (seed) tubers. They can, however, also be grown from sexually produced (botanical) seed, i.e. True Potato Seed (TPS). The use of TPS for potato tuber production is not a new technology. Plant breeders use TPS to generate new cultivars. Farmers in the Andes have been using this technology ever since they started domesticating potatoes. Also Asian farmers and Irish immigrants in the Northern America are known to have used botanical seeds, usually to replace their degenerated material or to produce planting material when seed tubers were not available. In 1977 the International Potato Center (CIP) started research on the use of TPS as an alternative to the use of seed tubers for potato production.

The advantages of using TPS for potato production are especially relevant for developing countries where the availability and costs of good quality seed tubers are strongly limiting potato production (Umaerus, 1987; Malagamba, 1988). The most important advantages are that TPS is easier to store and transport than seed tubers, whereas most virus and tuber-borne diseases are not transmitted from the plant to the botanical seed. Moreover, farmers do not need to save a part from the harvest for next planting. Because of these advantages, TPS can be better and cheaper planting material than seed tubers. Large distances from seed tuber producing areas and availability of labour further increase the potential of the technology in comparison to the use of seed tubers.

The high requirements for good seed germination, delicateness of the seedlings, slow initial development of the crop, the larger number and smaller size of tubers produced, and the genetic variation within the crop are considered disadvantages of the use of TPS. However, these disadvantages can be overcome by using suitable genetic material and appropriate production technology. The genetic material presently being used shows relatively low levels of segregation for seedling vigour, plant maturity, tuber dry matter and tuber dormancy. On the contrary, at present, the genetic variation is considered a potential advantage in relation to pest and disease resistance which merits to be further explored. Furthermore, the identification of new hybrid crosses with increased seedling vigour and shorter growing periods has greatly improved the potential of the TPS technology. Moreover, the development of post-harvest practices have contributed importantly to improving quality and performance of TPS (Pallais, 1991; 1994).

The availability of improved genetic material and the increased physiological quality of the seed has recently resulted in a significant expansion of the interest in TPS technology. In some areas the interest is renewed after an initial phase of on-farm evaluation of earlier selected genetic material and adaptation of the technology to farmers' conditions, while in other areas the interest is more recent (CIP, 1992; Pallais, 1994). In some of these areas the production conditions meet a set of criteria which were expected to favour the adoption of the TPS technology: tropical (low-elevation) areas where good quality seed tubers are expensive or not available, and small-farmers with abundant available family-labour (India, Indonesia, Paraguay, Nicaragua). However, the TPS technology has also been taken up by farmers under conditions where this was not directly foreseen: large-scale commercial farmers in arid, irrigated conditions (Egypt, Peru).

1.2. TPS utilization systems

Potatoes produced from TPS are called seedling tubers. They can be produced by different sowing and transplanting methods (Figure 1.1). TPS can be sown directly in the field or in nursery beds, and seedlings can be left in place or be transplanted (Wiersema, 1984; 1985, Malagamba, 1988). Seedling tubers can be sold as ware potatoes or be used as seed tubers. These different practices in combination with possible variation in planting dates and number of multiplications, make the TPS technology flexible and adaptable to location-specific conditions (agro-ecological conditions, labour costs, market prices). It can therefore be an excellent basis for a potato seed (tuber) supply system.

The production potential of a crop grown from TPS is at least similar to that of a crop grown from seed tubers. Since plants grown from TPS generally produce more tubers per stem than plants grown from tubers and because these tubers tend to be smaller, potato production from TPS is especially suitable for seed(ling) tuber production. The most commonly used technology at present probably is the production of seedling tubers in nursery beds. When using TPS in nursery beds, the high requirements of conditions for good seed germination and seedling growth can be met more easily. Furthermore, seedling tuber production in nurseries does not require high labour inputs for transplanting, plants do not suffer a transplant shock and crop management is better controlled in small protected areas than in the field. By sowing in nursery beds, it is possible to produce seedling tubers off-season, thereby creating the possibility to prolong the growing season and to produce planting material with the right physiological condition for planting in the field. With improved genetic material coming available and increased seed quality, it is possible, however, that in the future direct sowing will be the most-used TPS based production system.

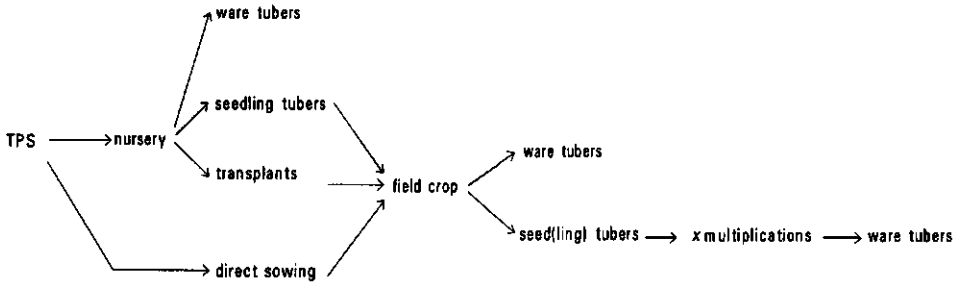

Figure 1.1. Schematic presentation of possible TPS utilization systems.

1.3. Production of TPS: the objectives of the study

The availability of good quality, economically priced (botanical) seed is of paramount importance for the success and further expansion of the TPS technology (Pallais, 1987; 1994). Efficient production of high quality TPS is therefore essential.

A potato plant can produce one or more inflorescences, each with one or more flowers. After successful fertilization, flowers develop into berries with seeds. Some clones form berries with seeds from open pollination, but presently most TPS used for potato tuber production is hand pollinated hybrid seed. Whereas the purpose of growing potatoes (from TPS or seed tubers) is the harvest of tubers, i.e. below-ground reproductive storage organs, for the production of the botanical seed the objective is growth and development of inflorescences, i.e. above-ground reproductive structures. Different from many other plant species, in potato, stem and leaf production continues while inflorescences in different stages of development are producing flowers, berries and seeds. The simultaneous development of different plant parts and the alternating purpose of growing potatoes for tuber or botanical seed production requires the understanding of possibilities to control the development of the different plant structures in potato.

The objective of this study was to define production practices that maximise quantity and quality of TPS produced, and contribute to the understanding of above-ground development in potato. In the first phase of the study, components determining seed production and factors that affect them were explored and investigated. As pollen production and pollination are important cost factors in hybrid TPS production, assessment of differences in production potential between flowers on a plant or in a field is meaningful. Furthermore, because increasing size of the seed produced can contribute importantly to increasing seed quality, identification of factors and production practices that increase seed size was an important objective of the research. This study only considered differences in seed quality between treatments of one genotype within a production field.

Since flower production was an important factor determining the quantity of seed produced from a plant or a field, qualitative and quantitative analysis of this component were the objectives in the second phase of the study. The effect of temperature and photoperiod on above-ground development of the potato plant was studied in order to understand the variation in flower production over seasons within a location, and between locations. The cultivars used in the experiments were not only selected on the basis of their genetic potential as TPS parent, but also because of the range of plant types they represented. The cultivar Atzimba was included in all experiments.

1.4. Outline of the thesis

The first part of this thesis addresses field experiments with different genotypes, in three contrasting agro-ecological zones in Peru. In these experiments, the production potential of different inflorescences and flowers on a potato plant for production of TPS was assessed. In Chapters 2 and 3, berry set, seed set and seed weight of TPS production from different inflorescence positions on

a potato shoot and from different flowers in an inflorescence were analysed. Chapters 4 and 5 describe the effects of stem density on flowering and seed production. In Chapter 4, the number of inflorescences per plant, flower production per inflorescence, berry and seed set, and seed weight are analysed. In Chapter 5, the temporal patterns of flower production at different stem densities were evaluated and related to seed production characteristics. Artificial extension of the photoperiod as a practice to increase flower and seed production was studied in a warm tropical environment (Chapter 6). Nitrogen applications, pruning of lateral stems and time of berry harvest were also evaluated as potential factors and practices in TPS production (Chapters 2 and 4).

The results of experiments which were carried out under controlled conditions to improve the insight in the physiology of flowering in potato and its photothermal control are presented in Chapter 7. These results in combination with an extensive literature review were used to define a conceptual model of shoot structure and development in potato, with special attention for inflorescence and flower production. This model forms the basis for the definition of components that determine flower production and assessment of their responses to temperature and photoperiod.

Chapter 9 integrates the information on flowering and seed production, discusses the relevance of effects of environment and the implications for TPS production practices.

Chapter 2

EFFECTS OF INFLORESCENCE POSITION, NITROGEN TREATMENT, AND HARVEST DATE OF BERRIES ON FLOWERING AND SEED PRODUCTION

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2 EFFECTS OF INFLORESCENCE POSITION, NITROGEN TREATMENT, AND HARVEST DATE OF BERRIES ON FLOWERING AND SEED PRODUCTION

Additional keywords: number of flowers per inflorescence, berry set, seed quality

Summary

Flowering and true seed production from different order inflorescences in potato (*Solanum tuberosum* L.) were evaluated in two experiments. The number of flowers per inflorescence, berry set, berry weight, number of seeds per berry and seed weight generally decreased from primary inflorescences to tertiary inflorescences and inflorescences on lateral stems. The possible relation with carbohydrate distribution is discussed. Quality of the seeds produced from the different orders of inflorescences was a function of seed size; larger seeds showed better germination, emergence and seedling growth. Late harvest of berries increased berry weight and number of seeds per berry from primary inflorescences. Application of additional nitrogen during the flowering period did not affect flowering or differences between inflorescence positions in seed production, but it significantly decreased the number of seeds per berry. The practical implications of these results for true seed production are discussed.

2.1. Introduction

Advanced technology for the production of ware potatoes (*Solanum tuberosum* L.) as well as seed potatoes from True Potato Seed (TPS) has been developed for use in third world countries (Wiersema, 1986; Umaerus, 1987; CIP, 1988; Malagamba, 1988). Methods for the production of high quality TPS are essential to fully realize the potential of this technology. Since potatoes are commonly propagated vegetatively, little is known about the factors affecting yield and quality of TPS produced under field conditions.

The main stem of a potato shoot terminates in an inflorescence, the primary inflorescence, and shoot growth continues by apical lateral branching (Figure 2.1; Reestman & Schepers, 1971). Depending on the cultivar and environment, a shoot may develop several orders of branching, each terminating in an inflorescence of the corresponding order. Thus, inflorescences on higher orders of branching are younger and flower later. Lateral stems can emerge from lower buds on the main stem and may also produce inflorescences. TPS yield and quality may vary with the position of inflorescences since flowers and seed at each position are formed during different stages of plant development. Effects of the position of inflorescence on fruit and seed production have been reported for lettuce (Soffer & Smith, 1974), carrot (Borthwick, 1931; Hawthorne et al., 1962), celery (Thomas et al., 1979), parsnip (Hendrix, 1984; Gray & Steckel, 1985), cereals (see Gray & Thomas, 1982) and tomato (Hatcher, 1940; Hood, 1959; Pet & Garretsen, 1983).

High levels of nitrogen fertilizer in potato promote flowering (Bamberg & Hanneman, 1988), increase (Pallais et al., 1987) or decrease (Upadhya et al., 1985) seed weight and improve seed quality (Pallais, 1986). The effect of N on TPS production from inflorescences situated at different positions has not been studied.

This paper reports the effect of inflorescence position on yield and quality of TPS, as well as the effects of nitrogen fertilization and harvest date of berries.

2.2. Materials and methods

Experiments were planted at two experimental stations of the International Potato Center (CIP) in Peru. Experiment 1 was planted on October 25, 1984 at Huancayo, 3,200 m.a.s.l. Experiment 2 was planted on June 30, 1985 at Lima, 240 m.a.s.l.

2.2.1. Treatments and experimental design

The effect of inflorescence position on TPS production was studied by restricting seed production to the following inflorescences (Figure 2.1):

P : Seed production restricted to primary inflorescences only.

PS : Seed production restricted to primary and secondary inflorescences.

PST : Seed production from primary, secondary and tertiary inflorescences.

PSTL : Seed production from all inflorescences, including lateral stems. This treatment was applied only in Experiment 2.

Inflorescences other than those indicated in each treatment were not pollinated and did not develop berries spontaneously. Treatments PST (Experiment 1) and PSTL (Experiment 2) were used to study differences between primary, secondary, tertiary and lateral-stem inflorescences. Primary inflorescences of treatments P, PS, PST and PSTL were compared to study competition between the inflorescences on a main stem.

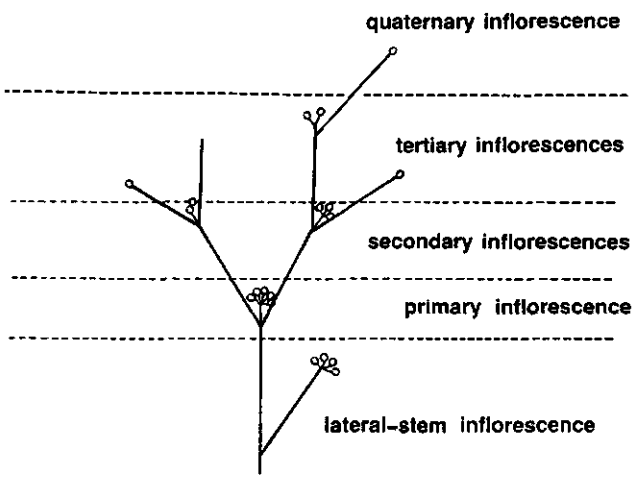

Figure 2.1. Diagram of a flowering potato stem, showing the successive orders of branching and flowering.

In Experiment 2 there were two N treatments:

- N_1: 45 kg N per ha at planting and 45 kg N per ha three weeks after planting, applied as ammonium nitrate (33% N).
- N_2: as N_1 plus 3 additional applications of N as urea (44 % N) at 40 kg N per ha per application during the flowering period.

At planting, fertilizer was applied in the rows, and the additional applications were applied as a side dressing.

To study possible interactions between berry maturity and nitrogen treatment in Experiment 2, primary berries were harvested on two dates. The early harvest was carried out 30 days after flowering (d.a.f.), when the berries started maturing, and the late harvest 50 d.a.f., when berries started to drop. Berries of secondary, tertiary and lateral-stem inflorescences were harvested about 50 d.a.f.

In Experiment 1, seed tubers of the cultivars Atzimba, CEX-69.1 and Yungay were planted in a split-plot design with 3 replications. Clones were assigned to main plots and the treatments P, PS and PST to sub-plots. In Experiment 2, seed tubers of the cv. Atzimba were planted in a split-split-plot design with 3 replications. The nitrogen treatments were assigned to main-plots, the treatments P, PS, PST and PSTL to sub-plots and harvest dates to sub-sub-plots. The number of plants per sub-plot (Experiment 1) and sub-sub-plot (Experiment 2) was 60 and 5 respectively. One above-ground stem per plant was sampled and used for TPS production.

For statistical analysis of differences between inflorescence positions, means were separated by a series of t-tests (Tables 2.1 and 2.2). The analysis of variance in which inflorescence position was considered as a treatment resulted in similar mean separations, so the S.E.'s of these analyses are given to simplify the presentation. Data of berry and seed production from different inflorescence positions in Experiment 1 (Table 2.2) were analysed by clone because tertiary inflorescences of Yungay failed to produce seeds. Data on the proportion of large berries, berry set and germination were transformed for statistical analysis (Tables 2.2, 2.3 and 2.4).

2.2.2. Seed production methods

In both experiments, planting distance within rows was 0.5 m. The distance between rows was 1.50 m in Experiment 1 and 1.40 m in Experiment 2. Shoot length reached up to 1 m and plants were trellised with cotton strings tied between wooden stakes as described for tomato by Geisenberg & Stewart (1986). Nitrogen fertilization in Experiment 1 was the same as N_1 in Experiment 2. In both experiments 100 kg P and 75 kg K per ha were applied at planting. Plants were not hilled.

Flowers were pollinated in the morning, 3 to 4 times a week, and each flower was pollinated once after anthesis. The pollen source was flowers harvested from field-grown male parent plants in the afternoon and left overnight to dry. Pollen, extracted from the flowers using a vibrator, was stored in gelatine capsules and taken to the field in black plastic film containers with silica gel. Flowers of Atzimba and CEX-69.1 were emasculated before anthesis and pollinated with pollen of the clone R-128.6. Flowers of Yungay in Experiment 1 were pollinated with a bulk pollen of Andigena clones. In Experiment 1, an average of 4 berries per inflorescence was produced and other flowers were pruned. In Experiment 2 all flowers of the treatment inflorescences were pollinated. After berry set, net bags were tied around the inflorescences to prevent berry loss.

2.2.3. Data collection and harvest procedures

The number of flowering inflorescences, their position and number of flowers in the treatments PST (Experiment 1) and PSTL (Experiment 2) were recorded. The age of berries from inflorescences of different orders at harvest was kept similar by maintaining the same period of time between pollination and harvest. Berries, harvested 65 d.a.f. (Experiment 1) and 30 or 50 d.a.f. (Experiment 2) were weighed and separated into large, medium and small size grades. Berries with a diameter of more than 32 mm for Atzimba and Yungay and more than 26 mm for CEX-69.1 were classified as large. All berries smaller than 23 mm were classified as small. Seed was extracted from a sample of 5 berries per treatment from each harvest in Experiment 1, and 8 berries per grade per treatment in Experiment 2. After extraction and drying, seeds were separated into fractions of large (>1.7 mm), medium (1.7-1.5 mm) and small (1.5-1.2 mm) sized seed, using round-hole sieves. The 100-seed weight of each fraction was determined from 3 samples of 100 seeds which had been dried to a constant weight over silica gel.

2.2.4. Seed tests

In a first test, seeds were sown from the progeny Atzimba x R-128.6 produced at the high nitrogen level (N_2) in treatment PSTL of Experiment 2. The effects of the following factors on seed quality were analysed: order of inflorescence (primary, secondary and tertiary), berry size (large and small), and seed size (large and small). Seed quality was measured by the rate and percentage of germination or emergence, and the early seedling growth. The seeds had been stored for 26 to 30 weeks over silica gel in a dessicator at 15-20 °C. After storage they were soaked for 24 hours in a solution of 1,500 ppm gibberellic acid (GA). Of each treatment, three samples each of 100 seeds were sown in a completely randomized design in nursery beds during the cool season in Lima. Replicates of the field experiment were maintained as replicates in the test. The nursery beds were 1 m wide bamboo constructions (Wiersema, 1985), filled with 20 cm of a 1:1 mix of sand and shredded peat moss. Seeds were sown at 4 x 20 cm spacing. Rates of fertilizer applied per square meter of bed were 13.1 g P at sowing, and 5.0 g N and 2.1 g K 8 days after emergence. Similar N and K applications were repeated 15 and 22 days after emergence which was recorded at regular intervals. Above-ground parts of the seedlings were harvested for determination of fresh and dry weights when the first plots reached full ground cover, 41 days after sowing. Three samples of 100 seeds, each from the same treatments, were germinated on filter paper in Petri dishes at 15-20 °C in light. In a second test, medium sized seeds of the progeny Atzimba x R-128.6 from the treatment PSTL in Experiment 2 were sown in nursery beds. The effects of the following factors were analysed: order of inflorescence (primary, secondary and tertiary), nitrogen levels (N_1 and N_2) and harvest dates (H1 and H2). The seeds had been stored for 42-46 weeks and were not treated with GA. The treatments were sown in a completely randomized design. Other procedures were similar to those described for the first test.

2.3. Results

2.3.1. Plant growth and flowering

Plants grew to a height of up to 50 cm (Atzimba, CEX-69.1) and 100 cm (Yungay), and developed

Table 2.1. Flowering characteristics of inflorescences developed at different positions on the plant[a].

Clone	Position of inflorescence	Number of inflorescences per plant	Number of flowers per inflorescence	Number of flowers per plant	Total number of flowers per plant
EXPERIMENT 1					
Atzimba	primary	2.0 bc	10.1 a	20 b	
	secondary	3.4 b	6.0 b	19 b	
	tertiary	1.6 bc	3.9 c	7 c	
	quaternary	0.8 c	1.3 d	1 c	
	lateral branches	8.0 a	9.6 a	76 a	123
CEX-69.1	primary	2.0 bc	12.2 a	24 b	
	secondary	3.8 b	6.8 b	27 b	
	tertiary	3.2 b	6.4 b	19 b	
	quaternary	0.2 c	3.3 c	1 c	
	lateral branches	9.6 a	9.8 a	97 a	168
Yungay	primary	2.0 bc	12.5 a	25 b	
	secondary	2.6 b	8.0 b	22 b	
	tertiary	0.4 c	3.6 c	1 c	
	quaternary	0.0 c	0.0 c	0 c	
	lateral branches	7.6 a	7.2 b	57 a	105
S.E.		0.3	0.6	3	
EXPERIMENT 2[b]					
Atzimba	primary	2.4 bc	11.2 a	26 a	
	secondary	3.7 a	6.7 b	25 a	
	tertiary	1.8 c	5.5 c	10 c	
	quaternary	-	-	-	
	lateral branches	3.1 ab	5.5 c	17 b	78
S.E.		0.3	0.3	2	

[a] Means in a column followed by a common letter are not significantly different at $P<0.05$ (t-test).
[b] Means of nitrogen treatments N_1 and N_2.

an average of 2.0 above-ground main stems in Experiment 1 and 2.8 in Experiment 2. Primary, secondary and tertiary inflorescences of the cultivars Atzimba and CEX-69-1 (Experiment 1) started flowering 50, 75 and 90 days after planting (d.a.p.), respectively. Primary and secondary inflorescences of Yungay started flowering 75 and 90 d.a.p. Lateral stems started flowering between 60 and 90 d.a.p. Atzimba, Yungay and CEX-69-1 matured 150, 164 and 171 d.a.p., respectively. The number of flowers per inflorescence was greatest for primary inflorescences and decreased with the order of the inflorescence (Table 2.1). The number of flowers per inflorescence of lateral stems was intermediate between those of primary and tertiary inflorescences.

Table 2.2. Effect of inflorescence order[a] on the characteristics of berry and seed production in three clones (Experiment 1) and two N levels (Experiment 2).

EXPERIMENT 1

Order of inflorescence	Proportion of large berries (%)			Number of seeds per berry			100-seed weight (mg)		
	Atzimba	CEX-69.1	Yungay	Atzimba	CEX-69.1	Yungay	Atzimba	CEX-69.1	Yungay
primary	25 b (27)[c]	48 a (40)	22 b (25)	154 ab	146 a	276 a	77.9 a	60.6 a	75.2 a
secondary	35 a (35)	42 a (41)	37 a (37)	163 a	144 a	256 a	78.7 a	61.4 a	75.4 a
tertiary	23 b (27)	42 a (41)	-	141 b	132 a	-	75.7 b	57.1 b	-
S.E.	(1.6)	(1.5)	(1.8)	4	5	7	0.4	0.4	0.6

EXPERIMENT 2

Order of inflorescence	Berry set (%)	Berry weight (g)	Number of seeds per berry	100-seed weight (mg)
primary	89 a (71)[c]	16.5 a	217 a	68.5 a
secondary	87 ab (70)	14.5 b	214 a	66.6 ab
tertiary	83 b (67)	13.0 c	190 b	64.4 b
lateral	61 c (52)	11.7 d	190 b	64.1 b
S.E.	(1)	0.5	6	0.9
N-level[b]				
N_1	82 (65)	14.3	206	66.3
N_2	79 (63)	13.6	198	65.5
	ns	ns	*	ns
S.E.	1.3	2.2	1.3	0.3

[a] Means in a column followed by a common letter are not significantly different at $P<0.05$ (t-test).
[b] Means over inflorescence positions: ** = significant at $P<0.01$, * = significant at $0.01<P<0.05$, ns = not significant.
[c] Transformed values (arcsin) in parenthesis.

Table 2.3. Effect of the treatments[a] P, PS, PST and PSTL on the characteristics of berry and seed production from primary inflorescences in three clones (Experiment 1) and at two harvest dates (Experiment 2).

EXPERIMENT 1

Treatment	Proportion of large berries (%)			Number of seeds per berry			100-seed weight (mg)		
	Atzimba	CEX-69.1	Yungay	Atzimba	CEX-69.1	Yungay	Atzimba	CEX-69.1	Yungay
P	34 a (35)[c]	44 a (42)	31 a (31)	150 a	140 a	263 a	80.9 a	61.8 a	77.2 a
PS	28 ab (30)	48 a (43)	30 a (30)	152 a	137 a	268 a	79.3 bc	60.7 a	77.1 a
PST	25 a (27)	48 a (40)	22 b (25)	154 a	146 a	276 a	77.9 c	60.6 a	75.2 b
S.E.		(1.8)			6			0.5	

EXPERIMENT 2

Treatment	Berry weight (g)	Number of seeds per berry	100-seed weight (mg)
P	17.6 a	222 a	70.2 a
PS	16.8 a	229 a	68.3 b
PST	16.8 a	229 a	68.1 b
PSTL	16.5 a	217 a	68.5 b
S.E.	0.4	4	0.5
Harvest date			
H_1	16.6	217	69.0
H_2	17.3	232	68.6
	*[b]	**	ns
S.E.	0.2	4	1.0

[a] Means in a column followed by a common letter are not significantly different at $P<0.05$ (Duncan's Multiple Range test).
[b] ** = significant at $P<0.01$, * = significant at $0.01<P<0.05$, ns = not significant (F-test).
[c] Transformed values (arcsin) in parenthesis.

In Experiment 1, more than 50% of the total number of flowers per plant developed on lateral stems (Table 2.1). The primary and secondary inflorescences together developed over 30% and tertiary inflorescences developed 6 and 12% of the total number of flowers per plant in Atzimba and CEX-69-1, respectively. In Yungay, 45% of the total number of flowers per plant developed at the primary and secondary inflorescences, whereas the tertiary inflorescences developed less than 1%. The number of quaternary inflorescences was negligible in all clones. In Atzimba, Experiment 2, 66% of the total number of flowers per plant developed on primary and secondary inflorescences and 22% developed on lateral stems. The application of additional nitrogen in Experiment 2 did not affect flowering and plant senescence.

2.3.2. Berry and TPS production from inflorescences of different orders

In Atzimba (Experiment 2) the percentage of flowers producing berries after pollination (berry set) was significantly lower in tertiary and lateral-stem inflorescences than in primary and secondary inflorescences (Table 2.2). Similarly, berry set of tertiary inflorescences in Experiment 1 was lower than that of primary and secondary ones. Quaternary flowers did not produce berries.

The secondary inflorescences of Atzimba (Experiment 1) and Yungay produced the largest berries (Table 2.2). However, in general, berry weight and size, number of seeds per berry and 100-seed weight decreased from lower to higher position inflorescences. Combining the data on berry set and number of seeds per berry showed that in Experiment 2 tertiary and lateral-stem inflorescences had 27 and 40% less seeds per pollination, respectively, than primary inflorescences and their total number of large seeds per flower was 42 and 52% lower compared to primary inflorescences. Additional N in treatment N_2, Experiment 2, did not affect berry set of main-stem inflorescences, but berry set of lateral-stem inflorescences was significantly lower in treatment N_2 than in N_1 (55% vs. 68%). Additional N significantly reduced number of seeds per berry and tended to reduce berry weight and 100-seed weight (Table 2.2).

2.3.3. Berry and seed production from primary inflorescences

In Atzimba (Experiments 1 and 2) and Yungay, primary berries in treatment P were larger than those in treatment PST and PSTL (Table 2.3). In each clone seeds from primary inflorescences in treatments P were heavier than in treatments PST and PSTL, but differences were significant only in Atzimba (Experiments 1 and 2). The number of seeds per primary berry was not significantly different in the treatments P, PS, PST and PSTL.

Late harvested primary berries were heavier and had more seeds than early harvested ones (Table 2.3) and late harvesting resulted in more and a greater proportion of large seeds, and more seeds per plant. Harvest date of the primary berries did not affect seed production of later flowering inflorescences.

2.3.4. Total TPS production per plant

In Experiment 2, treatment PS produced more large, medium and small sized seeds than treatment P (Figure 2.2). Treatment PST produced more medium and small sized seeds than treatment PS, resulting in a significantly larger total number of seeds per plant. Seed yield from treatment PSTL,

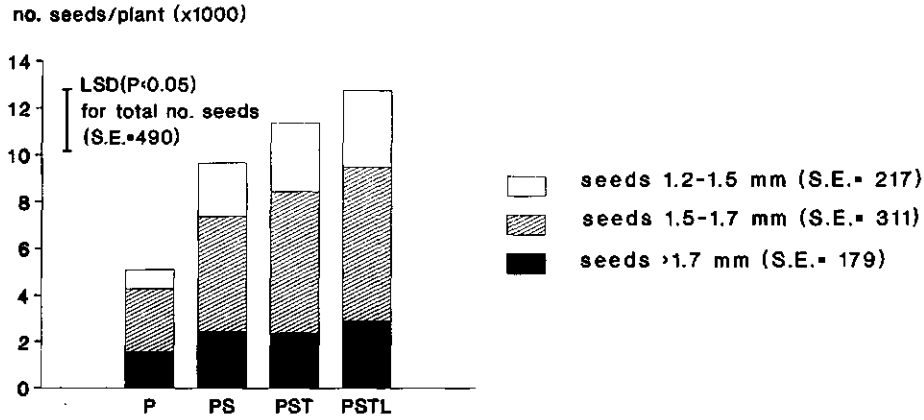

Figure 2.2. Effect of the use of inflorescences of different orders on the seed yield and size distribution in Atzimba (Experiment 2)[a].

[a] P = seed production on Primary inflorescences, PS = seed production on Primary and Secondary inflorescences, PST = seed production on Primary, Secondary and Tertiary inflorescences, PSTL = Seed production on all inflorescences.

which included seed production from lateral stems, was not significantly different from treatment PST. Of the seeds in treatment PSTL, 75% was produced from primary and secondary inflorescences. Total seed yield per plant was similar for the treatments N_1 and N_2.

2.3.5. Seed tests

The position of the inflorescences at which the seed was produced in treatment PSTL did not affect germination, emergence and above-ground seedling weight. Large seeds showed better germination and earlier emergence than small seeds (Table 2.4). Large seeds produced more above-ground biomass than small seeds during the first 41 days after sowing. The second test showed that the application of additional N and harvest date had no significant effect on germination and seedling growth of PSTL seeds.

2.4. Discussion

2.4.1. Position of inflorescences

The general decrease in number of flowers per inflorescence, berry set, berry and seed weight and number of seeds per berry from primary to higher position inflorescences suggests that conditions

Table 2.4. Effect of seed size on germination, emergence and seedling growth.

Seed size	Petri dishes			Nursery beds				
	germination (%)			emergence (%)			weight per seedling 41 das[a]	
	6 das	8 das	12 das	8 das	10 das	20 das	fresh (g)	dry (mg)
Large	37(37)[c]	94(76)	99(1.2)	60(51)	90(72)	96(79)	2.27	16
Small	34(35)	91(72)	98(1.2)	43(41)	84(64)	94(76)	1.60	12
	ns[b]	*	**	**	**	*	**	**
S.E.	(1.5)	(1.0)	(0.03)	(1.6)	(1.0)	(0.7)	0.1	0.6

[a] das = days after sowing.
[b] ** = significant at $P<0.01$, * = significant at $0.01< P<0.05$, ns = not significant (F-test).
[c] Transformed values (arcsin) in parenthesis.

for flowering and seed production were less favourable for the later flowering inflorescences. There was no indication that this was attributable to changes in temperature, daylength or light conditions, factors which are believed to contribute to differences between tillers in cereals and grasses (Langer & Ryle, 1959). Since additional N in Experiment 2 did not affect flowering and plant maturity, N supply was judged to be adequate. Differences in seedproduction were not associated with differences in berry age, since all berries were harvested a similar number of days after pollination. Seed crops of lettuce, parsnip, carrot and celery, are normally harvested only once and the lower weights of seeds from later flowering inflorescences are probably related to differences in seed age and maturity. Differences between inflorescences may have been due to reduced availability of assimilates for higher position inflorescences. There is no information on tuberization in the experiments, but flowering and tuber growth are supposed to start at about the same time. The onset of tuber growth is associated with increased partitioning of assimilates to the tubers (see Dwelle, 1985). Longer photoperiods (Bodlaender, 1963; Turner & Ewing, 1988), increased N levels (Bamberg & Hanneman, 1988; Krauss, 1985) and higher (night) temperatures (Marinus & Bodlaender, 1975; Turner & Ewing, 1988) influence hormone levels and assimilate partitioning, resulting in delayed tuber development and stimulated shoot growth and flowering. Improved flower production by reducing carbohydrate partitioning to the tubers has also been demonstrated by tuber pruning and grafting on tomato (Thijn, 1954; Upadhya et al., 1985). The reduction in photosynthesis that is concomitant with the onset of plant senescence, affects particularly the latest inflorescences, those which are harvested when the plants are maturing.

Although tuber growth is generally assumed to be the principal limitation for flowering in potato, other sinks are also involved. After flowering started, shoot growth continued and needed assimilates. In tomato, competition between flowering inflorescences and young leaves has been demonstrated (De Zeeuw, 1954; Kinet, 1977), while at a later stage the leaves proximate to the inflorescence are the principal assimilate sources for the fruits (see Ho & Hewitt, 1986). Similar

sink-source relations in a potato shoot would explain the small effect of seed production at higher inflorescence positions on primary inflorescences.

Furthermore, the development of fruits and seeds at primary inflorescences can restrict the flowering of young higher position inflorescences, as was found for tomato (Marre & Murneek, 1953; Verkerk, 1957). Dominant sink activity of primary inflorescences would be related with the earlier sink establishment and stronger sink activity of seeds in comparison with flowers. Moreover, a primary inflorescence was a stronger sink than later inflorescences because they produced more seeds and sink activity is related with hormone production from the seeds (Varga & Bruinsma, 1976; Sjut & Bangerth, 1984).

Competition with tuber production and shoot growth, decreasing photosynthesis when plants start maturing and later sink establishment, all combined decrease flowering and seed production from lower to higher inflorescence position. Development of the proximate leaves as a sink, increasing sink activity of inflorescences after seed set and distribution of assimilates over a smaller number of berries and seeds, together explain the relatively small reductions in number of seeds per berry and 100-seed weight of higher position inflorescences, in comparison to differences in number of flowers per inflorescence.

2.4.2. Clones, nitrogen and harvest date of berries

Flowering is determined by the interaction between genotype, daylength and temperature (Bodlaender, 1963). Differences between clones were therefore specific for the conditions of the experiments. However, in each of the clones, flower and seed production was lowest at the highest position inflorescences.

The tendency of the extra N applications in Experiment 2 to reduce berry and seed production suggests that N levels were supra-optimal for TPS production. These results agree with those from Upadhya et al. (1985) for potato seeds and with reports on other seed crops (Vittum & Tapley, 1953; Shasha'a et al., 1976; George et al., 1980). Possibly, the extra N stimulated shoot development, thereby increasing competition between shoot and inflorescences.

Heavier berries and more seeds per berry of late harvested primary inflorescences indicate that berry and seed growth continued up to harvest time. Apparently, some seeds smaller than 1.15 mm at the time of the early harvest were included in the late harvest.

2.4.3. Seed quality

The position of the inflorescence from which the seeds were produced did not affect seed quality when seeds of similar size were compared. Since larger seeds showed faster germination and better seedling growth and since the inflorescence position affected seed size, we conclude that the effect of inflorescence position on seed quality was associated with seed size. When the second seed test was carried out, the seed was too old to find possible effects of the inflorescence position on the seed dormancy.

2.4.4. Practical implications

TPS is best produced from primary and secondary inflorescences since those had best berry and seed set and produced heavier seed and consequently produced more and better quality seed per

pollination. Although reductions in berry and seed set and seed size were relatively small (Table 2.2), combining these differences into yield per pollination showed that productivity of tertiary and lateral-branch inflorescences was much lower than that from primary inflorescences. Harvesting seed from tertiary and lateral-stem inflorescences may be practical, but its economics will depend on costs of labour, prices of seed and other considerations. Inflorescences from different orders have to be harvested separately, because berry age and maturity can affect seed quality. Since the effect of inflorescence position on quality was a function of seed size, the seed produced from different inflorescences can be mixed and graded to select for quality. Late, mature harvest of the berries increases total seed yield and seed size. The effect of N on TPS production and seed quality needs further study. Further research is also needed on sink-source relations and the interaction between sinks in potato, with special reference to the reproductive processes. Better understanding and possible manipulation of these processes could improve methods to produce high quality TPS.

Chapter 3

RELATION BETWEEN BERRY WEIGHT, NUMBER OF SEEDS PER BERRY AND 100-SEED WEIGHT WITHIN INFLORESCENCES

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3 RELATION BETWEEN BERRY WEIGHT, NUMBER OF SEEDS PER BERRY AND 100-SEED WEIGHT WITHIN INFLORESCENCES

Additional keywords: *Solanum tuberosum* L., TPS, seed number, seed weight, berry weight, flower position

Summary

In three potato cultivars (*Solanum tuberosum* L.), Atzimba, R-128.6 and Serrana, the effect of the position of the flower in the inflorescence on berry weight, number of seeds per berry and 100-seed weight was analysed. Mean berry weight, number of seeds per berry and 100-seed weight decreased from proximal to distal flower position, except the 100-seed weight of Serrana. The relation between berry weight and number of seeds per berry was positive and highly significant. The relationships between 100-seed weight and number of seeds, and between 100-seed weight and berry weight were weak and not consistent for all cultivars. Within and between flower position correlations are illustrated and discussed. In Atzimba and R-128.6, pollination of flowers or harvesting berries from proximal positions only could improve average 100-seed weight.

3.1. Introduction

Using true potato seed (TPS) for potato tuber production has proven to be a viable alternative to the use of seed tubers, especially in developing countries (Malagamba, 1988). For the development of efficient TPS production practices, it is important to understand the sources of variation of berry number, seed number per berry and seed size in both open pollinated (O.P.) and hybrid seed production. In contrast with O.P. seed production, hybrid TPS production requires hand pollination, which offers the possibility to select the most productive flowers for seed production, i.e. flowers with a high percentage of berry set, a high number of seeds per berry and large seeds.

Variation in berry and seed production for different inflorescence positions was described earlier (Almekinders & Wiersema, 1991). Variation for different flower positions within inflorescences has not been explored in potato. In tomato, egg plant and other Solanaceae crops, most cultivars produce the largest berries at the proximal flower positions of an inflorescence (Marré & Murneek, 1953; Nothmann & Rylski, 1983; Bangerth & Ho, 1984). Since there is a positive relation between berry size and seed number (Varga & Bruinsma, 1976; Pallais, et al., 1986), proximal flower positions probably also produce most seeds. However, it is not clear how flower position relates to 100-seed weight. Relations of 100-seed weight with number of seeds per berry as well as with berry weight in tomato and in potato were found negative, positive or absent (Hatcher, 1940; Richardson & Currence, 1953; Dempsey & Boynton, 1965; Pet & Garretsen, 1983; White, 1983; Upadhya et al., 1985; Pallais et al., 1986; Groot et al., 1987; Randhawa & Bhargava, 1994).

As within a seed lot, seed weight is positively correlated with rate and percentage of germination, and seedling vigour, seed production practices should be directed to the production of heavy seeds.

This paper discusses for three cultivars the relationships between berry weight, seed number per berry and seed weight for the individual flower positions and when data are pooled for the entire inflorescence.

3.2. Material and methods

Single-stem plants of *Solanum tuberosum* L., cultivars Atzimba, R-128.6 and Serrana were grown from seed tubers, planted at a 20 x 20 cm spacing in nursery beds on the experimental station of the International Potato Center in San Ramon, Peru, in 1988. Per cultivar, 24 plants with a total of 14-18 flowers per primary inflorescence were used for TPS production. All flowers of primary inflorescences were hand pollinated at anthesis with pollen from the clone 104-12.LB. Berries were harvested 40 days after pollination when they were mature. Berries at the first (proximal), third, fifth and the seventh (distal) position (Figure 3.1) were weighed individually, after which the seed was extracted from each berry separately, dried to a constant weight over silicagel, weighed and counted.

3.3. Results

3.3.1. Means of cultivars and flower positions

Cultivar means. Cultivars differed in mean berry weight with the highest mean weight for Atzimba and the lowest for Serrana. Seed number per berry differed in the same sequence; Atzimba had the

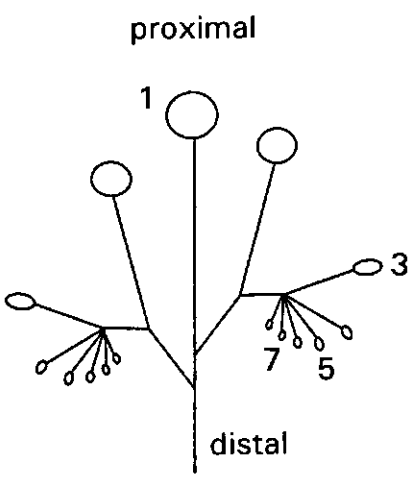

Figure 3.1. Diagram of a potato inflorescence, showing the different flower positions.

Table 3.1. The effect of flower position on mean berry weight, mean number of seeds per berry and mean 100-seed weight in the cultivars Atzimba, R-128.6 and Serrana after pollination with pollen of the cultivar 104-12.LB.

Flower position	Berry weight (g)			No. seeds per berry			100-seed weight (mg)		
	Atzimba	R-128.6	Serrana	Atzimba	R-128.6	Serrana	Atzimba	R-128.6	Serrana
1 st	9.5	4.4	3.9	193	170	140	60.4	58.5	66.8
3 rd	8.1	4.0	3.4	171	163	128	58.8	57.7	67.7
5 th	7.9	3.6	2.9	166	130	109	53.1	52.1	66.7
7 th	7.1	3.3	2.8	156	126	86	53.4	45.5	69.1
Mean	8.2	3.8	3.3	171	147	116	56.4	53.6	67.6
$LSD_{(P<0.05)}$	1.3	0.4	0.4	25	29	18	2.5	2.5	2.0

highest number of seeds, followed by R-128.1 and Serrana (Table 3.1). However, Serrana had the highest 100-seed weight (Table 3.1), while R-128.6 had the lowest. Thus, on the level of cultivar means, 100-seed weight did not correlate with berry weight or seed number per berry.

Flower position. In all three cultivars (Table 3.1), mean berry weight and mean seed number per berry, and in Atzimba and R-128.6 also 100-seed weight, decreased from proximal to distal flower position. In Serrana 100-seed weight did not correlate with flower position, indicating that there was no overall relationship between mean 100-seed weight and flower position for cultivars.

3.3.2. Regression analysis of single data

Berry weight and seed number per berry. According to Varga and Bruinsma (1976) fruit growth within the tomato inflorescence is a function of the sink activity exerted by the developing seeds. For that reason, berry weight (y) is plotted against the seed number per berry (x) (see Figure 3.2 for Atzimba).

Regression analysis showed that in all three cultivars the correlation between seed number per berry and berry weight was significant when data of the entire inflorescence were pooled, as well as for the individual flower positions, except flower position 7 in Serrana. Since flower positions did not differ significantly in regression coefficients and in intercepts, Table 3.2 only contains the regression parameters for the total inflorescences. The absence of any flower position effect on the relationship between berry weight and seed number per berry suggests that the differences in berry weight between flower positions presented in Table 3.1 can be fully explained from differences in seed number per berry.

100-Seed weight and seed number per berry. Table 3.3 presents the correlation coefficients between 100-seed weight and seed number per berry for single flower positions and when data for the total inflorescences were pooled, in the three cultivars. Significant correlations for single flower positions and/or the total inflorescence were found only in Atzimba and R-128.6. In Atzimba

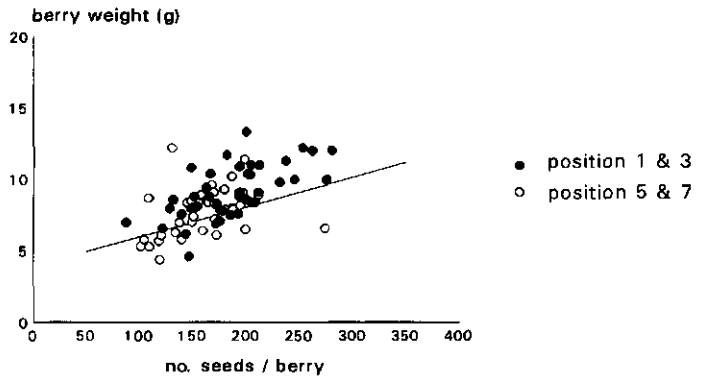

Figure 3.2. The relation between berry weight and number of seeds per berry for different flower positions in the cultivar Atzimba.

Table 3.2. Regression equations ($y = a + bx$) and correlation coefficients (r) for the relation between berry weight (y) and seed number per berry (x) for the total inflorescences of cultivars Atzimba, R-128.6 and Serrana.

	a	b	r	n
Atzimba	3.55	0.028	0.63**	89
R-128.6	1.94	0.013	0.76**	89
Serrana	1.16	0.018	0.75**	93

** $P<0.01$

significant correlations were all negative, in R-128.6 significant negative as well as positive correlations were found. The reason for the lack of correlation in Serrana was that at a similar variation in berry weight compared with Atzimba and R-128.6, there was little variation in seed weight (data not shown). The overall conclusion from Table 3.3 is, that correlations between 100-seed weight and seed number per berry were weak and inconsistent.

Figure 3.3 illustrates why in Atzimba despite systematic negative correlations for individual flower positions (Table 3.3), the between flower position correlation for seed weight and seed number per berry was positive (Table 3.1): the distal flower positions had on average lower seed numbers per berry and in same ranges of seed numbers a lower mean seed weight than the proximal positions.

100-Seed weight and berry weight. The cause of the positive relation between the flower position means for 100-seed weight and berry weight in Atzimba and R-128.6 in Table 3.1 is further analysed in Table 3.3. Calculations from the individual berry data showed that this correlation was significant for the total inflorescence, but not consistent for the individual flower positions. The reason for the latter is illustrated for R-128.6 in Figure 3.4: along with high 100-seed weights in the entire range of berry weights in all flower positions, especially low-weight berries at the more distal flower positions had more frequently a low 100-seed weight.

The inconsistency of the correlation at the level of single flower positions, suggests that the lower means for both characters at the more distal flower positions in Table 3.1 were not causually related but depended on additional factors.

Table 3.3. Coefficients of correlations between 100-seed weight (y, mg) and the number of seeds per berry (x), and between 100-seed weight (y, mg) and berry weight (x, g) for the individual flower positions, within and between flower positions and for the total inflorescence from crosses in three cultivars.

Flower position	100-seed weight (y) and seed number (x)			100-seed weight (y) and berry weight (x)		
	Atzimba	R-128.6	Serrana	Atzimba	R-128.6	Serrana
First	-0.45 **[a]	-0.47 *	0.09 ns	-0.07 ns	-0.15 ns	0.05 ns
Third	-0.58 **	-0.01 ns	0.19 ns	-0.06 ns	0.32 ns	0.42 *
Fifth	-0.37 ns	0.49 *	-0.36 ns	0.51 *	0.30 ns	-0.08 ns
Seventh	-0.36 ns	0.24 ns	-0.12 ns	0.13 ns	0.11 ns	0.49 *
Within	-0.39 **	0.18 ns	-0.06 ns	0.16 ns	0.15 ns	0.19 ns
Between	0.83 ns	0.99 **	-0.68 ns	0.87 ns	0.97 *	-0.35 ns
Total	-0.13 ns	0.33 **	-0.13 ns	0.34 **	0.33 **	0.13 ns

[a] ** = $P<0.01$, * = $0.01<P<0.05$, ns = not significant.

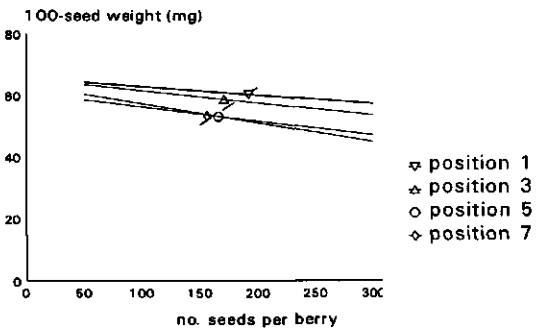

Figure 3.3. Mean 100-seed weight and number of seeds per berry, and the relationship between 100-seed weight and number of seeds per berry averaged over inflorescences for different flower positions in inflorescences of the cultivar Atzimba.

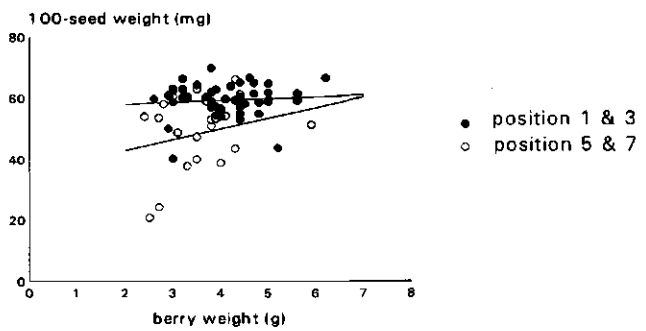

Figure 3.4. The relation between 100-seed weight and berry weight for different flower positions in the cultivar R-128.6.

The reason for the lack of a consistent correlation between berry weight and seed weight in Serrana was the limited variation in seed weight in Serrana (Table 3.3), already mentioned.

3.4. Discussion and conclusions

The finding that the largest berries were produced at proximal positions agrees with results in tomato and other crops (Marré & Murneek, 1953; Nothmann & Rylski, 1983). Also in agreement with the literature is the positive correlation between berry weight and seed number per berry found for the total inflorescence. In all three cultivars used in this experiment, Atzimba, R-128.6 and Serrana, this relationship was not affected by flower position. This supports the hypothesis that fruit growth is causually related to the seed number per fruit (Varga & Bruinsma, 1976).

Our data show that because of flower position effects, correlations based on data of the total inflorescence can give misleading information. A clear example is the significant positive relation between 100-seed weight and berry weight for the total inflorescence in R-128.6, while there was no relationship between the two characters within positions (Table 3.3). Figure 3.3 showed the reverse example of systematic negative correlations for within flower positions, whereas the correlation for the total inflorescence was not significant, due to the fact that the means for flower positions were positively correlated.

The effect of flower position may partly explain the conflicting relationships between 100-seed weight and seed number per berry, and 100-seed weight and mean berry weight that are reported in the literature. Cultivar differences, growing conditions and other plant factors may also have an effect on these relationships.

Practical implications. Proximal flower positions were more productive than distal flower positions: they produced more seeds and in the inflorescences of Atzimba and R-128.6 they also produced heavier seed. This means that harvesting berries from proximal positions only would increase mean 100-seed weight in these two cultivars. Elimination of smaller berries from the total berry harvest of the inflorescences would have a similar effect. However, both practices reduce total seed yield. In hybrid seed production a practical option for increasing mean seed number per berry and 100-seed weight may be to exclude distal flower positions from pollination. Especially where labour is expensive and pollen availability is limited, this option should be considered. Moreover, leaving distal positions unused may improve seed production at proximal flower positions.

Since in our study only simultaneously flowering primary inflorescences were used and the range over which seed number varied was relatively small, the relations and options discussed need to be verified over a wider range of conditions and in different years.

Chapter 4

EFFECTS OF STEM DENSITY AND PRUNING OF LATERAL STEMS ON FLOWERING AND SEED PRODUCTION

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4 EFFECTS OF STEM DENSITY AND PRUNING OF LATERAL STEMS ON FLOWERING AND SEED PRODUCTION

Additional keywords: number of flowers per inflorescence, berry set, seed quality

Summary

Field experiments were carried out to evaluate the effect of stem density and pruning of lateral stems on flowering and true seed production in potato (*Solanum tuberosum* L.). Increasing stem density reduced flowering, berry and seed production from every inflorescence in all cultivars. Increasing density increased the proportion of primary flowers in the total number of flowers per plant and reduced the proportion of flowers on lateral stems, but its effect on the quality of the seed production was small. Differences in total seed production were principally determined by differences in flowering. There was an interaction between stem density and cultivars for the number of flowers produced and on the yield of true seed per m^2. Pruning lateral stems enhanced flowering of the main stem and decreased the total number of flowers per plant, but it did not affect berry and seed production from main-stem flowers.

4.1. Introduction

Appropriate field practices for the production of True Potato Seed (TPS) need to be established following the introduction of an advanced technology of potato production from TPS (Wiersema, 1986; Song & Vander Zaag, 1987; Hoang et al., 1988; Malagamba, 1988). Wide row spacing and staking of the plants facilitate the field operations of hybrid TPS production (CIP, 1985). However, there is little information on the effects of plant density in the row on either flowering or TPS production. Data of Mok (1985) show that although increasing plant density increased the number of flowers and seed weight per m^2, it decreased number of flowers per plant and berry set. Stem density may also affect seed size and weight and, importantly, it has been demonstrated that increased TPS weight and size improved germination and seedling growth (Dayal et al., 1984; Acuña, 1985; Almekinders & Wiersema, 1991).

In tomato, pruning young growing leaves stimulates flowering and fruit development (De Zeeuw, 1954; Aung & Kelly, 1973) and pruning lateral stems of potato has been reported to improve flowering and seed production (M.D. Upadhya, pers. comm.).

This paper reports the results of two experiments that were designed to evaluate the effect of stem density and of pruning lateral stems on flowering and TPS production.

4.2. Material and methods

Experiments were carried out at the experimental station of the International Potato Center in Huancayo (3300 m above sea level), Peru. Experiments 1 and 2 were planted on October 25, 1984, and November 11, 1985, respectively.

4.2.1. Treatments and experimental design

For Experiment 1, seed tubers (40-60 g) of the cultivars Atzimba, CEX-69.1 and Yungay were planted in a split-split-plot design with 3 replications. Cultivars were assigned to main plots, pruning treatments to sub-plots and stem density to sub-sub plots. The planting rows were 1.5 m apart and the sub-sub plots each consisted of 15 plants, 50 cm apart within a row. In the treatments with 1-stem and 3-stem plants, 1 and 3 above-ground main stems were allowed to develop and additional emerging stems were removed. To evaluate the effect of pruning, lateral stems developing from above-ground buds on the main stem (Figure 2.1) were removed weekly during a 5-week period, starting 15 days after emergence. Thereafter no new lateral stems developed. One stem per plant was sampled for TPS production.

In Experiment 2, seed tubers (50-60 g) of the cultivars Atzimba, Yungay and Renacimiento were planted in a split-plot design with 4 replicates. Cultivars were assigned to the main plots and density treatments to the sub-plots. Planting distances were 60, 30 and 15 cm witin rows that were 1.50 m apart. Sub-plots were single rows 7.20 m long of which 60 cm at each end was discard border. Within each treatment, two selections of 10 main stems each were used for TPS production. For the first selection ten early flowering stems were marked and for the second selection ten stems which flowered about 10 days later. Flowering data showed that primary inflorescences of late flowering stems were most representative of the average primary inflorescence. Therefore, data from these inflorescences were used to determine total seed production from primary inflorescences. For the same reason, data from secondary inflorescences of early flowering stems were used to determine total seed production from secondary inflorescences.

4.2.2. Seed production and data collection

At planting, 45-25-30 kg N-P-K per ha was applied in the rows and 3 weeks later 45 kg N per ha was applied as a side dressing in both experiments. In Experiment 2, 25 kg per ha of additional N as urea (44% N) was applied weekly during the flowering period (6-8 applications). Flowers of Atzimba and CEX-69.1 in Experiment 1 and of Atzimba and Yungay in Experiment 2 were pollinated after anthesis with pollen of the clone R-128.6. Flowers of Renacimiento were left to form berries naturally by open pollination (O.P.). In Experiment 1, inflorescences on main stems were used for TPS production. Four berries were allowed to develop at each inflorescence, the other flowers being removed. Flowers on lateral stems of unpruned plants were not pollinated and did not produce O.P. berries. In Experiment 2, all flowers of selected stems were used for TPS production. Berries were harvested separately from the different inflorescence positions and from different samplings. The time between pollination and berry harvest was 75-85 days for each treatment and inflorescence position. After harvest, the berries were graded into large, medium and small classes. Berries with a diameter of more than 34 mm for Renacimiento, more than 32 mm for Atzimba and Yungay and more than 26 mm for CEX-69.1 were classified as large. For Renacimiento, berries smaller than 32 mm and for the other clones berries smaller than 23 mm were classified as small. Berries were also weighed and seeds were extracted from eight berries per grade per treatment. All other practices and procedures of seed production were identical to those described by Almekinders & Wiersema (1991).

4.2.3. Seed tests

Seed quality, as measured by germination, emergence and seedling growth, was recorded for medium-sized seeds from medium-sized primary berries from all cultivars and density treatments in Experiment 2. Seeds, which had been stored for 22-26 weeks over silica gel at 15-20 °C, were soaked for 24 h in a 1500 ppm Gibberellic Acid (GA) solution before sowing. Of each treatment, 4 samples of 100 seeds were sown in nursery beds filled with a substrate of sand and peatmoss. Emergence was recorded and seedlings were weighed 41 days after sowing. Three samples of 100 seeds of each treatment were germinated in Petri dishes. Conditions and practices of the tests were identical to those described for other tests by Almekinders & Wiersema (1991).

4.3. Results

4.3.1. Plant growth and flowering

Shoot development of clones in Experiment 1 has been described by Almekinders & Wiersema (1991). In Experiment 2, stem height increased with stem density. Plants of cv. Atzimba grew to a height of 1 meter and matured 150 days after planting (d.a.p.), whereas those of cv. Renacimiento grew to 2 m, matured more than 200 d.a.p., and produced much more above-ground biomass. Shoot development of cv. Yungay was intermediate between that of Atzimba and Renacimiento. Planting density did not affect the onset and duration of flowering.

Since there was no interaction between stem density, pruning and cultivars ($P>0.25$), the effects of stem number and pruning on flowering in Experiment 1 are presented in separate tables as means over other treatments (Tables 4.1 and 4.2). Single-stemmed plants and plants with 3 stems produced similar numbers of primary inflorescences per stem, but 3-stem plants developed fewer higher position inflorescences and fewer lateral-stem inflorescences, and fewer flowers per inflorescence and fewer flowers per stem than 1-stem plants (Table 4.1). The proportion of the total number of flowers on lateral stems was smaller in 3-stem plants than in 1-stem plants. Three-stem plants formed a larger percentage of the total number of flowers on primary inflorescences. Pruning lateral stems increased the number of tertiary inflorescences on the main stems (Table 4.2). Pruned plants produced more flowers per inflorescence and a larger total number of flowers on their main stems. However, lateral stems of unpruned plants developed many flowers, resulting in a larger total number of flowers per plant than on pruned plants. For unpruned plants, the total number of flowers on 1-stem and 3-stem plants (125 and 140 flowers) did not significantly differ, but pruned 1-stem plants formed fewer flowers (59) than pruned 3-stem plants (102).

In Experiment 2, plants spaced 60, 30 and 15 cm apart produced averages of 9, 16 and 27 stems per m^2, respectively. The effects of stem density on flowering were similar to the effects in Experiment 1: higher stem density decreased the number of flowers per inflorescence, the number of inflorescences per stem and the number of flowers per stem (data not presented). Primary inflorescences formed 67 and 81% of the total number of flowers per plant at low and high stem density, respectively. Few lateral stems developed on plants in Experiment 2 and they formed only 8 and 2% of the total number of flowers at low and high stem density. Increasing stem density increased the number of flower per m^2 in Yungay and Renacimiento (Figure 4.1).

Table 4.1. Effect of number of main stems per plant and inflorescence positions on number of inflorescences per stem, number of flowers per inflorescence and number of flowers per plant (Experiment 1). Means of three clones and two pruning treatments.

Inflorescence position	Number of inflorescences per stem			Number of flowers per inflorescence			Number of flowers per plant		
	1 stem	3 stems	F-test[a]	1 stem	3 stems	F-test	1 stem	3 stems	F-test
Primary	1.0	1.0	ns	12.6	11.7	ns	12.6	35.2	**
Secondary	1.9	1.6	**	8.1	7.3	ns	15.5	35.4	**
Tertiary	2.2	1.9	**	6.5	5.0	**	15.7	15.6	ns
Quarternary	0.8	0.3	*	3.6	2.8	ns	3.5	2.2	ns
Lateral stems	4.3	1.4	**	5.1	3.8		44.6	32.0	*

[a] ** = significant at $P<0.01$, * = significant at $0.01<P<0.05$, ns = not significant.

Table 4.2. Effect of pruning of lateral stems and inflorescence position on number of inflorescences per stem, number of flowers per inflorescence and number of flowers per plant (Experiment 1). Means of three clones and two stem density treatments.

Inflorescence position	Number of inflorescences per stem			Number of flowers per inflorescence			Number of flowers per plant		
	not-pruned	pruned	F-test[a]	not-pruned	pruned	F-test	not-pruned	pruned	F-test
Primary	1.0	1.0	ns	11.6	12.8	ns	22.9	25.0	**
Secondary	1.7	1.8	ns	6.9	8.6	**	22.4	28.5	**
Tertiary	0.9	1.7	**	4.6	7.0	**	9.2	22.2	ns
Quarternary	0.2	0.5	ns	1.5	4.9	*	1.0	4.7	ns
Lateral stems	8.4	-		8.9	-		76.6	-	

[a] ** = significant at $P<0.01$, * = significant at $0.01<P<0.05$, ns = not significant.

4.3.2. Seed production

In Experiment 1, tertiary inflorescences produced smaller berries, fewer seeds per berry and smaller seeds than primary and secondary inflorescences (Almekinders & Wiersema, 1991), but there was no interaction between inflorescence position and the number of stems per plant. Primary, secondary and tertiary inflorescences of 3-stem plants produced smaller berries and smaller seeds than those of 1-stem plants. Three-stem plants of CEX-69.1 produced fewer seeds per berry than 1-stem plants, but in Atzimba and Yungay the number of stems did not affect seed number per berry. Pruning lateral stems did not affect berry and seed production per flower from main stems (Table 4.3).

Table 4.3. Effects of number of stems per plant on the fraction of large berries, number of seeds per berry and 100-weight in three clones (Experiment 1). Means of primary, secondary and tertiary inflorescences, and pruned and not-pruned plants.

Number of stems per plant	Fraction of large berries (%)			Number of seeds per berry			100-seed weight (mg)		
	Atz[a]	CEX	Yun	Atz	CEX	Yun	Atz	CEX	Yun
1	32	50	35	148	154	266	78.1	60.8	76.8
3	23	35	24	159	126	266	76.8	58.6	73.9
F-test[b]	ns	*	ns	ns	*	ns	ns	**	*

[a] Atz = Atzimba, CEX = CEX-69.1, Yun = Yungay.
[b] ** = significant at $P<0.01$, * = significant at $0.01<P<0.05$, ns = not significant.

Table 4.4. Effect of stem density on berry set, berry weight, number of seeds per berry and 100-seed weight of the total production in three cultivars (Experiment 2).

Density (stems/m^2)	Berry set (%)			Berry weight (g)			Number of seeds per berry (mg)			100-seed weight (mg)		
	Atz[a]	Yun	Ren	Atz	Yun	Ren	Atz	Yun	Ren	Atz	Yun	Ren
9	78	84	54	14.3	13.1	18.3	234	332	375	69.8	67.6	78.3
16	75	77	53	13.8	12.0	16.1	211	326	351	69.1	67.2	77.8
27	78	74	51	14.1	11.2	15.6	221	296	325	70.6	65.9	77.6
LSD($P<0.05$)[b]	ns			1.2			32			ns		

[a] Atz = Atzimba, Yun = Yungay, Ren = Renacimiento.
[b] For comparing means in columns.

As in Experiment 1, increasing stem density in Experiment 2 reduced berryset, berry weight, seed number per berry and 100-seed weight of primary and secondary inflorescences (data not presented). Increasing stem density significantly reduced the average berry weight and number of seeds per berry of the total production per plant in Yungay and Renacimiento, in Experiment 2 (Table 4.4). The differences induced in Atzimba and in berry set and 100-seed weight of the total production in Yungay and Renacimiento were small and not significant.

Increasing stem density decreased total seed and tuber yield per plant in all three cultivars. There was an interaction between stem density and cultivar for seed production per m^2 (Figure 4.1); in Atzimba, stem density did not affect seed production per m^2, whereas in Renacimiento production of all size grades increased with the stem density and in Yungay production was larger at intermediate and high stem density than at low stem density. However, the difference between the intermediate and high stem density treatments in Yungay was not significant. Increasing stem density increased tuber yield per m^2 in all three cultivars (Figure 4.1).

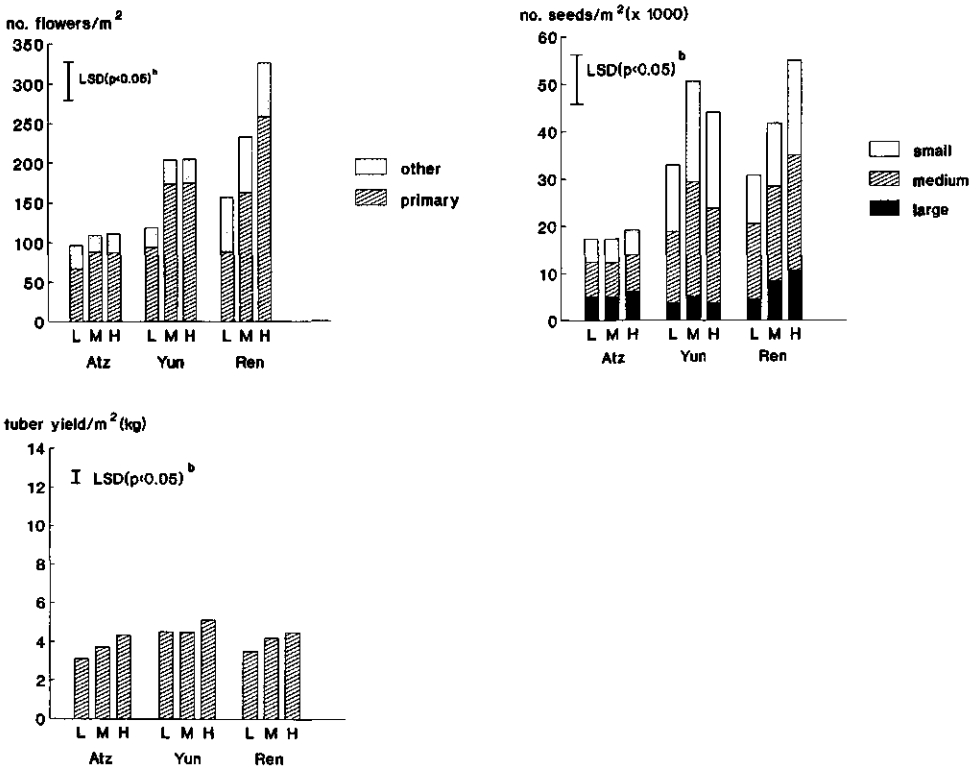

Figure 4.1. The effect of stem density[a] on number of flowers, tuber yield and number of seeds per m^2 in the cultivars Atzimba, Yungay and Renacimiento (Experiment 2).

[a]) L = low (9 stems/m^2), M = intermediate (16 stems/m^2) and H = high (27 stems/m^2).
[b]) for comparisons within a clone.

4.3.3. Seed tests

Germination, emergence and seedling growth were not affected by stem density of the parent plants (data not presented). Seeds of Renacimiento germinated and emerged later and slower and had a lower total germination and emergence percentage than seeds of Atzimba and Yungay. Seedlings from Atzimba seed produced more bio-mass in the 41 days after sowing than those from Yungay and Renacimiento.

4.4. Discussion

4.4.1. Stem density and flowering

Conditions for the production of higher position inflorescences on the main stem were less favourable for 3-stem plants than for 1-stem plants. All stems in Experiment 1 formed a primary

inflorescence, but 3-stem plants formed fewer higher position inflorescences than 1-stem plants not because higher position inflorescences aborted, but because shoot growth ceased at an earlier stage of development on the 3-stem plants. Also, three-stem plants developed fewer nodes per stem and fewer orders of branches than 1-stem plants. Thus, increasing stem density concentrated flowering in primary inflorescences because shoot growth ceased earlier and development of lateral stems was reduced.

Increasing stem density reduced the number of flowers per inflorescence at each of the inflorescence positions. The effect was not significant for primary inflorescences in Experiment 1 (Table 4.1), but it was consistent in both Experiment 1 and 2. This shows that there was competition between stems from an early stage of growth, although the row distances were wide and the stem density within the row was low, especially in Experiment 1. Effects of stem density are generally attributed to competition for light, water and nutrients. Nitrogen supply and soil moisture were judged to be adequate, but competition between stems for light is evidenced by the observation that stem internodes in Experiment 2 were longer in the high density treatments.

4.4.2. Stem density and seed production

Increasing stem density reduced 100-seed weight of harvests from each inflorescence position. However, the effect of stem density on average 100-seed weight of the total seed yield was small (Table 4.4), because of the larger contribution of primary inflorescences to the total harvest at higher stem densities. Primary inflorescences produced heavier seed than other inflorescences so that their larger contribution at higher stem densities compensated for the stem density effect on each of the inflorescence positions. Similarly compensated were the effects on berry set, berry weight and number of seeds per berry of each of the inflorescence positions. Differences in productivity and changes in contribution of inflorescences to the total harvest have also been reported for grasses (Meijer, 1984), cereals (Darwinkel, 1978), carrot (Gray & Steckel, 1983), parsnip (Gray et al., 1985) and tomato (Fery & Janick, 1970). Like potato, these crops can develop various orders of flowering and reported effects of stem density are also generally small.

There were no differences in quality between seed of similar size from the three density treatments. Other work has shown that larger and heavier seeds from a seed lot are more vigorous (Dayal et al., 1984; Acuña, 1985; Almekinders & Wiersema, 1991) and that differences between harvests from the various inflorescence positions were associated with seed size (Almekinders & Wiersema, 1991). However, since the effect of stem density on the average 100-seed weight of the total seed production was small, it follows that the effect of stem density on seed quality was also small.

In all three cultivars (Experiment 2), the effects of stem density on berry set, number of seeds per berry and 100-seed weight were small compared to the differences in total number of seeds produced. Thus, seed production per plant and per m^2 was principally determined by differences in the number of flowers. The different responses of the three cultivars to stem density seemed to be related to earliness and the amount of above-ground biomass produced. The earliest maturing cultivar, Atzimba, produced the least biomass and developed fewest flowers per plant and at higher stem density the reduction in its number of flowers per stem was compensated by the larger number of stems per m^2 (Figure 4.1). The cultivar Renacimiento matured last and had the

largest number of flowers per plant; it also had the strongest shoot development, suggesting an earlier and more intensive inter-stem competition than Atzimba and Yungay. However, the number of flowers per stem was less affected by increasing stem density and the number of flowers per m^2 increased with the stem density. Yungay was intermediate between Atzimba and Renacimiento in shoot development, maturity and in its response in flowering. Differences between the three cultivars in tuber production were not related to shoot development. Thus, the effects of stem density on tuber, flower and TPS production do not necessarily coincide.

4.4.3. Pruning

The enhancement of the development and flowering of higher position inflorescences on main stems by the pruning of lateral stems, demonstrated that there was competition between different sinks in a shoot. Flowering inflorescences on main stems competed for resources with developing lateral stems. Assimilates produced by lateral stems on unpruned plants in a later stage did not improve berry and seed production from the main stems. These results agree with the suggestion made by Almekinders & Wiersema (1991) that inflorescences are supplied by different sources during flowering and seed production.

4.4.4. Practical implications

Higher stem density generally reduced 100-seed weight, berry set, berry weight and the number of seeds per berry. However, the differences were small for total berry and seed production per plant and per m^2. The effect on seed quality was associated only with seed size. Since differences in seed weight of the total harvests were small, the effect of stem density on TPS production was principally determined by its effects on the number of flowers. The experiments showed that for maximum number of flowers and seeds per plant, wide planting distances within the row are required. In some clones increasing stem density can increase the number of flowers per m^2 and, thereby, the seed production per m^2. Since pruning of lateral branches decreased the total number of flowers per plant and did not affect seed production, there is no benefit to be gained from pruning lateral stems under conditions of my experiment. However, since flowering of main stems was stimulated, pruning lateral stems may prove useful with poor flowering clones and under conditions less favourable for flowering.

Chapter 5

EFFECT OF PLANT DENSITY ON THE INFLORESCENCE PRODUCTION OF STEMS AND THE DISTRIBUTION OF FLOWER PRODUCTION

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5 EFFECT OF PLANT DENSITY ON THE INFLORESCENCE PRODUCTION OF STEMS AND THE DISTRIBUTION OF FLOWER PRODUCTION

Additional keywords: *Solanum tuberosum* L., branching, TPS, seed production

Summary

A knowledge of the pattern of flowering and seed production is required for the development of large-scale field production of True Potato Seed (TPS). At the highland experimental station of the International Potato Center in Peru, data on flowering and seed production were collected from three cultivars planted at three densities.

Main stems in which flowering was delayed ceased shoot growth at an earlier stage and produced fewer inflorescences. Inflorescences produced later had fewer flowers, a lower berry set and yielded less seed. Inflorescences flowering at the same time performed similarly, irrespective of their position on the plant. Increasing plant density resulted in cessation of shoot growth at an earlier stage and concentrated inflorescence and flower production at primary positions of early-flowering shoots. With cvs Renacimiento and Yungay a higher plant density increased the percentage of flowers produced in the first three weeks of the flowering period, but with cv. Atzimba the effect of plant density on the distribution of flower production was off-set by a slower stem development.

5.1. Introduction

The interest in the use of True Potato Seed (TPS) for potato production in tropical countries (Wiersema, 1986; Malagamba, 1988) and in TPS production has been increasing. To develop and evaluate methods for the large-scale field production of TPS, an understanding of the flowering pattern of a potato plant and its relation with TPS production is essential.

Potato shoots show a rather fixed pattern of branching and production of inflorescence positions (Almekinders & Wiersema, 1991; Vos, 1995). The numbers of leaves that a main stem produces before developing an inflorescence position seems somewhat fixed and the number of leaves that an apical branch produces depends on the order of branching; the influence of other factors appears to be limited (Jones & Borthwick, 1938; Firman et al., 1991; Almekinders, 1992; Vos & Biemond, 1992). The orders of apical branching that a shoot develops and lateral branch development from lower buds on the main stem depend on the cultivar and environmental conditions. When shoot growth is favoured, several orders of branching can develop. This results in the production of inflorescences of different age and at different positions on the shoot, which is associated with differences in flowering and seed production (Almekinders & Wiersema, 1991). Differences between stems in time of emergence and rate of development may contribute to differences between inflorescences in flowering and seed production.

This paper describes, for three cultivars, differences between stems in production of inflorescences and the effect of plant density on distribution over time of flower production.

5.2. Material and methods

The experiment was carried out at the highland experimental station (12° S, 3300 m above sea level) of the International Potato Center (CIP) in Huancayo, Peru. Well-sprouted 40-50 g seed tubers of cvs Atzimba, Yungay and Renacimiento were planted on November 22, 1986, in a split-plot design with 4 replications. Cultivars were assigned to the main plots and plant densities to the sub-plots. Each sub-plot consisted of a 7.20 m long row with 15, 30 or 60 cm between plants, resulting in high, medium and low stem densities. Distance between the rows was 1.50 m. Outside rows and 60 cm at both ends of each treatment row were borders. Plants were not hilled and they were trellised with cotton string tied between wooden stakes. At planting, 45 kg N as ammonium nitrate (33% N), 25 kg P and 30 kg K per ha were applied in the rows. Thirty days after planting a further 45 kg N per ha in the form of ammonium nitrate (33% N) was applied as a side dressing. Following recommendations for the production of high quality seed (Pallais et al., 1987), supplemental N was applied weekly during the flowering period as a side dressing. Cultivars Atzimba and Yungay received 6, and Renacimiento a total of 8 supplemental N applications at a rate of 25 kg per ha in the form of urea (44% N).

The three cultivars planted belonged to the species *Solanum tuberosum* subsp. *tuberosum*, but cv. Renacimiento is much more an 'andigena'-type cultivar than cv. Atzimba, while cv. Yungay is intermediate between these two cultivars.

Numbers of above-ground stems were recorded in each treatment. At weekly intervals new flowering inflorescences were marked and their position and number of flowers were recorded. Flowering of a primary inflorescence marked the start of flowering of an above-ground stem. The flowering period was defined as the period over which new inflorescences and flowers were produced.

In each treatment, two selections of ten above-ground stems were used for TPS production: ten stems which started flowering in the first week of the flowering period of each cultivar and ten stems which started flowering about 10 days later. These stems are referred to, respectively, as early and late stems. All flowers of selected stems were used for TPS production. Flowers of cvs Atzimba and Yungay were hand pollinated with pollen of the cultivar R-128.6. Flowers of cv. Renacimiento were not pollinated because, unlike those of cvs Atzimba and Yungay, they formed berries naturally from open pollination. Berries from primary and secondary inflorescences of early and late stems were harvested as separate treatments. Each treatment was harvested 75-85 days after pollination and berries were graded in large, medium, and small size classes. Seed was extracted from eight berries per grade and separated into fractions of large (>1.7 mm), medium (1.5-1.7 mm) and small sized (<1.5 mm) seed. Hundred-seed weight of the fractions was determined after drying the seed to a constant weight over silicagel.

5.3. Results

5.3.1. Plant growth and flowering

Plant growth of the three cultivars in this experiment was described by Almekinders (1991,

Experiment 2). *Increasing plant density significantly decreased the number of above-ground stems* per plant (Table 5.1). Flowering started 6, 7 and 8 weeks after planting with cvs Atzimba, Yungay and Renacimiento, respectively, and new primary inflorescences appeared over a period of 6 weeks (Figure 5.1). Secondary and lateral-branch inflorescences started flowering 2 (cv Atzimba) to 3 (cvs Yungay and Renacimiento) weeks later and new ones appeared over the following 3-4 week period. Plant density did not affect the start or the length of the period over which new inflorescences were produced or plant senescence.

5.3.2. Production of inflorescences

Increasing plant density decreased the percentage of flowering stems in all varieties (Table 5.1). Also it reduced the number of primary, secondary and lateral-branch inflorescences per plant from 7.4 to 4.2, 4.3 to 1.6 and 2.0 to 0.3, respectively. Increasing plant density from low to high increased the percentage of the inflorescences produced at primary positions from 56 to 71%.

At low plant density in cvs Atzimba and Yungay, a larger number of stems per plant produced a primary inflorescence in the first 3 weeks of the flowering period than at high density (Figure 5.1). With cv. Renacimiento, the differences between the treatments in the first three weeks of the flowering period were not significant. During the last three weeks of primary inflorescence production, all three cultivars produced significantly more primary inflorescences when grown at low rather than at high plant density (Table 5.1).Medium plant density treatments gave intermediate

Table 5.1. The effect of plant density[a] in three cultivars on the number of above-ground main stems, the total number of primary inflorescences and the distribution of primary inflorescence production.

Cultivar	Plant density[a]	No. stems/ 10 plants	No. primary inflorescences / 10 plants				
			Total	W1[c]	W2	W3	W4+5+6
Atzimba	L	72	62 (86)[b]	8.8	15.3	**25.0**[d]	12.8
	M	68	47 (69)	5.6	14.6	**18.9**	8.0
	H	54	25 (48)	3.8	7.1	**9.0**	4.4
Yungay	L	83	80 (97)	15.5	**22.8**	16.0	26.0
	M	81	73 (91)	16.1	**31.8**	12.8	12.6
	H	68	43 (64)	7.6	**16.0**	11.7	7.9
Renacimiento	L	97	95 (98)	2.8	**27.5**	18.0	47.0
	M	72	68 (94)	4.1	**28.8**	13.8	20.9
	H	63	57 (90)	5.1	**21.4**	16.4	13.9
$LSD_{(P<0.05)}$[e]		11	13	5.1	8.8	6.4	12.0

[a] L = low, M = medium and H = high plant density.
[b] Percentage of the number of stems.
[c] Weeks of the flowering period.
[d] The maximum primary inflorescence production is printed in bold.
[e] For comparisons within of one cultivar.

results in cvs Atzimba and Renacimiento, but in cv. Yungay the number of primary inflorescences per plant when grown at low and medium densities were not significantly different (Figure 5.1).

At the low plant density, respectively 53, 43 and 25% of all inflorescences were produced in the first three weeks of the flowering period in cvs Atzimba, Yungay and Renacimiento. At high plant density, these figures were respectively, 62, 62 and 49% (data not presented).

5.3.3. Production of flowers

In each treatment and cultivar, later flowering primary inflorescences generally produced fewer flowers than earlier ones (Figure 5.2). Similarly, later flowering secondary inflorescences produced fewer flowers than earlier ones. Also few lateral-branch inflorescences developed but the later flowering ones produced fewer flowers than the earlier ones. With inflorescences produced within a particular week, increasing stem density decreased the number of flowers of inflorescences at each position and for each cultivar, but there was no significant interaction of the effect of density with the time of flowering (data not presented). Also differences in numbers of flowers of primary and secondary inflorescence was only significant for cv. Yungay in the 13th week after planting (Figure 5.2). The few inflorescences produced on lateral branches generally had fewer flowers than inflorescences on the main shoots. The average number of flowers over the flowering period was respectively 9.9, 5.3 and 4.2 for primary, secondary and lateral-branch inflorescences (LSD = 0.4, $0.01 < P < 0.05$).

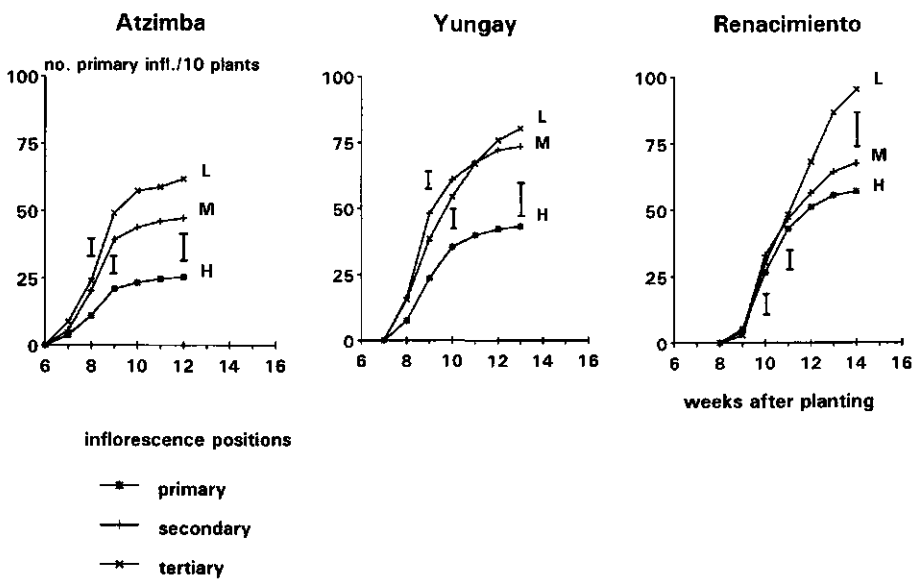

Figure 5.1. The effect of plant density (L = low, M = intermediate and H = high plant density) on numbers of primary inflorescence positions per plant for the cultivars Atzimba, Yungay and Renacimiento. Bars indicate LSD($0.01 < P < 0.05$).

With cv. Atzimba, increasing plant density decreased the number of flowers per plant and did not significantly increase the number of flowers per m^2, the percentage of the total number of flowers produced at primary inflorescence positions or the percentage of flowers produced in the first three weeks of the flowering period (Figure 5.3). With cvs Yungay and Renacimiento, increasing plant density also decreased the number of flowers per plant, but it increased the total number of flowers per m^2 and the percentage of flowers produced by primary inflorescences. With both cultivars, increasing plant density increased the percentage of flowers produced in the first 3 weeks of the flowering period: at high plant density, cvs Yungay and Renacimiento produced respectively 75 and 66% of all flowers in the first 3 weeks, whereas 66 and 39% were produced at low plant density.

5.3.4. Flowering and seed production of early and late main stems

All stems selected for TPS production produced a primary inflorescence (Table 5.2). The early flowering stems produced more secondary inflorescences than the late flowering ones (Table 5.2) and more secondary inflorescences at low than at high plant density. Almost all later-flowering stems ceased shoot growth before producing a secondary inflorescence. Secondary inflorescences on early stems and primary inflorescences on late stems produced fewer flowers, had lower berry set and berry weight, produced fewer seeds per berry and seeds with a lower 100-seed weight than

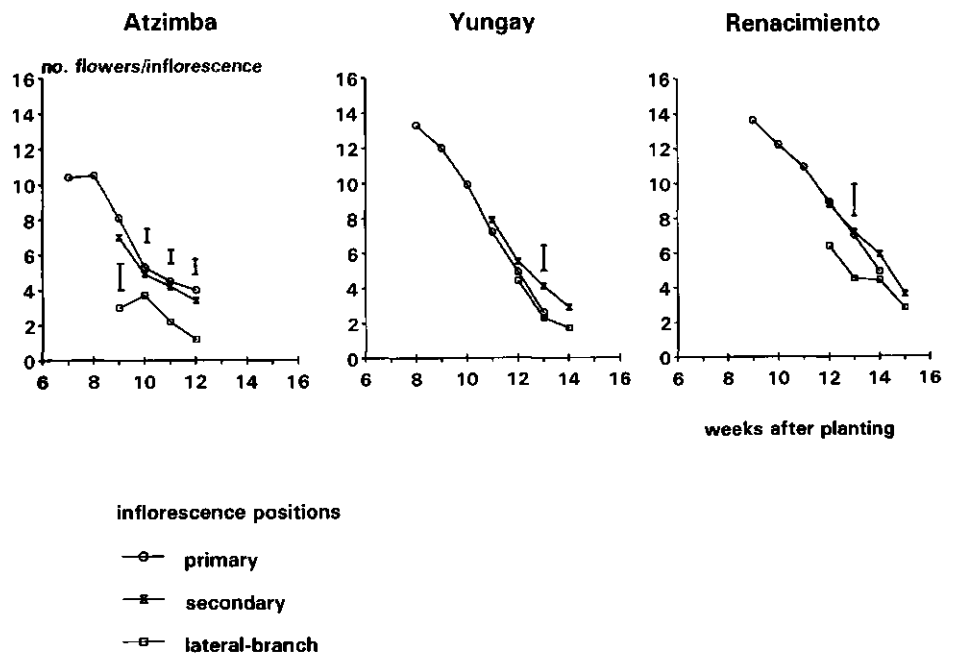

Figure 5.2. The number of flowers per inflorescence produced at primary, secondary and lateral-stem positions for the cultivars Atzimba, Yungay and Renacimiento (means of three plant density treatments). Bars indicate LSD($0.01 < P < 0.05$) for differences between inflorescence positions within particular weeks.

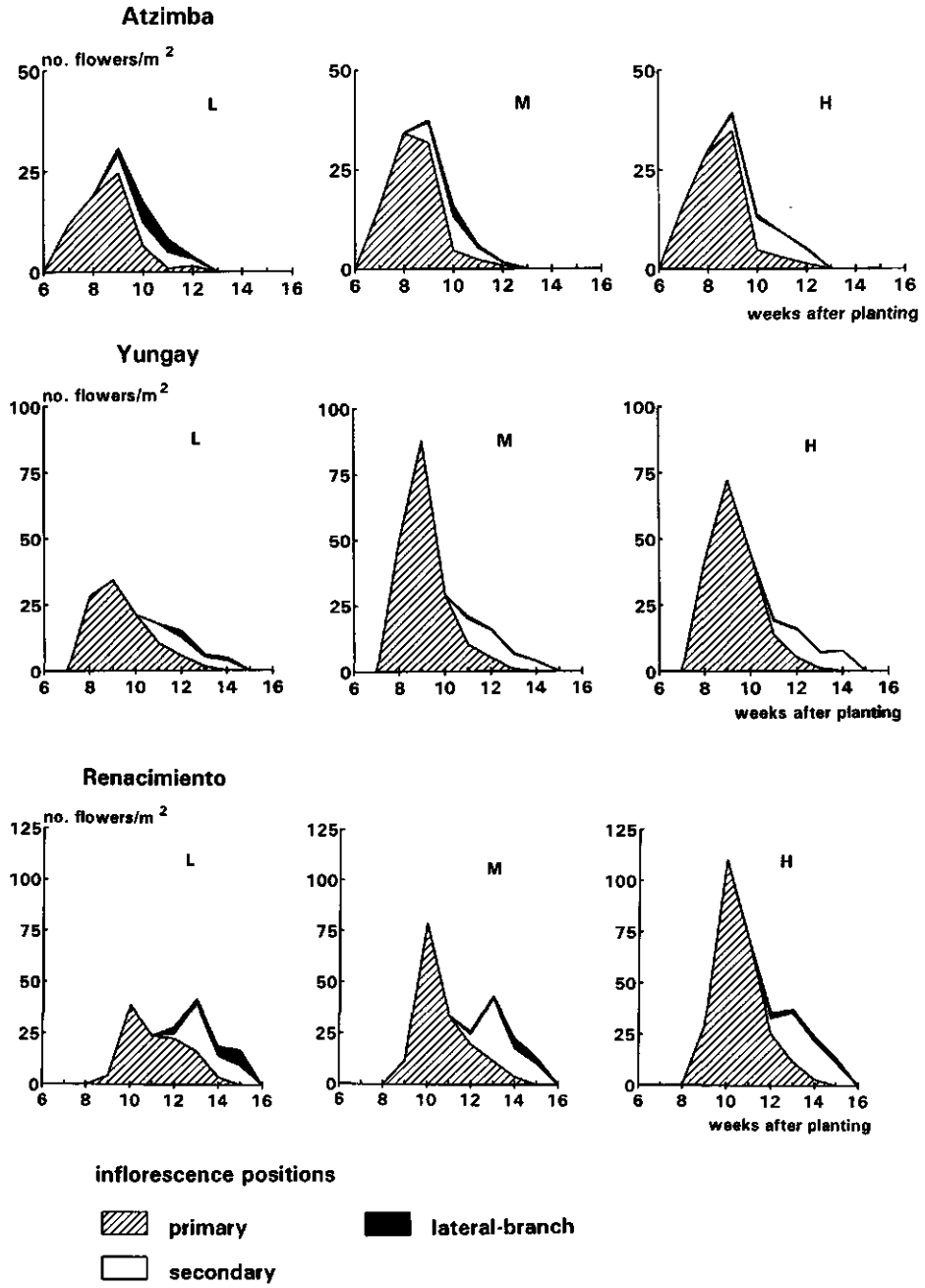

Figure 5.3. Distribution of flower production per m^2 from different inflorescence positions for the cultivars Atzimba, Yungay and Renacimiento at three plant densities (L = low, M = intermediate and H = high plant density).

Table 5.2. Flowering and seed production of selected early and late flowering stems[a] (means of three cultivars and three plant densities).

Inflorescence	No. inflorescences per 10 stems	No. flowers per inflorescence	Berry set (%)	Berry weight (g)	No. seeds per berry	100-seed weight (mg)
Early primary	10	13.2 a	76 a	17.0 a	324 a	74.0 a
Early secondary	8	5.8 c	69 b	13.1 c	292 b	70.6 b
Late primary	10	10.1 b	71 b	14.5 b	296 b	71.8 b
Late secondary	1	-	-	-	-	-

[a] Mean separation within columns with *t*-tests for differences between primary and secondary inflorescences on the same stem and anova for other differences: means followed by a common letter are not significantly different at $P<0.05$.

primary inflorescences on early stems (Table 5.2). Primary inflorescences on the late stems flowered slightly earlier than secondary inflorescences on the early stems; they produced more flowers and larger berries than secondary inflorescences on the early stems, but berry set, number of seeds per berry and 100-seed weight were not significantly affected. Secondary inflorescences and lateral-branch inflorescences on late stems failed to produce berries and seeds. There were no interactions with plant density for flowering, berry and seed production from early and late stems.

5.4. Discussion

5.4.1. Dynamics of inflorescence production

Later-flowering shoots produced fewer inflorescences, which was associated with cessation of shoot growth at an earlier stage. Shoots that produced a primary inflorescence earliest continued growth through development of apical branches, and produced secondary inflorescences 2-3 weeks later. Shoots that produced a primary inflorescence later ceased growth at an earlier stage, and only few of them succeeded in producing a secondary inflorescence. The shoots that were latest in producing a primary inflorescence ceased growth before producing a secondary inflorescence. Probably the shoots that ceased growth before producing a primary inflorescence were the last to emerge or the slowest to develop. These shoots may have developed from deeper planted, smaller or slower developing sprouts on the seed tuber or they developed as below-ground branches from axillary buds on the underground part of a main stem. Since large row distances were used and plants were not hilled, it is likely that below-ground branches developed in all treatments. At lower density, plants probably developed more below-ground branches which could explain the larger number of stems per plant in those treatments (Table 5.1). The smaller number of primary inflorescences that were produced during the last three weeks of the flowering period in high density treatments was a result of both a smaller number of 'late' stems and the cessation of shoot growth at an earlier stage. Because of the earlier cessation of shoot growth, a larger number of 'late' stems did not succeed in producing primary inflorescence. Also the number of stems that did

not produce a secondary inflorescence increased. Thereby, inflorescence production at high density was more concentrated at primary positions and on early flowering shoots. Similar effects of plant density on inflorescence production were found for tomato (Fery & Janick, 1970). In winter wheat, increased plant density reduced tiller production and the ear development of the later produced tillers (Darwinkel, 1978). Increasing plant density in carrot and parsnip also increased the proportion of the total number flowers and seeds which were produced by the primary inflorescence positions (Gray & Steckel, 1983; Gray et al., 1985).

With cv. Renacimiento, the concentration of inflorescence production at primary positions and on early-flowering shoots in the high plant density treatments was associated with a higher percentage of the total number of inflorescences produced in the first 3 weeks of the flowering period. However, with cv. Atzimba the concentration of inflorescence production was partly compensated by a slower shoot development. This slower development can be deduced from the fact that at high density a smaller number of stems produced a primary inflorescence in the first 3 weeks of the flowering period than at low density. Assuming that all stems produced the same number of leaves before developing an inflorescence, a lower leaf production rate is implied. With cv. Yungay, competition delayed leaf production at high plant density, but there was no difference between the treatments with low and medium plant densities.

5.4.2. Dynamics of flower production

Within a specific week, the inflorescence position did not affect numbers of flowers per inflorescence (Figure 5.2) and differences in berry and seed production of inflorescences which flowered at about the same time were relatively small (Table 5.2). This indicates that the time of flowering was a better indicator for its performance than its position. Late produced inflorescences, i.e. inflorescences at a higher position or on a later flowering shoot, probably produced less flowers per inflorescence (Figure 5.1) and had reduced berry and seed production (Table 5.2) because there was stronger competition for light and carbohydrates than during the development of earlier inflorescences.

The pattern of flower production (Figure 5.3) largely reflected the pattern of inflorescence production. However, with cvs Yungay and Renacimiento, the effect of plant density on the distribution of the flower production was smaller than on the distribution of inflorescence production. Plants in the low density treatments produced a larger percentage of the inflorescences in the last weeks of the flowering period, but the effect of those late inflorescences on the flower production was reduced because they produced fewer flowers per inflorescence.

5.4.3. Practical implications

The results demonstrate that flowering and TPS production of a selection of above-ground main stems which start flowering at the same time are not representative for all stems of a potato crop of multi-stem plants. For practical purposes, inflorescence position is not important and inflorescences can be classified according to the time they start flowering: later-flowering inflorescences produce fewer flowers and fewer and smaller seeds per berry. Increasing stem density can increase flower production per m^2 and the proportion of flowers produced in the first part of the growing season. In large-scale TPS production distribution of flower production over time is important because of the labour needed for emasculations and pollinations.

Chapter 6

THE EFFECT OF PHOTOPERIOD ON FLOWERING AND TPS PRODUCTION IN THE WARM TROPICS

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6 THE EFFECT OF PHOTOPERIOD ON FLOWERING AND TPS PRODUCTION IN THE WARM TROPICS

Additional keywords: shoot length, orders of branching, inflorescence position

Summary

Three similar field experiments with five cultivars were carried out to evaluate the effect of a 5-hour extension of the natural daylength and a 3-hour night break on flowering and TPS production in the warm tropics. Shoot length, number of inflorescence positions per plant and number of flowers per inflorescence varied considerably between the experiments. In each experiment, the supplementary photoperiods delayed cessation of shoot growth and thereby increased the orders of branching and the number of inflorescence positions per plant. The photoperiod treatments significantly increased the number of flowers at the last produced inflorescence positions, but not at other ones. Pollen production and quality, berry set, seed set and 100-seed weight were not affected by the photoperiod treatments. TPS production was characterized by variation in flowering and low and variable seed production per flower.

6.1. Introduction

Potatoes in the warm and humid tropical areas are mostly grown by small farmers as a cash crop and for home consumption (Horton & Sawyer, 1985). Because good quality seed tubers are usually expensive or not available, the use of True Potato Seed (TPS) has good prospects for potato production in those conditions. Because TPS can reduce seed costs and help farmers to be less dependent on conventional seed sources (Malagamba & Monares, 1988), the possibility of TPS production in these areas needs to be evaluated.

In the cooler tropical conditions, European cultivars produce short stems, and tuberize and mature early (Demagante & Vander Zaag, 1988; Burton, 1989). Under such conditions flowering is reported to be poor (Pallais, 1985; Upadhya et al., 1985; Umaerus, 1987). However, short-day adapted Andigena-type cultivars may flower abundantly in the cool tropics (Burton, 1989; Almekinders & Wiersema, 1991). In the warm and humid tropics, a short daylength is accompanied by high day and night temperatures, which accelerate plant development, increase branching, increase the number of leaves of the sympodial shoot, and delay tuberization and plant maturity (Marinus & Bodlaender; 1975, Ewing, 1981). Extending the photoperiod has much the same effect on plant development and tuberization as high temperature (Clarke & Lombard, 1939; Bodlaender, 1963; Demagante & Vander Zaag, 1988; Turner & Ewing, 1988). The effects of longer photoperiods are more intense at higher temperature, but there are large differences in cultivar responses (Snyder & Ewing, 1989).

Increased shoot growth is usually associated with improved flowering, berry and seed production (Marinus & Bodlaender, 1975; Demagante & Vander Zaag, 1988; Turner & Ewing, 1988), which can be explained by an increased number of inflorescences or by more flowers per inflorescence. The production of inflorescence positions on a potato shoot is associated with a

rather fixed pattern of leaf production and branching (Almekinders & Wiersema, 1991; Vos, 1995). After the production of a primary inflorescence a shoot continues growth through apical branching. A stem can produce various orders of branching, with inflorescence positions terminating each branch. Longer photoperiods and higher temperatures increase the number of sympodial leaves (Ewing & Struik, 1992), which is associated with more orders of branching and more inflorescence positions. They also stimulate lateral stem development from lower buds on the main stem and the production of inflorescence positions on those stems. The initiation of the first inflorescence does not require photoperiodic induction and its position on the shoot is not affected by the photoperiod (Jones & Bothwick, 1938; Clark & Lombard, 1942). Effects of the photoperiod on the number of differentiated flower buds and on flower bud abortion may depend on the light intensity (Jones & Borthwick, 1938; Clarke & Lombard, 1942; Werner, 1942).

High temperatures reduce pollen fertility and fruit set in tomato (Kuo et al., 1978), but no data are available from potato about pollen fertility, berry and seed set or the quality of TPS produced under warm tropical conditions.

This paper reports experiments with TPS production in the warm tropical environment of San Ramon, Peru. Effects of extension of the photoperiod and night break were evaluated as practices to improve flowering. The effect of these treatments on plant development and seed production was examined.

6.2. Material and methods

Three similar experiments were carried out at the experimental station of the International Potato Center in San Ramon, Peru (11° S, 800 m above sea level), during three successive seasons. Planting dates and conditions during the experiments are presented in Table 6.1. Single-stem plants of 5 clones (Atzimba, R-128.6, LT-7, DTO-28 and Serrana) were grown from tubers in nursery beds filled with a 20 cm layer of substrate (1:1 mixture of peat moss and soil on a volume basis). The nursery beds were adequately fertilized and watered. Three photoperiod treatments were compared:
- Short Day (SD): natural daylength.
- Long Day (LD): natural daylength + 5 hours supplemental light from 1800 h - 2300 h.
- Night Break (NB): natural daylength + 3 hours supplemental light from 000 h - 300 h.

For supplemental light in the treatments LD and NB, one 100 W incandescent light bulb was used per m^2. The distance between the lamps and the top of the canopy decreased as the plant height increased during the season. Black plastic curtains separated the nursery beds with different photoperiod treatments from 1800 h until early next morning. Each photoperiod treatment had three replications of 12 single-stem plants per clone.

Flowers were not emasculated and were pollinated after anthesis with pollen from the clones R.128-6 (Experiment 1) and 104-12.LB (Experiments 2 and 3). The pollen used in Experiment 2 had a low viability, due to the fact that it had been inappropiately stored for several months. Berries were harvested when mature, at about 30 days after pollination. Seed production, harvesting and processing of berries and seed were as described by Almekinders & Wiersema (1991). Pollen quality was evaluated by an in vitro-germination technique, adapted from Mortenson

Table 6.1. Details of Experiments 1-3.

	Planting date		Natural daylength (hours)	Temperature (°C, seasonal average)		Start of flowering (d.a.p.)[a,b]	Tuber harvest (d.a.p.)
				Max.	Min.		
Expt 1	dry season 1988	July 19	11.35-12.07	32.9	17.3	31-34	86
Expt 2	rainy season 1988/89	November 8	12.27-12.26 (max. 12.40)	31.4	19.3	32-35	96
Expt 3	dry season 1989	June 19	11.30-11.43	31.0	16.2	35-37	70

[a] Days after planting.
[b] Earliest and latest flowering cultivar.

et al. (1964), and by colouring with aceto-carmine (Belling, 1921). Pollen production was estimated by extracting and weighing pollen from samples of 8-10 flowers. Because bumble bees were actively foraging on the potato flowers, those flowers were collected early in the morning. The flowers of primary, secondary and other order inflorescences were counted. In Experiment 1, lateral stems with inflorescences also developed from the lower buds on the main stem. In Experiment 2, lateral stems were pruned at an early stage, and in Experiment 3 no lateral stems developed. The total number of inflorescence positions was the sum of the total number of flowering inflorescences and the number of aborted inflorescences, i.e. inflorescences of which all flower buds had dropped before anthesis. Shoot length was measured at tuber harvest. In Experiment 1, plants in the SD treatments were mature at harvest, whilst those in the LD and NB treatments were still green. In Experiments 2 and 3, tubers were harvested when all plants were mature. In each experiment tubers were weighed.

The experiments were carried out under strict pest and diseaese control, so that *Phytophthora infestans, Alternaria solani* and larvae of tuber moth (*Phthorimaea operculella*) were prevented. However, in the 1988-89 rainy season (Experiment 2) contamination of the substrate with *Pseudomonas solanacearum* could not be avoided. Wild bees (*Trigona* spp.) and *Diabrotica* damaged some stigmas, ovaries and corollas of the flowers in Experiment 2.

Seeds from the three photoperiod treatments of Atzimba and LT-7 (Experiment 1) were evaluated for germination, 6-7 months after harvest. From each treatment, three samples of 100 medium-sized seeds (diameter 0.15 - 0.13 cm) produced from primary inflorescences were germinated on wet filterpaper in Petri dishes at 25 °C and 24 h light. Before sowing, seeds had been soaked for 24 hours in gibberellic acid (1500 ppm).

6.3. Results

6.3.1. Shoot development and flowering

After producing 15 - 16 leaves, the main stems formed a primary inflorescence. Shoot growth continued through two apical branches which each formed 4 - 8 leaves before producing a

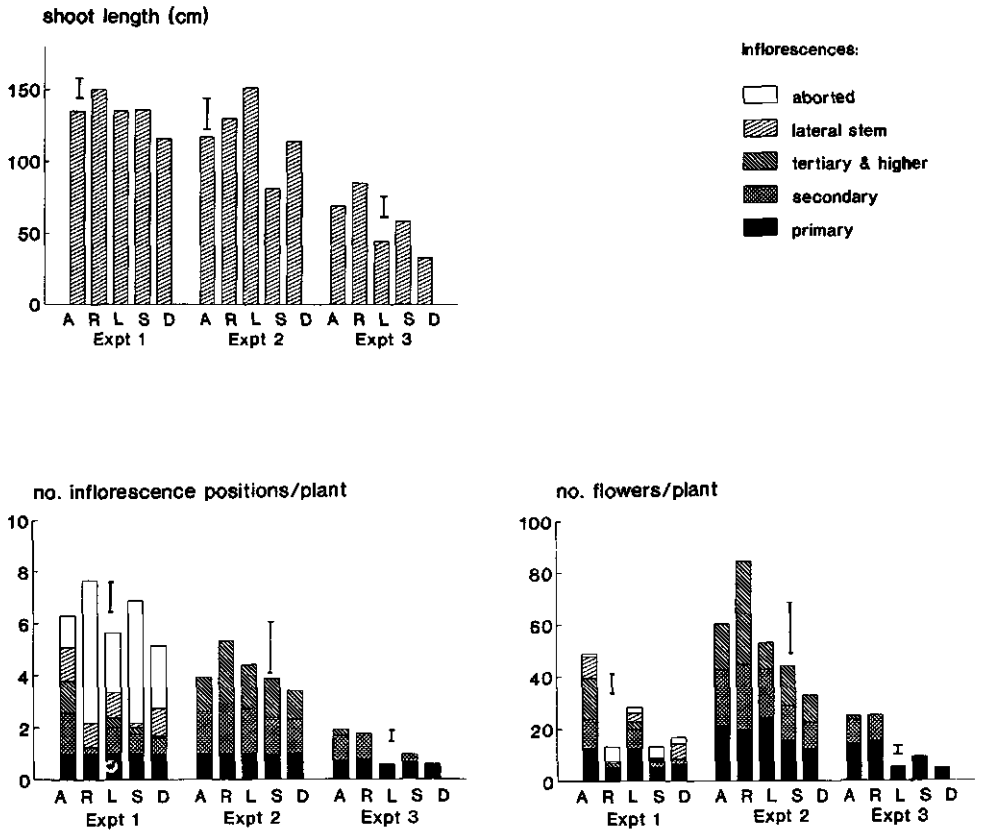

Figure 6.1. Shoot length, number of inflorescence positions and number of flowers at different positions on the plant for five cultivars in three experiments in San Ramon. Bars are LSD($0.01 < P < 0.05$) for comparisons within experiments (A = Atzimba, R = R-128.6, L = LT-7, S = Serrana, D = DTO-28).

secondary inflorescence. Tertiary stems and stems of following orders developed in a similar way, but they formed fewer and a more variable number of leaves before producing an inflorescence. This growth pattern was not affected by the treatments; however, the stage at which shoot growth ceased depended on the photoperiod treatment, the cultivar and the experimental conditions.

Shoot length and number of inflorescence positions were largest in Experiment 1 and smallest in Experiment 3 (Figures 6.1 and 6.2). In Experiment 1, many inflorescences at secondary and higher positions on the main shoot aborted, particularly in R-128.6 and Serrana. The number of flowering inflorescences per plant (Figures 6.1 and 6.2), number of flowers per inflorescence (Table 6.2) and number of flowers per plant were largest in Experiment 2 and lowest in Experiment 3.

Over the three experiments, R-128.6 produced the longest shoots and the largest number

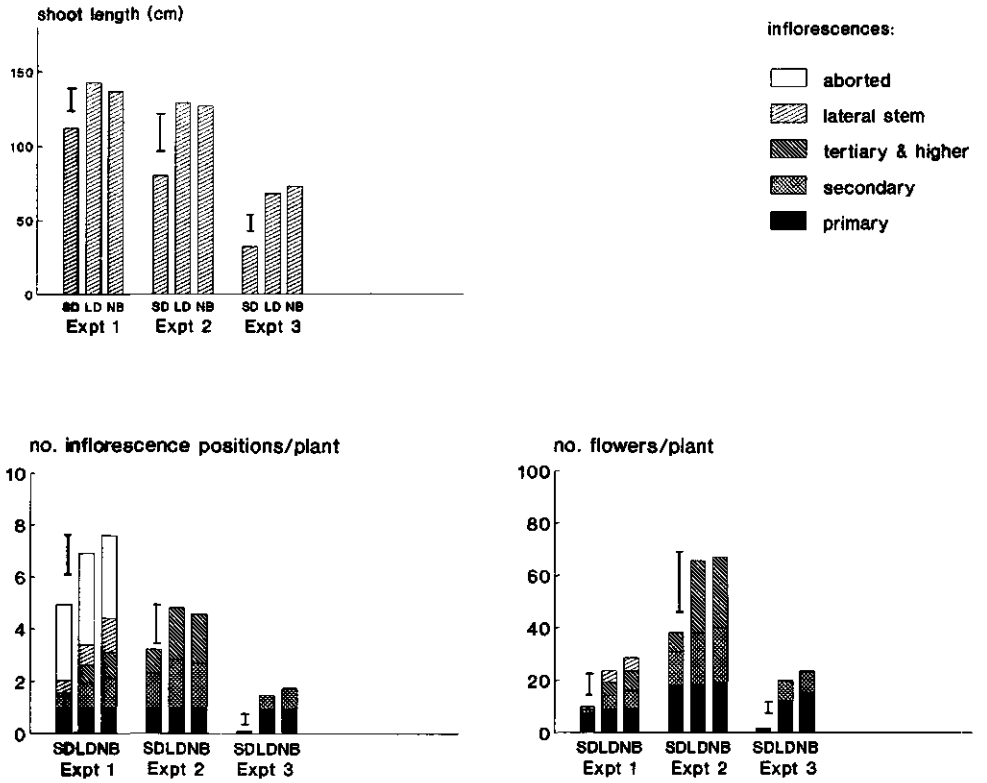

Figure 6.2. Effect of photoperiod treatments on shoot length, the number of inflorescence positions and flowers at different positions on the plant in three experiments in San Ramon (mean of five cultivars). Bars are LSD($0.01 < P < 0.05$) for comparisons within experiments (SD = short days, LD = long days, NB = night break).

of inflorescence positions and was the last to mature (Figure 6.1). Except for the shoot length of Serrana in Experiment 2, DTO-28 produced the shortest shoots and the fewest inflorescence positions and flowers per plant and was the first to mature. The start of flowering varied little between experiments and cultivars (Table 6.1).

In each experiment the plants in the LD and NB treatments grew significantly taller than in the SD treatments (Figure 6.2). In Experiment 2, plants of Serrana and DTO-28 in the NB treatments were not significantly taller than those in the SD treatment, which is probably an effect of the contamination of those treatments with *Pseudomonas solanacearum*. Plants in the LD and NB treatments produced more inflorescence positions and flowers (Figure 6.2), and matured later than the ones in the SD treatments. The effect of the photoperiod treatment on the number of flowers per inflorescence depended on the position of the inflorescence, cultivar and experiment (Table 6.2). The LD and NB stimulated lateral stem development in Experiment 1, but did not significantly

Table 6.2. Number of flowers per inflorescence of primary, secondary and tertiary order, of five cultivars in three successive experiments in San Ramon.

	Experiment 1 (1988)					Experiment 2 (1988-89)					Experiment 3 (1989)				
	Atz[a]	R-128.6	LT-7	Serr[b]	DTO-28	Atz	R-128.6	LT-7	Serr	DTO-28	Atz	R-128.6	LT-7	Serr	DTO-28
Primary inflorescence															
SD	13.4	6.8	7.4	6.3	3.6	18.6	23.3	24.7	13.0	10.4	3.5	4.5	-	-	-
LD	13.4	3.7	14.3	4.9	7.8	21.9	17.1	22.9	15.6	15.1	18.0	18.2	8.1	10.1	6.4
NB	11.4	5.1	16.1	5.5	8.6	20.0	19.1	24.0	14.2	11.7	21.6	17.2	8.2	13.8	5.0
$LSD_{(P<0.05)}$[c]			5.4					4.9					2.8		
Secondary inflorescence															
SD	3.4	1.9	2.0	1.9	1.0	7.8	11.5	10.1	6.8	6.2	-	-	-	-	-
LD	8.0	1.6	6.4	2.6	1.8	14.5	12.4	9.7	9.1	8.1	8.3	9.5	-	3.0	-
NB	8.2	2.3	5.8	2.3	3.3	13.0	13.5	11.8	8.5	7.8	11.5	12.3	-	4.9	-
$LSD_{(P<0.05)}$			2.8					3.2							
Tertiary inflorescence															
SD	2.6	1.7	-	0.1	0.9	3.2	6.5	5.4	3.1	1.3	-	-	-	-	-
LD	8.0	3.7	6.4	0.8	0.3	8.1	9.5	8.0	6.3	5.0	-	-	-	-	-
NB	7.6	3.1	5.8	2.4	1.2	7.8	9.1	9.3	6.0	5.8	-	-	-	-	-
$LSD_{(P<0.05)}$			4.3					4.9							

[a] Atz = Atzimba, [b] Serr = Serrana.
[c] For comparison between treatment means of the same or different clones.

Table 6.3. Berry set, number of seeds per berry and 100-seed weight. Averages of three photoperiod treatments for five cultivars.

	Berry set (%)			No. seeds per berry			100-Seed weight (mg)		
	Expt 1 1988	Expt 2 1988-89	Expt 3 1989	Expt 1 1988	Expt 2 1988-89	Expt 3 1989	Expt 1 1988	Expt 2 1988-89	Expt 3 1989
Atzimba	37	25	49	127	117	146	55.2	60.3	59.7
R-128.6	1	23	50	-	98	138	-	62.9	59.4
LT-7	13	29	35	155	82	188	53.7	63.8	54.6
Serrana	29	18	87	97	80	128	69.7	67.8	64.1
DTO-28	25	24	25	117	42	163	57.8	63.2	58.4
$LSD_{(P<0.05)}$	11	9	15	20	9	7	4.6	2.9	1.3

increase the number of inflorescences and flowers on those stems (Figure 6.2). Differences between the LD and NB treatments were not significant. There was no effect of the photoperiod on the start of flowering. In the treatments LD and NB, leaf inclination was more erect (especially during the night and in the early morning) and flowers opened later than in the SD treatment.

6.3.2. Pollen, seed and tuber production

Depending on the clone, pollen production varied from 0.2 to 1.5 g fresh weight per flower, less than 25% of the quantities normally produced in Huancayo and Lima (C.J.M. Almekinders, unpublished). In vitro germination of the pollen was extremely low and variable (0-10%). Percentage of colouring of the pollen with aceto-carmine ranged from 0 to 40%, depending on the clone and the season. There was no indication that the photoperiod treatments affected pollen production per flower or fertility.

Table 6.4. Germination of seeds (%) produced from Atzimba and LT-7 in three photoperiod treatments in Experiment 1.

Photoperiod treatments	Days after sowing					
	5		13		21	
	Atzimba	LT-7	Atzimba	LT-7	Atzimba	LT-7
Short days	45(42)[a]	36(37)	88(70)	89(70)	94(75)	98(83)
Long days	20(27)	9(15)	84(66)	61(52)	91(73)	74(64)
Night break	32(35)	30(33)	80(64)	87(69)	90(73)	97(82)
$LSD_{(P<0.05)}$[b]	(15)		(14)		(15)	

[a] Transformed values (arcsin) in parenthesis.
[b] For comparison between treatment means (transformed values) of the same or different clones.

There was large variation between seasons, cultivars and treatments for berry weight (data not presented), berry set, number of seeds per berry and 100-seed weight (Table 6.3). However, differences were not consistent and there was no significant effect of the photoperiod treatments. Total seed production per plant, which is determined by the number of flowers per plant, berry set and number of seeds per berry, varied considerably over the seasons and per cultivar (data not presented). There was no effect of the photoperiod treatments on the germination of the seeds produced from Atzimba and LT-7 in the 1988 dry season (Table 6.4).

Average tuber yields were 256, 281 and 263 g fresh weight per plant in Experiments 1, 2 and 3, respectively (data not presented). In Experiment 1, tuber yields were larger in the SD treatment than in the LD and NB treatments. There was a significant interaction between the photoperiod treatments and the cultivars for the tuber yield in Experiment 2. In Experiment 3, tuber production for the SD treatments applied to Atzimba and R-128.6 were significantly larger than for the LD and NB treatments, while for LT-7, Serrana and DTO-33 the photoperiod treatments did not affect tuber production.

6.4. Discussion

6.4.1. Season

Flowering in Experiments 1 and 2 was better than in Experiment 3 because plants developed taller shoots with more orders of branching and, consequently, more inflorescence positions. Most shoots in the SD treatment in Experiment 3 ceased growth before producing a primary inflorescence position and plants matured early. Low night temperatures in the third and fourth week after planting (± 13 °C) probably resulted in early tuberization and cessation of shoot growth, while the higher temperatures in Experiments 1 and 2 counteracted the effect of the natural short daylength on tuber and shoot growth.

Although conditions were favourable for shoot growth and the production of inflorescence positions in both Experiments 1 and 2, they were not favourable for flower development in Experiment 1; primary inflorescences developed fewer flowers and many flower buds of secondary and higher position inflorescences on main stems aborted. Since the sympodial shoots developed more leaves after the production of these inflorescence positions, the abortion of flower buds may be explained by competition for assimilates with the young developing leaves, similar as can occur in tomato (De Zeeuw, 1954; Kinet, 1977). However, no explanation can be given for the variation between Experiment 1 and Experiment 2. Differences in mean temperatures and natural daylength (Table 6.1), but also other factors, such as differences in light quality and intensity, or in day and night temperature regimes may have influenced assimilate attraction by the inflorescences.

Comparisons between the average tuber yields in the 3 experiments are difficult because of the differences in plant maturity at harvest in Experiment 1 and the contamination with *Pseudomonas solanacearum* in Experiment 2. Pruning of lateral stems in Experiment 2 probably stimulated the flowering of the shoot to some extent (Almekinders & Wiersema, 1991), but without influencing the treatment effects.

6.4.2. Cultivar

In general, later maturing cultivars showed prolonged shoot growth and produced more orders of branching, more inflorescence positions and more flowers per plant, and tended to produce lower tuber yields. The cultivars represented a range of genotypes, of which R-128.6 and DTO-28 were the extremes. R-128.6 is a short-day adapted Andigena-type cultivar, which produced long shoots and low tuber yields, probably because the high temperature strongly delayed cessation of shoot growth and tuberization. DTO-28, a Tuberosum-type cultivar selected for high temperature and short daylength conditions, showed early cessation of shoot growth and produced high tuber yields in all three experiments. The other three cultivars were intermediate between Tuberosum and Andigena type. There was no clear relation between the type of cultivar and the effect of the photoperiod treatments on shoot growth and tuber production.

6.4.3. Photoperiod treatment

The extended photoperiod (LD) and night break (NB) increased the number of flowers per plant, principally because they produced more inflorescence positions as a result of prolonged sympodial shoot growth and more orders of branching. LD and NB increased the number of flowers at the last produced inflorescence positions, because they delayed the cessation of shoot growth. When a shoot ceases growth, most assimilates are diverted to the tubers, photosynthesis decreases and the plant starts to mature. Thus, the last produced inflorescence often cannot fully develop and flower buds may abort because of a shortage of assimilates. Since shoot growth continued for much longer in the LD and NB treatments, the inflorescences had more time to develop. Although these inflorescences competed with vegetative shoot growth, they had more assimilates available, resulting in less flower bud abortion and a larger number of flowers at the last produced inflorescence positions. The photoperiod treatments did not affect the number of flowers at lower inflorescence positions or the abortion of inflorescences in Experiment 1. This agrees with work of Turner & Ewing (1988), which also showed that the effect of photoperiod on the number of flowers per inflorescence was larger for the later inflorescences. This indicates that photoperiod did not affect the distribution of assimilates between shoot and inflorescences.

The higher tuber yields of the SD treatments in Experiment 1 indicate that LD and NB delayed tuber production. The tuber yields in Experiment 3 show that when all plants were harvested at maturity, delayed plant maturity in the LD and NB treatments compensated for the delayed tuberization in LT-7, Serrana and DTO-28. However, in Atzimba and in R-128.6, tuber yields were larger in the SD treatments, suggesting a strong effect of the photoperiod treatments on the tuber initiation. In Atzimba and R-128.6 in Experiment 3, the reduction of the tuber yield in the LD and NB treatments was associated with increased shoot development and flowering, but no such relationship existed for the other three cultivars.

6.4.4. Feasibility of TPS production in the warm tropics

Since potato shoots developed several orders of branching and inflorescence positions under short-day and high temperature conditions, some clones may flower better in warm than in a cooler tropics. This can be particularly important for cultivars that mature early in cooler tropical locations and cease shoot growth before producing an inflorescence. Shoot growth and number of

inflorescence positions was further increased by an extended photoperiod and a night break, thus improving flowering and seed production. However, flower bud abortion in Experiment 1 showed that increased production of inflorescences does not always result in increased flower production. Data from these experiments suggest that low and variable berry set, and low pollen production and fertility have to be considered as factors that seriously limit TPS production in the warm tropics. The quality of seed produced under high temperature is probably lower because of its lower weight and size as compared to seed produced in other locations (Almekinders & Wiersema, 1991). However, the effect of high temperature on seed quality can only be assessed in more controlled conditions.

It can be concluded that extension of the photoperiod or a night break increase flowering and seed production in the warm tropics, principally through delaying the cessation of shoot growth and increasing the number of inflorescences per plant. However, large variation in flowering between seasons, low and variable TPS production per flower and high pest and disease pressure increase costs of the seed production in the warm tropics.

Chapter 7

PHOTOTHERMAL RESPONSE OF SYMPODIUM DEVELOPMENT AND FLOWERING UNDER CONTROLLED CONDITIONS

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7 PHOTOTHERMAL RESPONSE OF SYMPODIUM DEVELOPMENT AND FLOWERING UNDER CONTROLLED CONDITIONS

Additional keywords: potato, *Solanum tuberosum* L., sympodial development, leaf production, flowering, photoperiod, temperature

Summary

In two phytotron experiments with different cultivars (Experiment 1: cvs Atzimba and Van Gogh; Experiment 2: cvs Spunta and Désirée), temperature and photoperiod effects on sympodial development, stem, leaf and flower production of potato (*Solanum tuberosum* L.) shoots were investigated. In both experiments, short-day (SD) and long-day (LD) treatments were combined with average temperatures ranging from 15 to 27 °C. In Experiment 1, data of the entire shoot were collected, whereas in Experiment 2 only leaf and flower production of the main and secondary stems were measured.

In Experiment 1, increasing temperature at SD and LD, and increasing photoperiod at 15 °C increased the number of lateral stems, the numbers of inflorescences and leaves of the sympodium, and of the entire shoot. The photoperiod response at 25 °C was not consistent. In Experiment 2, the number of flower primordia and survival of flower primordia of individual inflorescences increased with the photoperiod and with temperature up to 23 °C. At 27 °C in Experiment 2, flower development was suppressed.

Total leaf and flower production per plant were largely a function of lateral stem production. Increasing temperature and photoperiod increased the number of leaves of individual stems in most treatments. However, the effects on leaf as well as flower production of individual stems were relatively small, except for the effect of a temperature increase from 23 to 27 °C in Experiment 2. The photoperiodic response of the 'time till flowering' of individual stems was facultative SD or daylength-neutral, depending on the cultivar and stem position.

7.1. Introduction

The use of True Potato Seed for potato tuber production has stimulated the interest in the reproductive development of potato (cf. Burton, 1989). Whereas the effects of temperature and photoperiod on the vegetative growth and development of the potato plant have been investigated extensively (cf. Ewing & Struik, 1992), qualitative and quantitative information concerning their effects on flowering is limited. Furthermore, the available information, referring to a wide range of temperature and photoperiod conditions, is in some instances contradictory (cf. Burton, 1989).

Increasing temperature and/or photoperiod enhances branching, increases number of leaves of the shoot and delays tuberization (cf. Ewing & Struik, 1992). Longer days and/or artificial extension of the photoperiod usually result in more abundant flowering (cf. Driver & Hawkes, 1943). Increasing temperature is reported to improve flowering (Marinus & Bodlaender, 1975; Turner & Ewing, 1988). However, since the term flowering is generally loosely applied, it is in most cases not clear how temperature and photoperiod improve flowering. Increased flower production

has been reported as result of an increased number of inflorescences (Almekinders, 1992a), an increased number of flower buds (Werner, 1942; Turner & Ewing, 1988) and reduced flower bud abortion (Werner, 1942; Bodlaender, 1963; Turner & Ewing, 1988). Furthermore, negative effects of high temperature and long photoperiods on flowering have also been reported (cf. Burton, 1989; Garner & Allard, 1923; Lundegårdh, 1966; Sadik, 1983).

Few studies report an effect of photoperiod on the start of flowering in potato. Most of these state that the onset of flowering was earlier under short-day conditions or not affected by the photoperiod (Garner & Allard, 1923; Doroshenko et al., 1930; Driver & Hawkes, 1943). On the basis of these reports, potato cultivars are usually classified as daylength-neutral or facultative short-day plants for time till flowering (Salisbury, 1963; Roberts & Summerfield, 1987). However, facultative long-day responses have also been observed (cf. Salisbury, 1963). Inflorescence formation in complete darkness (Jones & Borthwick, 1938; Clarke & Lombard, 1942; Leopold, 1949) and in continuous light (Clarke & Lombard, 1939; Werner, 1942) have been reported.

This paper presents results of two experiments under controlled conditions in which the quantitative effects of photoperiod and temperature on the different components of vegetative shoot development and flowering in potato were assessed. In both experiments, treatments representing tropical temperature and daylength conditions were included. In Experiment 1, we used a cultivar adapted to tropical conditions and used in experiments on different aspects of TPS production (Almekinders & Wiersema, 1991; Almekinders, 1992a), and a cultivar adapted to temperate, long-day conditions and known for its abundant flowering and high berry set under such conditions (Veerman & Van Loon, 1993). In Experiment 2, we used the main cultivars investigated in an extensive international research programme on the ecological adaptation of potato cultivars in the (semi-)tropics. Experiment 2 was designed to analyse the quantitative effects of ecological conditions on early tuber growth and dry matter partitioning. As a by-product, this experiment yielded precise data on flowering characteristics of a wider range of conditions than Experiment 1 could. Although the differences between the treatments of both experiments restrict the possibilities of comparing the results, the data are important as the use of growth chambers limited possibilities for replications.

The information from the two experiments is relevant for a better understanding of flowering and to modelling of shoot development.

7.2. Material and methods

7.2.1. Phytotron and plant cultivation

Two experiments were carried out in the phytotron of the Department of Agronomy, Wageningen Agricultural University. Growth chambers of approximately 14 m^2 each were illuminated with SON-T 400 W AGRO and HPI-T 400 W lamps (Philips, The Netherlands) in a 1:1 ratio, giving photosynthetically active radiation (PAR) of 100 to 150 W m^{-2} at 0.30 to 1.50 m above the floor during the day-light period. Extension of the photoperiod was achieved by incandescent light of 2-4 W m^{-2}. Relative humidity was maintained at 50-70%.

In Experiment 1, single-stem plants of the cvs Atzimba and Van Gogh were grown from sprouted tubers, planted in 10-l pots on January 29, 1990. In Experiment 2, single-stem plants were grown from sprouted seed tubers of the cvs Spunta and Désirée, planted in 20-l pots on November 18, 1993. The pots were filled with a 1:1 substrate mix (v/v) of potting soil and sand.

Every plant in Experiment 1 received a total of 3.4 g N, 1.9 g P, 4.7 g K, 1.7 g Mg, 1.2 g Ca and micro-nutrients in 5 applications of a nutrient solution during the period of 10 to 50 days after planting (DAP). Plants in Experiment 2 received a total of 4.0 g N, 1.0 g P, 4.6 g K, 0.5 g Mg and 0.8 g Ca and micro-nutrients in 10 applications of a nutrient solution. Plants were watered daily with tap water.

7.2.2. Treatments

Four different growth chambers were used in Experiment 1, one growth chamber for each combination of two photoperiods and two temperature regimes. In Experiment 2, eight growth chambers were used, i.e. one growth chamber for each combination of two photoperiods and four temperature regimes. In both experiments, a short-day and a long-day photoperiod treatment were applied, coded in the text as SD and LD, respectively. The SD and LD treatments in both experiments had a 12-h PAR period. In the LD treatments this period was extended with incandescent light. In Experiment 1, a 4-h extension was given after the PAR period and in Experiment 2, a 6-h extension was split into a 3-h period before and a 3-h period after the PAR period. Plants were exposed to the day-temperature during the PAR period and to the night-temperature during the rest of the time. Day/night temperature regimes in Experiment 1 were 20/10 and 30/20 °C. In Experiment 2, the day/night temperature regimes were 18/12, 22/16, 26/20 and 30/24 °C. Temperature treatments of both experiments are coded in the text by their average temperature (Experiment 1: 15 and 25 °C; Experiment 2: 15, 19, 23 and 27 °C). In both experiments there were 48 plants in each growth chamber, 24 plants of each cultivar.

In Experiment 1, the treatments 15 SD and LD were ended at 100 DAP (days after planting) and 120 DAP, respectively. The 25 °C treatments in Experiment 1 were ended 127 DAP. Experiment 2 was ended 102 DAP.

7.2.3. Terminology

Based on Danert (1957) and Vos (1995) the following terminology is used to refer to the different lateral stems which together with the main stems, form the potato shoot (Figure 7.1). The above-ground main stem (developing as a true main stem directly from the tuber, or from below-ground nodes on the true main stem) forms the first level of growth and terminates in the production of a 'primary' inflorescence. Lateral stems developing from above-ground axillary buds on the main stem are called 'secondary' stems and terminate in 'secondary inflorescences'. Together these stems form a second level of growth. Similarly, lateral stems and inflorescences developing axillary buds on secondary stems are called 'tertiary stems' and 'tertiary inflorescences'. Continuation of shoot growth gives rise to fourth and fifth levels of growth, and so forth.

After the main stem has formed an inflorescence, growth is mostly continued by the stems of the second, third and higher growth levels developing from the nodes n-1 and n-2 (n being the position of the last formed leaf on the main and lateral stems, as it is used throughout the rest of

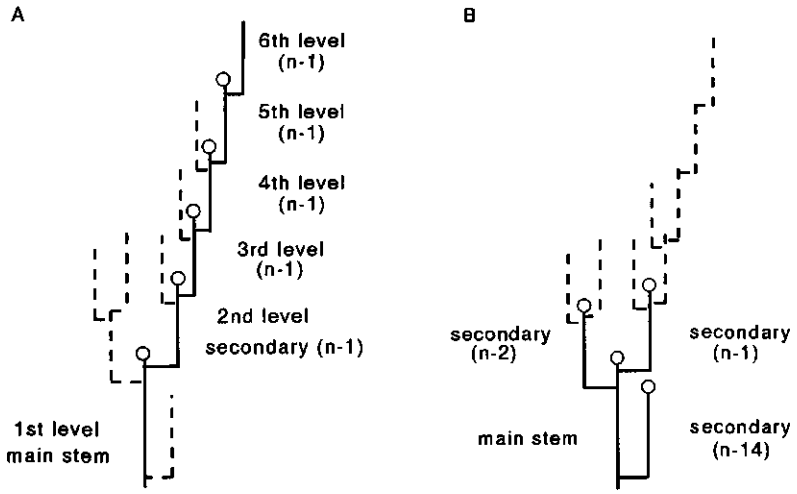

Figure 7.1. Diagrams of (A) the sympodium, composed of the main stem and the lateral stems of different levels of growth, developed successively from the nodes n-1, and (B) the main stem and secondary stems developed from the nodes n-1, n-2 and n-14.

the paper). Because lateral stems from the nodes n-1 usually develop more strongly than those from the nodes n-2, the total series of stems successively developing from the nodes n-1 gives the appearance of a single shoot (Vos, 1995), which is called a sympodium (Figure 7.1). With the 'entire shoot', we refer to the main stem and the entire constellation of lateral stems developing from one main stem. Stems developing from nodes n-1 and n-2 are briefly called 'apical laterals' ('apical secondary stem', 'apical tertiary stem', etc.). The lateral stems developing from the nodes on the basal part of a stem are here called 'basal laterals' ('basal secondary stem', etc.). The secondary lateral from the lowest above-ground bud on the main stem forming an inflorescence is coded as n-14, although its position on the main stem varied between n-14 to n-17.

In our experiments, a stem was considered to have 'completed' its development when it had formed a macroscopically visible terminal inflorescence. The formation of an inflorescence refers to the initiation of one or more flower primordia and their subsequent growth and development. Flower primordia survival is the proportion of flower primordia that develop into open flowers, i.e. flower primordia which do not abort before anthesis. Inflorescence survival is defined as the proportion of inflorescences that formed one or more open flowers. An aborted inflorescence is an inflorescence in which all flower primordia aborted before reaching anthesis. Flowering of an individual flower is referring to the opening of the flower. An inflorescence starts flowering with the opening of the first flower.

7.2.4. Data collection

In Experiment 1, the following data were recorded (between parentheses: n = the number of plants per treatment used for the observation):

- Numbers of days from planting till flowering of the primary inflorescence and secondary inflorescences from the nodes n-1, n-2 and n-14 ($n = 24$).
- Numbers of leaves of the main stem and secondary stems from the nodes n-1, n-2 and n-14 on the main stem (see Figure 7.1, $n = 24$). Only the numbers of leaves of stems which had completed their development were included in the statistical analysis.
- Numbers of flowers of primary inflorescences and secondary inflorescences on the stems from nodes n-1, n-2 and n-14 on the main stem ($n = 24$). Only flower positions with a peduncle larger than 0.8 cm at the time of harvest were counted as an opened flower.
- Total number of leaves of the sympodium and of the entire shoot ($n = 12$). New leaves appearing at the top of the stems where included when they had reached a length of about 1 cm.
- Total numbers of inflorescences of the sympodium ($n = 24$) and of the entire shoot ($n = 12$), and number of flowers of the entire shoot ($n = 12$). The number of inflorescences corresponds with the number of completed stems (Table 7.1).

With the exception of the number of days till the opening of the first flower of an inflorescence, all data were collected at the end of the experimental period.

In Experiment 2, number of leaves ($n = 12$), number of macroscopically visible flower primordia and flowers ($n = 6$) were counted for main stem and the secondary stem developing from the node n-1.

7.2.5. Statistical analysis

A Chi-square test was used to determine significance of different numbers of plants which produced inflorescences (Table 7.1) and numbers of inflorescences that developed open flowers (Table 7.4). Other data were analysed with standard analysis of variance. Since it was not possible to have replications of treatments at the growth chamber level simultaneously or over time and as the variation due to differences in (well-controlled) growth chambers is very small compared to plant-to-plant variation and variation among treatments, single plants were considered as experimental units. Estimated values, obtained through missing plot analysis, were used for those plants which had not produced a completed stem or flowering inflorescence, with correction for the degrees of freedom. Percentages of flower primordia survival (Table 7.5) were analysed after an arcsin transformation. Levels of statistical significance are presented in Table 7.7.

7.3. RESULTS

7.3.1. Plant development (Experiment 1)

Sympodium. All plants of the cvs Atzimba and Van Gogh in Experiment 1 developed a completed main stem, i.e. a main stem with a primary inflorescence (Table 7.1), and continued sympodial growth through development of apical secondary stems. The sympodium of plants of cv. Atzimba

Table 7.1. The number of plants, expressed as a percentage, in the treatments of Experiment 1 that produced a main stem and lateral stems (from node n-1) with an inflorescence in the successive levels of growth, the total number of stems (with inflorescences) of the sympodium (see Figure 1) and the entire shoot.

Cultivar	cv. Atzimba					cv. Van Gogh					$LSD_{(P<0.05)}$
Temperature (°C)	15		25		P^a	15		25		P^a	
Photoperiod	SD	LD	SD	LD		SD	LD	SD	LD		
level of growth											
first level (main stem)	100	100	100	100	-	100	100	100	100	-	
second level (n-1)	100	100	100	100	-	83	100	100	96	0.03	
third level (n-1)	96	100	100	96	0.56	21	71	50	50	<0.01	
fourth level (n-1)	25	83	100	96	<0.01	0	0	8	8	0.24	
fifth level (n-1)	0	0	63	96	<0.01	0	0	0	0	-	
total no.of stems sympodium	3.2	3.8	4.6	4.8		2.1	2.7	2.3	2.2		0.4
total no. of stems entire shoot	14.0	27.0	27.1	33.1		2.6	7.4	3.8	4.1		4.2

[a] Probability of Chi-square; test per cultivar on number of plants (n = 24).

formed more levels of growth than the ones of cv. Van Gogh (Table 7.1). Plants grown at 15 °C ceased leaf production earlier than the ones grown at 25 °C. In cv. Atzimba, this was associated with a sympodium consisting of fewer completed stems than at 25 °C (Table 7.1).

Fifty percent of the plants of the cv. Van Gogh grown at 25 °C developed a 'completed' third level, i.e. tertiary stems with inflorescences. The other 50% continued producing leaves without forming a visible secondary inflorescence, i.e. without completing its development. As a consequence, the sympodium of plants of cv. Van Gogh at 25 °C did not produce more (completed) stems than at 15 °C (Table 7.1).

At 15 °C, plants of both cultivars stopped leaf production earlier with SD than with LD. This resulted in a sympodium of fewer stems with 15 SD than with 15 LD (Table 7.1). At 25 °C, photoperiod did not significantly affect the number of stems of the sympodium at the end of the experiment. At this time, plants in 25 °C LD were still producing new leaves, while those in 25 °C SD had stopped producing leaves, but had not yet completely senesced. Average dry matter production of shoot and tubers was highest in the 15 LD treatments. It approximated 300 g per plant for cv. Atzimba and 190 g per plant for cv. Van Gogh.

Entire shoot. Fewer stems with inflorescences developed from the nodes further down the main stem than from node n-1 (data not presented). Fewer secondary stems with inflorescences developed from nodes n-2 and n-14 than from n-1, but more than from other nodes (data not presented). Shoots of cv. Atzimba were composed of a larger number of stems than the ones of cv. Van Gogh (Table 7.1).

At 25 °C in cv. Atzimba, more stems from the nodes n-2 to n-14 formed an inflorescence than at 15 °C, and at LD more than at SD, especially at 15 °C. These effects are reflected in the significant differences in total number of stems of the entire shoot (Table 7.1). In cv. Van Gogh, lateral stem development was poor, except in the treatment 15 LD, which accounted for the significantly larger number of stems of cv. Van Gogh in that treatment (Table 7.1).

7.3.2. Leaf production (Experiments 1 and 2)

In Experiments 1 and 2, the number of leaves produced per stem generally decreased from the main stem to higher levels of growth (data only presented for first and second level of growth; Table 7.2, Figure 7.2). In Experiment 1, the number of leaves produced by completed secondary stems increased from higher to lower positioned secondary stems (Table 7.2), and approached or even surpassed the number of leaves of the main stem.

At 25 °C in Experiment 1, main stems of the cv. Van Gogh produced more leaves than the ones of cv. Atzimba (Table 7.2). In Experiment 2, the cv. Spunta developed more main stem leaves than cv. Désirée (15.5 vs. 13.5), while secondary stems of cv. Spunta developed fewer leaves than the ones of cv. Désirée (6.2 vs. 8.4).

In Experiments 1 and 2, main stems and secondary stems produced more above-ground leaves before forming an inflorescence at 25 or 27 °C than at 15 °C (Table 7.2, Figure 7.2). The results of Experiment 2 indicate that the effect of temperature was larger in the upper temperature

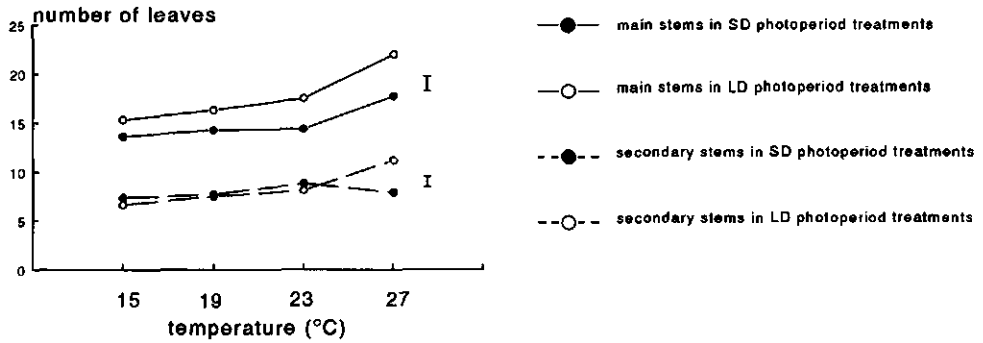

Figure 7.2. The effect of temperature and photoperiod on the number of leaves per main stem and per secondary stem from node n-1, in Experiment 2. Means of two cultivars. Vertical bars indicate the LSD($0.01 < P < 0.05$) for comparison of means of main stems and of secondary stems, respectively.

range. In Experiment 1, the total number of leaves of the sympodium and of the entire shoot were also larger for the plants at 25 °C than for the ones at 15 °C (Table 7.2).

There was no significant effect of photoperiod on the number of leaves of main stems in Experiment 1 (Table 7.2), whereas in Experiment 2 the number of leaves of main stems was significantly larger in the LD treatments (Figure 7.2). In contrast, secondary stems in Experiment 1 developed more leaves with LD than with SD (Table 7.1), while in Experiment 2 only in the treatment with the highest temperature secondary stems produced more leaves with LD (Figure 7.2). In Experiment 1, the effect tended to be larger for basal than for apical secondary stems in cv. Atzimba (Table 7.2).

In the 15 °C treatments of Experiment 1, the total numbers of leaves of the sympodium and of the entire shoot were higher at LD than at SD. In the 25 °C treatments, the photoperiod did not significantly affect the total number of leaves of the sympodium or the entire shoot, in spite of its effect on number of stems of the entire shoot. Other interactions between temperature, photoperiod and cultivars were not consistent. They varied for main stems and secondary stems, and they varied between the two experiments (Table 7.7).

7.3.3. Inflorescence production (Experiment 1)

Number of inflorescence positions. Since the formation of an inflorescence corresponds with the completion of stem development, the data on number of completed stems in Experiment 1 (Table 7.1) correspond with the number of inflorescence positions. Cv. Atzimba produced more inflorescence positions on the sympodium and on the entire shoot than cv. Van Gogh. For cv. Atzimba, total number of inflorescences on the sympodium and on the entire shoot was larger at

Table 7.2. The number of leaves produced by the main stem and completed secondary stems developing from the nodes n-1, n-2 and n-14 on the main stem, and the total number of leaves of the sympodium (see Fig. 7.1) and of the entire shoot in the treatments of Experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				LSD ($P<0.05$)
Temperature (°C)	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
main stem	15.9	16.0	18.5	18.4	15.3	15.5	19.8	20.7	0.7
secondary stem (n-1)	5.9	6.8	7.3	9.2	5.6	6.4	8.1	8.8	0.5
secondary stem (n-2)	8.5	8.7	9.2	11.0	5.2	6.1	9.8	15.0	1.8
secondary stem (n-14)[a]	13.8	16.2	16.2	20.1	-	-	-	-	1.5
total sympodium	31.0	41.8	48.0	48.3	25.5	32.3	54.0	56.5	2.9
total entire shoot	169.0	348.0	392.0	415.1	30.0	104.0	90.0	85.0	51.0

[a] Only data of all four treatments available of cv. Atzimba.

25 °C than at 15 °C (Table 7.1). For cv. Van Gogh, there were significant interactions between the effects of temperature and photoperiod for the number of inflorescences. Increasing temperature with LD significantly reduced the number of inflorescence positions of the entire shoot in cv. Van Gogh. At 15 °C, both cultivars formed more inflorescences on the sympodium with LD than with SD. At the end of the experiment, there was no difference in number of inflorescences on the sympodium between the treatments 25 °C SD and 25 °C LD. In cv. Atzimba, the entire shoot produced more inflorescence positions at 25 °C LD than at 25 °C SD, while in cv. Van Gogh there was no significant effect.

Number of days from planting to flowering. Primary inflorescences of the cv. Atzimba flowered earlier than the ones of cv. Van Gogh. Inflorescences of secondary stems from node n-1 in cv. Atzimba flowered earlier than inflorescences from other secondary stems. The number of days from emergence to flowering of primary and secondary inflorescences in Experiment 1 was smaller at 25 °C than at 15 °C (Table 7.3). Increasing temperature reduced the number of days till flowering more in cv. Atzimba than in cv. Van Gogh. LD significantly delayed flowering of the primary and the secondary inflorescences.

7.3.4. Flower production (Experiments 1 and 2)

Number of flower primordia per inflorescence. In Experiment 2, cv. Spunta formed more flower primordia per inflorescence than cv. Désirée (data not presented). The number of flower primordia per inflorescence increased with temperature up to 23 °C (Figure 7.3). In that temperature range, more flower primordia were produced with LD than with SD (Figure 7.3). In the 27 °C treatments only rudimentary inflorescences were visible and no individual flower primordia could be

Table 7.3. Number of days from planting till flowering of the primary inflorescence and the secondary inflorescences corresponding to the laterals developing from the nodes n-1, n-2 and n-14 on the main stem (see Figure 7.1) in Experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				LSD ($P<0.05$)
Temperature (°C)	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
main stem	45.8	47.8	33.9	35.0	46.8	48.2	37.3	37.4	1.0
secondary stem (n-1)[a]	56.9	61.3	42.5	45.8	-	-	-	-	1.7
secondary stem (n-2)[a]	61.5	66.3	45.0	47.6	-	-	-	-	2.0
secondary stem (n-14)[a]	57.6	59.8	44.8	49.1	-	-	-	-	4.7

[a] Only data of all four treatments available of cv. Atzimba.

distinguished. There were no significant interactions between temperature, photoperiod and cultivars for the effects on number of flower primordia per inflorescence (Table 7.7).

Inflorescence and flower primordia survival. Table 7.4 presents inflorescence survival in Experiment 1. Inflorescence survival of primary inflorescences was better than of secondary ones and inflorescence survival decreased from apical to basal secondary stems. In cv. Atzimba, high temperature significantly reduced inflorescence survival of the basal secondary stems, especially at SD. In cv. Van Gogh at 15 °C more primary and secondary inflorescences survived with LD than with SD.

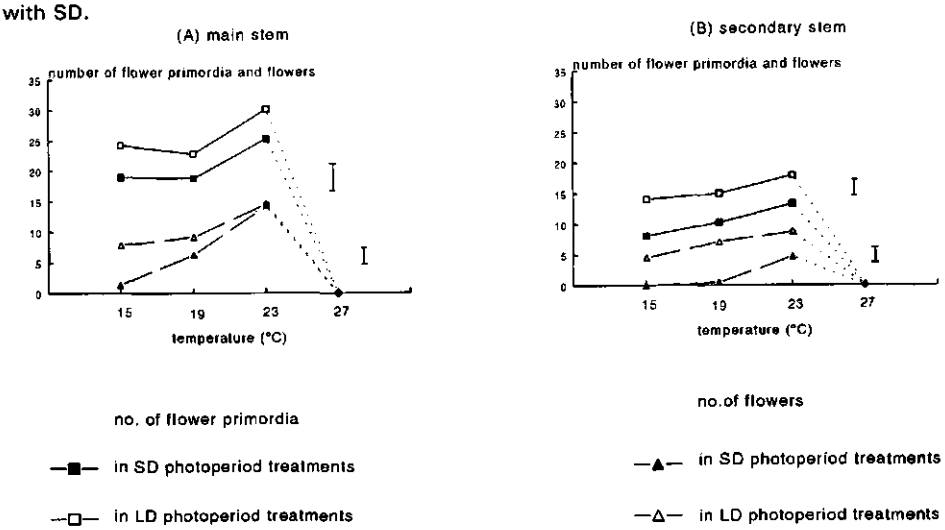

Figure 7.3. The effect of temperature and photoperiod on the number of flower primordia and number of flowers per inflorescences of main stems (A) and of secondary stems from node n-1 (B) in Experiment 2. Means of two cultivars. Vertical bars represent the LSD ($0.01<P<0.05$) for comparison of means of flower primordia and of flowers, respectively.

Table 7.4. Inflorescence survival in Experiment 1, as a percentage of the total number of primary inflorescences formed on the main stem, and on secondary stems developing from the nodes n-1, n-2 and n-14 (see Figure 7.1).

Cultivar	cv. Atzimba					cv. Van Gogh				
Temperature (°C)	15		25		P^b	15		25		P^b
Photoperiod	SD	LD	SD	LD		SD	LD	SD	LD	
main stem	100	100	100	100	-	62	100	75	67	-
secondary stem (n-1)	100	100	100	87	0.03	0	100	0	5	0.01
secondary stem (n-2)	96	100	100	83	<0.01	0	94	0	8	<0.01
secondary stem (n-14)[a]	71	75	23	65	<0.01	-	-	-	-	<0.01

[a] Only data of all four treatments available for cv. Atzimba.
[b] Probability of Chi-square; test per cultivar on number of plants (n = 24).

Table 7.5. The proportion of flower primordia of primary and secondary inflorescences that developed into open flowers (%), in the treatments with cvs Spunta and Désirée (Experiment 2).

	primary inflorescences				secondary inflorescences			
Cultivar	cv. Spunta		cv. Désirée		cv. Spunta		cv. Désirée	
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD
Temperature (°C)								
15	0 (1)[a]	0 (1)	25 (29)	85 (67)	0 (1)	0 (1)	0 (1)	39 (38)
19	2 (4)	8 (10)	71 (58)	91 (75)	3 (5)	18 (20)	7 (10)	74 (62)
23	39 (38)	21 (23)	91 (74)	89 (71)	32 (31)	12 (11)	37 (37)	88 (72)
27	-	-	-	-	-	-	-	-
$LSD_{(P<0.05)}$	(16)				(18)			

[a] Transformed values (arcsin) in parenthesis.

Table 7.6. The number of flowers per inflorescence of the main stem (primary inflorescence) and secondary stems developing from the nodes n-1, n-2 and n-14 on the main stem (see Figure 7.1), and the total number of flowers per plant in Experiment 1.

Cultivar	cv. Atzimba				cv. Van Gogh				LSD ($P<0.05$)
Temperature	15		25		15		25		
Photoperiod	SD	LD	SD	LD	SD	LD	SD	LD	
primary infl	16.0	18.8	27.8	28.4	5.6	26.2	11.8	25.8	2.9
secondary infl (n-1)	11.4	15.6	16.7	18.0	0.0	16.9	0.0	16.0	5.5
secondary infl (n-2)[a]	9.4	13.3	13.3	14.0	-	-	-	-	ns
secondary infl (n-14)[a]	8.5	11.0	6.0	5.3	-	-	-	-	3.9
entire shoot	65.0	184.0	215.0	352.0	3.0	73.0	9.0	16.0	35.0

[a] Only data of all four treatments available of cv. Atzimba.

In Experiment 2, flower primordia survival was higher in cv. Désirée than in cv. Spunta (Table 7.5). LD improved flower primordia survival in the temperature treatments 15 and 19 °C. However, in the 23 °C treatment, LD decreased flower primordia survival of primary and secondary inflorescences of cv. Spunta and increased it significantly in secondary inflorescences of cv. Désirée only. At 27 °C all inflorescences aborted, but the rudimentary inflorescences were smallest and more frequently invisible with LD, suggesting that the development of the flower primordia was arrested earlier with LD than with SD.

Number of flowers per inflorescence and the total number of flowers per plant. Secondary inflorescences developed fewer flowers than primary inflorescences (Table 7.6, Figure 7.3) and in cv. Atzimba, Experiment 1, the number of flowers of secondary inflorescences decreased with the position of the node from which the secondary stem developed.

In Experiment 1, more flowers were produced in the high temperature treatments by primary inflorescences of both cultivars, and by secondary inflorescences of cv. Van Gogh only (Table 7.6). The effect of temperature on the number of flowers of secondary inflorescences in cv. Atzimba varied with the position of the secondary stems on the main stem (Table 7.6). In Experiment 2, primary and secondary inflorescences developed most flowers at 23 °C (Figure 7.3). Inflorescences in the treatments with 15 and 19 °C developed fewer flowers, but the differences were not always significant. In Experiment 2, no open flowers were produced at 27 °C. The total number of flowers per plant (a function of the number of flowers per inflorescence and the number of inflorescences per plant) was higher in Experiment 1 at 25 °C than at 15 °C, only for cv. Van Gogh the difference was not significant (Table 7.6).

Primary inflorescences in Experiment 1 produced more flowers with LD in cv. Van Gogh, but not in cv. Atzimba (Table 7.6). The effect of photoperiod on the number of flowers of secondary inflorescences showed significant interaction with the cultivar and temperature effects (Tables 7.6 and 7.7). In Experiment 2, number of primary flowers was significantly higher with LD

than with SD in the three lower-temperature treatments in cv. Désirée, and significantly lower than SD for cv. Spunta at 23 °C (data not presented), resulting in significant interactions between temperature and cultivar (Table 7.7). Results were similar for secondary inflorescences, however, *significances were somewhat different (Table 7.7). Figure 7.3 with the number of flower primordia* and flowers, only presents means over the two cultivars. The numbers of flowers of the entire shoots were larger with LD than with SD treatments, except for Van Gogh at 25 °C (Table 7.6).

7.4. DISCUSSION

7.4.1. Sympodial development, leaf and inflorescence production

The effects of temperature and photoperiod on sympodial development in Experiment 1 were similar, with some exceptions. In general, the shoot produced more leaves, more (completed) stems and inflorescences with higher temperatures and longer photoperiods (Table 7.1). This was the result of increased branching and delayed cessation of sympodial growth, which agrees with effects reported by others (cf. Ewing & Struik, 1992). One exception was the lack of a clear response to photoperiod in the high temperature treatments, which is explained by the conclusion of the experiment before plants had completely ceased leaf production. The other exception was due to the results of the 25 °C LD treatment for cv. Van Gogh. In this treatment, inflorescence formation was suppressed compared to the treatment 15 °C LD. Leaf production in this treatment was not significantly different from 25 °C SD, principally because branching was suppressed. For the cv. Van Gogh, the 25 °C treatment was apparently supra-optimal for shoot development and LD further enhanced the negative effects of the high temperature.

Increasing temperature also increased the number of leaves of individual stems. Since in the temperature range of the experiments, thermal time for leaf primordia initiation is probably constant or increases with temperature, this means that increasing temperature delayed flower initiation expressed in thermal time (cf. Squire, 1990). The data on number of leaves per stem in Experiment 2 (Figure 7.2) show that the temperature effect was stronger in the range of the higher temperatures. Actually, for secondary stems of cv. Van Gogh in Experiment 1, and for main stems of cvs Spunta and Désirée in Experiment 2, the effect of high temperature on inflorescence formation was even larger than expressed by the presented data. Some of these stems continued leaf production without forming a macroscopically visible inflorescence, but leaf production of those stems was not included in the analysis, since they had not completed their development.

Increasing photoperiod had an effect on leaf production of individual stems similar to temperature, but the effect was less consistent: longer photoperiods significantly increased the number of leaves in some stems and did not affect it in others. The effect of photoperiod on number of leaves was most pronounced and consistent in the high temperature treatments. Together with the strong temperature effects, this resulted in serious delays in the onset of flower initiation in high temperature (>23-27 °C) and long day conditions.

Increased number of leaves and delayed flowering with higher temperature and longer photoperiods have been reported for tomato (Calvert, 1959; Hussey 1963; Kinet, 1977) and many other short-day plants. Jones & Borthwick (1938) also reported a larger number of leaves before

Table 7.7. Level of statistical significance of the main effects of temperature (T), photoperiod (Ph) and cultivar (C), and significance of possible interactions for variables from Experiments 1 and 2.

Experiment 1	T	Ph	Ph x T	C	C x T	C x Ph	C x T x Ph
total number of stems (Table 1)							
- sympodium	**	**	**	**	**	ns	ns
- entire shoot	**	**	*	*	**	*	ns
number of leaves (Table 2)							
- main stem	**	ns	ns	**	**	ns	ns
- secondary stem (n-1)	**	**	ns	ns	**	**	**
- secondary stem (n-2)	*	**	ns	**	ns	**	ns
- secondary stem (n-14)	**	**	ns	-	-	-	-
- sympodium	**	**	ns	**	**	**	**
- entire shoot	**	**	ns	**	**	**	**
number of flowers (Table 6)							
- main stem	**	**	ns	**	**	**	ns
- secondary stem (n-1)	ns	**	**	**	**	*	*
- secondary stem (n-2)	ns	ns	ns	-	-	-	-
- secondary stem (n-14)	**	ns	ns	-	-	-	-
- entire shoot	**	**	ns	**	**	**	**
Experiment 2							
no. leaves (Figure 3)							
- main stem	**	**	ns	**	**	ns	ns
- secondary stem	**	*	**	**	ns	ns	ns
main stem inflorescences (Figure 4A)							
- no. flower primordia	**	**	ns	**	ns	ns	ns
- no. flowers	**	**	*	*	ns	**	*
secondary stem inflorescences (Figure 4B)							
- no. flower primordia	**	**	ns	*	ns	ns	ns
- no. flowers	**	**	ns	**	ns	**	ns
flower primordia survival (transformed data, Table 5)							
- primary inlforescences	**	*	*	**	ns	*	ns
- secondary inflorescences	**	**	*	**	ns	**	ns

** = $P<0.01$; * = $0.01 \leq P<0.05$; ns = not significant, $P \geq 0.05$.

inflorescence initiation with higher temperature in potato. In contrast with the results from our experiments, they found that stems produced significantly more leaves with short daylengths, although differences were small. Also in our experiments, the effect of temperature and photoperiod on the number of leaves of the main stem were relatively small, particularly in the lower temperature ranges. It is therefore not surprising that number of above-ground leaves of the main stem has been considered a conservative characteristic, which varies between cultivars (Krijthe,

1962), but is little affected by growing conditions (Firman et al., 1991; cf. Vos, 1995).

7.4.2. Flower production

Flower primordia initiation. The results of Experiment 2 show that the number of flower primordia and the development of the primordia into opening flowers were enhanced by high temperature and long photoperiods, in the range up to 23 °C, which is in agreement with other reports (Clarke & Lombard, 1942; Werner, 1942; Turner & Ewing, 1988). However, in these earlier reports the significant effects possibly referred to inflorescences which were produced as the only and/or last ones of the sympodium. In these cases, the effects could be attributable to delayed cessation of sympodium development. Delayed cessation may allow the last formed inflorescences to fully complete development, instead of being curtailed during flower primordia initiation or during their subsequent development into open flowers, as compared with earlier cessation of sympodial growth, i.e. in treatments with lower temperature and shorter daylength. However, this cannot explain the effects in our experiments, since at least several fully developed leaves were formed after the primary and secondary inflorescences that were used for data collection. The differences thus indicate that temperature and photoperiod affect the rate of primordia initiation and/or the duration of the period of primordia initiation. Since the different photoperiod treatments in our experiments received approximately the same PAR in a similar number of hours, the responses are true photoperiod effects and not indirect effects via assimilate production.

Flower primordia survival. The positive effect of increasing photoperiod and temperature up to 23 °C on the flower primordia survival in Experiment 2 can be explained by an increased availability of assimilates to the flower buds. Because of increased dry matter partitioning to the shoots with increasing temperature and photoperiod, temperature for optimum shoot dry matter accumulation was higher than the one for maximum dry matter accumulation of the entire plant, especially at SD. This may have been associated with a more favourable assimilate supply to the inflorescences. At 27 °C, assimilate availability for the inflorescences may have been considerably decreased, whereas processes of senescence and abscission (Addicott & Addicott, 1982) or capacity of the primordia to utilise available assimilates (Dinar & Rudich, 1985) may also have affected flower primordia survival. Whereas all flower primordia aborted in the 27 °C treatments in Experiment 2, flower production was still high in the 25 °C treatments of Experiment 1. Although the use of different cultivars and differences in day-night temperature amplitudes do not allow comparison of the two experiments, it is conceivable that the higher night temperatures in Experiment 1 favoured flower primordia realisation, supposedly by enhancing the assimilate level in the shoot (Turner & Ewing, 1988).

Effects of photoperiod on the development of flower primordia into flowers at higher temperature tended to be opposite to effects at lower temperature. This is indicated by the flower primordia survival in Experiment 2: LD improved flower primordia survival in the two lower temperature treatments, but not at 23 °C. Furthermore, at 27 °C the rudiments of aborted inflorescences were smaller and more often macroscopically invisible with LD than with SD. This suggests that daylength extension under high temperature reduces assimilate supply to the

inflorescences. This suggestion is supported by the fact that shoot dry matter weights were lower in 27 °C LD as compared to the ones in 27 °C SD.

However, light intensity in the experiments was relatively low, particularly when taking into account the high temperatures applied in the treatments. It may therefore be assumed that assimilate levels in the plants were lower than what can be expected under field conditions. It is likely that this particularly affected the realisation of flower primordia.

Number of flowers. The effect of photoperiod and temperature on number of flowers per inflorescence is the product of the effects on number of initiated flower primordia and flower primordia survival. Since both latter variables increased with daylength and with temperature up to about 23 °C in Experiment 2, number of flowers per inflorescence showed an optimum at the same temperature. In the supra-optimal temperature range, flower primordia survival seemed to decrease abruptly with increasing temperature. In Experiment 1, there was a general trend of significantly more flowers with increasing temperature and daylength, however, there were many significant interactions, including those with cultivars and inflorescences positions (Table 7.7).

The effects of temperature and photoperiod on number of flowers per inflorescence were relatively small compared to the effects on sympodial growth and associated inflorescence production. As a consequence, the total number of flowers per plant was largely a reflection of the number of inflorescences per plant (Tables 7.1 and 7.2).

7.5. CONCLUSION

The increased leaf production per shoot with higher temperature and longer photoperiod is a resultant of an increased number of leaves of individual stems and of an enhanced branching. In contrast to the effect on the number of stems, the effects of photoperiod and temperature on leaf production of individual stems were moderate to small under conditions in which potatoes are normally grown, i.e. average temperatures lower than 23-27 °C. This means that inflorescence as well as total leaf production were largely determined by the effects on stem production.

Increasing photoperiod and temperature in the range below the optimum both increased the number of initiated flower primordia per inflorescence and flower primordia survival in Experiment 2. Because of the relatively small effect, number of flowers per shoot in this temperature range was mainly a function of the number of inflorescences. The fact that the effect on flower primordia survival was relatively small may be related to the low light intensity under which these plants were grown. At supra-optimal temperatures, the flower primordia survival became the determining factor in the flower production.

These conclusions emphasize that for a better understanding of responses of the total shoot and flower production, it is valuable to disintegrate sympodial shoot development and flower production into individual components and analyse the effects on each of those components.

The time till the onset of flower initiation of the shoot is determined by the response of the main stem, which produces the first inflorescence. While increasing temperature delayed flowering in all individual stems (expressed in number of leaves or thermal time), the effect of photoperiod

was less consistent. Cvs Spunta and Désirée in Experiment 2 behaved as quantitative short-day plants with respect to this response, because the shoot started flower initiation at an earlier stage under SD than under LD. The main stems of the cvs Atzimba and Van Gogh, however, showed a day-neutral reaction. In both Experiments the secondary stems tended to react differently from the main stems. This variation in response between cultivars and between stems indicate that photoperiodic sensitivity of flowering in potato may be influenced by other factors. Possible explanations for these different effects remain speculative.

Apart from delaying inflorescence initiation of individual stems, increasing temperature and photoperiod delay cessation of stem production, as well as tuberization (see Ewing & Struik, 1992). This delayed tuberization and the related delayed shift of assimilate partitioning possibly explain improved flower development with longer days and increasing temperature. Vegetative and generative development in potato is associated with a complex pattern of assimilate distribution between the different sinks in a potato plant. This pattern, the effect of temperature and photoperiod on this pattern, and the possible relations with flowering will be further discussed in chapter 8.

Chapter 8

SHOOT DEVELOPMENT AND FLOWERING

submitted as:

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8 SHOOT DEVELOPMENT AND FLOWERING

Additional keywords: assimilate partitioning, flower primordia survival, flower production, photoperiod, stem production, temperature, time to flower primordia initiation, tuber initiation

Summary

The shoot system of potato is a constellation of individual stems with terminal inflorescences. Shoot development is quantified by the stem production. Stem development is quantified by leaf and flower primordia production per stem, functions of rate and duration of leaf and flower primordia initiation. The effect of the position of the stem in the shoot system on number of leaves and flowers per stem is evaluated.

Flowering of individual stems is described by 'time to flower primordia initiation' (expressed in number of leaves produced) and 'flower production' (function of production and realisation of flower primordia. Increasing temperature and photoperiod increase the number of stems per shoot and number of leaves and flower primordia per stem through prolonging the period of stem production per shoot and primordia production per stem; they affect flower primordia survival by altering assimilate production and partitioning.

The photothermal response of the number of leaves per stem is small compared to the response of stem production; at higher temperatures flower primordia survival becomes the principal factor determining flower production.

The similarity of signals leading to flower primoridia initiation and tuberisation, and the relation between shoot and tuber growth are analysed.

8.1. Introduction

Development of shoots, tubers and sexual reproductive structures of potato (*Solanum tuberosum* L.) is strongly influenced by environmental factors. While tuberization and its response to environmental factors have been extensively investigated (see Gregory, 1965; Ewing & Struik, 1992), the insight into the above-ground shoot development, particularly with respect to flowering, and its relation with whole plant physiology are still underdeveloped. One reason for pursuing this insight is practical: there is an increased interest in sexual reproduction of potato, since the use of true potato seed (TPS) as a basic propagule for seed tuber or ware potato production has become a viable alternative to the use of seed tubers (Umaerus, 1987; Malagamba, 1988; Pallais, 1994). Another reason is more fundamental: a better understanding of the development of different types of orthotropic and diageotropic shoots will contribute to the overall understanding and predictability of responses of the potato plant to environmental variation. The third reason for pursuing insight into development of flower structures is the suggestion that the signals involved in induction and

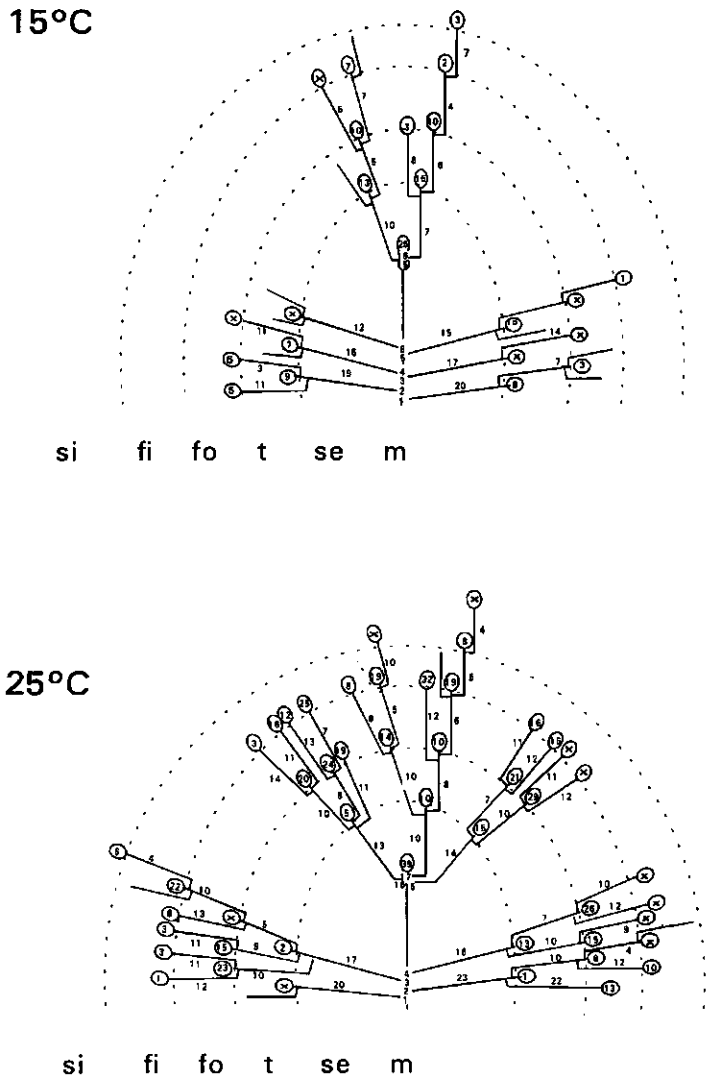


Figure 8.1. Diagram of the shoot system of two plants of Atzimba, grown under 16 h photoperiods at 15 and 25 °C (24-h average). The shoot systems are presented as constellations of stems of first (m = main stem), second (se), third (t), fourth (fo), fifth (fi) and sixth (si) order. The numbers on the main stem indicate the node position from which secondary stems with inflorescences developed. The numbers located near the secondary stems and stems from higher levels of growth indicate the number of leaves produced. The circles represent the inflorescences terminating the individual stems and numbers in the circles indicate the number of flowers of inflorescences. Aborted inflorescences are indicated by a cross within the circle. Data from Almekinders & Struik, 1994.

initiation of flowers are similar to the ones involved in tuberization (Chailakhyan et al., 1981; Martin et al., 1982; Helder, 1993), and that flowers and tubers compete for assimilates (East, 1908; Krantz, 1939; Thijn, 1954; Jessup, 1958; Pallais, 1987). Therefore, it is useful to try and relate initiation and further development of both flowers and tubers and integrate possible relations in a basic concept of potato plant development.

In this paper vegetative and generative shoot development up to flowering are reviewed. After a general qualitative and quantitative description of the shoot development and flowering, (8.2), we will analyse the different components that quantify the development, with special reference to flower production (8.3). The responses of the components to environmental variation, particularly those to temperature and daylength (8.4), and the relation between signals and assimilate partitioning regulating growth and development of the different plant structures are discussed (8.5).

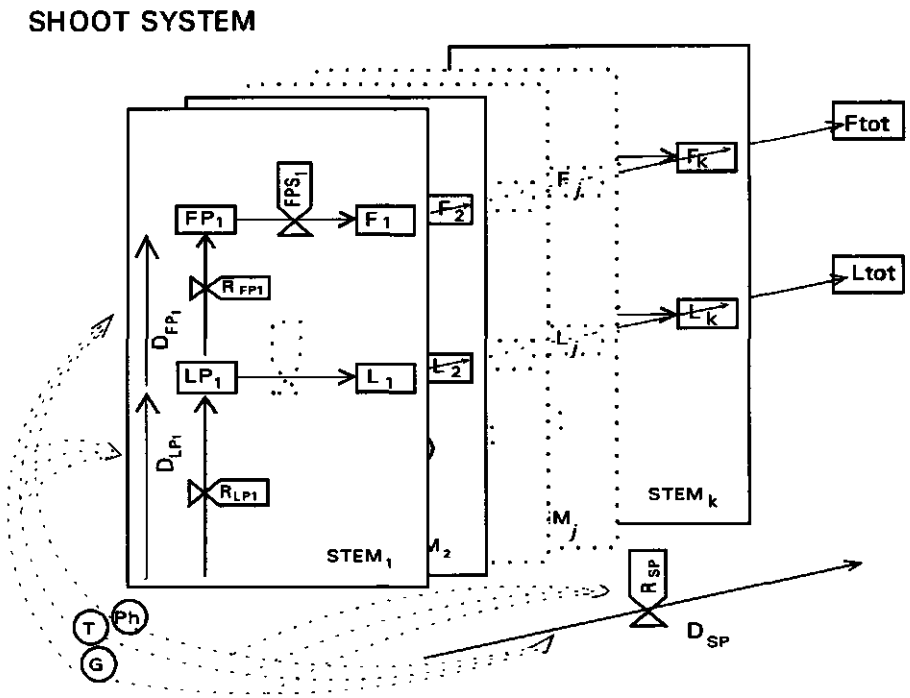
8.2. Description of shoot structure and flowering in potato

8.2.1. Qualitative description of shoot structure and flowering

A potato plant developing from a seed tuber consists of one or more above-ground, leafy shoots. Each shoot is a system of one or more individual stems and has, potentially, an indeterminate growth habit. The growth habit of each individual stem is determinate: it produces leaves and completes its development with the formation of a terminal inflorescence (Danert, 1957; Almekinders & Struik, 1994; Vos, 1995).

An above-ground main stem is the first stem of a shoot system, forming the first level of growth. There are two types of above-ground main stems: true main stems developing directly from the tuber, and the ones developing from below-ground buds on the true main stem. After a main stem completes its development with the production of a 'primary inflorescence', lateral-stem development is enhanced. All above-ground lateral buds on the main stem have the potential to develop into secondary stems. Together, secondary stems form a second level of growth. Secondary stems complete their development with the formation of a terminal inflorescence which is called a 'secondary inflorescence'. Continuation of shoot growth from lateral buds gives rise to third, fourth and following levels of growth, with corresponding inflorescences (see Figure 7.1). The position of a stem in the shoot system is defined by the level of growth of which it forms a part, and the position of the node on the previous stem from which it developed. Usually, stems of higher growth levels produce fewer leaves before initiating an inflorescence than the ones of lower levels (Almekinders & Struik, 1994).

The buds in the axils of the leaves just below the inflorescence usually develop stronger than those in the axils of other leaves, which causes asymmetry in the development of the shoot (Vos, 1995). The central axis of the shoot system consists of the main stem and the stems subsequently developing from the nodes just below the inflorescence, usually from the node *n-1* (*n* being the position of the last formed leaf of a stem). This central axis of the shoot is called a sympodium (Bell, 1991, p. 250; Almekinders & Struik, 1994).



abbreviation	description	units
R_{LP1}, ... R_{LPj},..., R_{LPk}	Rate of leaf primordia initiation of stem 1,... *j*,... k	# number.time^{-1}.degrees Celsius^{-1}
D_{LP1}, ... D_{LPj},..., D_{LPk}	Duration of leaf primorida initiation of stem 1,... *j*,... k	time.degrees Celsius
LP_1, ... LP_j,..., LP_k	Leaf primordia of stem 1,... *j*,..., k	# number
L_1, ... L_j,..., L_k	Leaves of stem 1,...*j*,..., k	# number
R_{FP1}, ... R_{FPj},..., R_{FPk}	Rate of flower primordia initiation of stem 1,... *j*,... k	# number.time^{-1}.degrees Celsius^{-1}
D_{FP1}, ... D_{FPj},..., D_{FPk}	Duration of flower primorida initiation of stem 1,..*j*,..., k	time.degrees Celsius
FP_1, ... FP_j,..., FP_k	Number of flower primordia of stem 1,... *j*,..., k	# number
FPS_1, ... FPS_j,..., FPS_k	Flower primordia survival	# number
F_1, ... F_j,..., F_k	Number of flowers of stem 1,... *j*,..., k	# number
R_{SP}	Rate of stem production	# number.time^{-1}.degree^{-1}
D_{SP}	Duration of stem production	time.degrees Celsius
L_{tot}	Leaves of total shoot system	# number
F_{tot}	Flowers of total shoot system	# number

Figure 8.2. Schematic diagram of a (potato) shoot system, describing leaf, flower and stem production and the influence of temperature (T), photoperiod (Ph) and genotype (G) on the different variables. For further explanation of the diagram, see 8.2.3.

The shape of the shoot system and the total number of stems produced by the shoot are functions of the proportion of nodes developing into lateral stems and the number of growth levels produced. The proportion of nodes that actually develop lateral stems is related to the intensity of apical dominance. Duration of shoot growth determines the levels of growth that are produced. Interactions between environmental factors and genotype influence the proportion of nodes that develop stems and the cessation of shoot growth. Figure 8.1 illustrates the effect of temperature on the shape and the number of stems of the shoot system of plants of cv. Atzimba under LD conditions. Increased duration of shoot development at 25 °C resulted in production of more stems of third, fourth, fifth and sixth level of growth than at 15 °C. At 25 °C more buds on apical and basal parts of the main stem tended to develop into stems than at 15 °C, whereas at 15 °C more buds on the middle part developed.

Stems that formed an inflorescence are defined as completed stems. The number of stems that completed their development determines the number of inflorescence positions produced by the shoot system. Axillary buds that cease growth before realising an inflorescence do not further develop and do not give rise to higher order stems. If shoot growth ceases before the main stem completes its development, then the shoot does not produce any inflorescence position at all.

Potato inflorescences are single or compounded cymes and the number of flowers per inflorescence and per cyme depends on the genotype, the environment and on the position of the inflorescence in the shoot system. The position of the inflorescence corresponds with the above-described definition of stem position. Usualily, inforescences at higher positions produce fewer flowers than the ones at lower positions (Almekinders & Wiersema, 1991; Almekinders & Struik, 1994).

8.2.2. Assimilate partitioning in the plant and flowering

In potato, leaves, flowers and (true) seeds can grow simultaneously above-ground, while at the same time stolons and tubers are being formed below-ground. Total assimilate production and its partitioning determine growth and development of the different structures.

After tuberization, the rate of total (and shoot) dry matter production may still increase for some time, but the assimilate partitioning starts to shift from the shoot to the tubers. While assimilate partitioning to the tubers increases (Van Heemst, 1986), at some point the rate of shoot dry matter production starts to decrease. Finally, when the shift of assimilate partitioning is realised and all assimilates are partitioned to the tubers, shoot growth ceases. This means that assimilate availability in the shoot is becoming increasingly short and that the last formed stems are arrested during leaf or flower primordia initiation, or their realisation.

The rate of realising the complete shift of assimilate partitioning from shoot to tubers varies between cultivars and depends on temperature and photoperiod (Kooman, 1995). Such differences in the rate of the shifting of assimilate partitioning are also likely to influence inflorescence development. Realisation of the complete shift in a short time curtails the assimilate supply in the shoot abruptly. With a slower rate of shifting, the assimilate supply in the shoot probably decreases more gradually.

Assimilate availability strongly influences development of flower primordia into mature flowers (Vince-Prue, 1975; Kinet, 1977; Kinet & Sachs, 1984). The changing patterns of assimilate production and its partitioning between above- and below-ground sinks causes a typical situation *for each inflorescence and each developing flower within an inflorescence*. Although patterns of assimilate production and partitioning have been studied extensively in relation to tuberization (see Ewing & Struik, 1992), little is known about their relation to flower development in potato.

8.2.3. Quantitative description of shoot development and flowering

Shoot development. To describe the above-ground shoot development and its responses quantitatively, the approach of analysis of photothermal flowering responses in legumes (Roberts & Summerfield, 1987) was adapted and elaborated for potato.

In the quantitative description, shoot system development is expressed as a function of leaf, flower and stem production, which is schematically presented in Figure 8.2. The vegetative apex of each stem initiates leaf primordia for some time (D_{LP_j}) until it switches to a reproductive mode and flower primordia initiation (FPI) is started. The reproductive stem apex initiates flower primordia for some time (D_{FP_j}). The numbers of leaf and flower primordia produced by stem j (LP_j and FP_j) are, respectively, a function of the rate and (thermal) duration of leaf primordia initiation (R_{LP_j} and D_{LP_j}), and a function of the rate and (thermal) duration of flower primordia initiation (R_{FP_j} and D_{FP_j}). Durations of leaf and flower primordia initiation can be expressed in time (day) or in thermal time (°C day). Rates of primordia initiation can be expressed per time unit (per day) or per thermal time unit (per °C day).

We call the subsequent development of flower primordia (FP_j) into open flowers (F_j), i.e. flowers in the stage of anthesis, 'realisation'. The success of flower primordia realisation of a particular stem is quantified by the proportion of flower primorida survival (% FPS_j). The number of flowers produced per stem (F_j) is a function of FP_j and % FPS_j.

The number of stems per shoot (k) is considered a function of the rate and (thermal) duration of stem production (R_{SP} and D_{SP}). D_{SP} approximately equals the period of time from emergence to the cessation of shoot growth.

The total number of leaves and flowers of the entire shoot system (L_{tot} and F_{tot}, respectively) are a function of number of stems per shoot (k) and the number of leaves and flowers of the individual stems (L_j and F_j).

Flowering. In this paper, flowering in potato is described by the 'time to the start of flower primordia initiation (FPI)' and 'flower production'. The time taken to the start of flowering (or its reciprocal value 'progress to flowering'; see Roberts & Summerfield, 1987), is important to describe the rate of development of the vegetative phase of a stem. The time to the onset of flowering (opening of the first flower) is commonly used as a practical measure of this phase. However, this also comprises flower primordia realisation, which we do not consider part of the vegetative phase. We therefore use 'time to FPI'.

Because the time to initiation of the first flower primordium (more or less) corresponds with

the duration of leaf primordia initiation (D_{LP_j}), the number of leaves preceding the inflorescence (LP_j) can be used as a (relative) measure for the time to FPI (Vince-Prue, 1975; Roberts & Summerfield, 1987).

Components of flower production. Based on the quantitative description of development of the potato shoot system, the total flower production of a potato shoot system is defined as

$$F_{tot} = \sum_{j=1}^{k} FP_j * FPS_j$$

in which k represents the number of completed stems per shoot system. The total number of flowers per plant is a function of the number of flowers per shoot (F_{tot}) and the number of shoots per plant. The number of shoots per plant is determined by the number of emerging sprouts, growing directly from the tuber (true main stems) and from below-ground buds on a true main stem.

Photothermal responses of flowering. Of the influence of environmental factors on 'time to FPI' and flower production in potato, we will only consider temperature and photoperiod and effects of assimilate supply as influenced by environment and the internal regulatory mechanisms. The effect of temperature and photoperiod on the number of leaf and flower primoridia per individual stem (LP_j and FP_j) is a function of the effects on R_{LP_j} and D_{LP_j}, and on R_{FP_j} and D_{FP_j}.

Generally, R_{LP_j} increases with temperature to a maximum, and a further increase in temperature reduces R_{LP_j} (Hussey, 1963; Thiagarajah & Hunt, 1982; Squire, 1990). Since in the range of suboptimal temperatures usually the thermal time needed for the initiation of a leaf primordium is constant (Squire, 1990), R_{LP_j} expressed per thermal-time unit is independent of temperature. Therefore, expression of 'time to FPI' in LP_j or thermal time measures the rate of vegetative development in this temperature range independent of the temperature effect on R_{LP_j} (Vince-Prue, 1975).

In this same temperature range, R_{FP_j} probably also increases with temperature and is constant when expressed per thermal-time unit. Photoperiod has possibly little effect on R_{LP_j}, as in tomato and wheat (Hurd, 1963; Miglietta, 1992), and is likely to have little effect on R_{FP_j} when photosynthetically active radiation (PAR) or its distribution is not varying around a critical level. In potato genotypes in which flowering is sensitive to photoperiod, photoperiod probably affects D_{LP_j} and D_{FP_j}, as it does in many other species. For example, an effect of photoperiod on D_{FP} has been demonstrated for cereals (Allison & Daynard, 1976; Rahman & Wilson, 1977).

Effects on the 'time to FPI' and on the different components of flower production may interact. For individual stems, a shorter time to FPI may result in a smaller apex at the start of FPI and a smaller leaf area supporting the development of the apex. Such effects may reduce FP_j and FPS_j. For example, Ellis et al. (1992) explained the effect of photoperiod on rate of tassel emergence in maize as the effect of a larger assimilate availability, resulting from a larger number of leaves at the start

of tassel initiation. When assimilate levels in the plant are critical, such effects on the size or the photosynthetic apparatus may also affect D_{FPj} or FPS_j.

An internal feed-back mechanism can regulate flower primordia realisation in potato in relation to assimilate production. An increase of FP_j may be partly off-set by lower FPS_j, as a larger FP_j increases competition for assimilates. A higher rate of flower primordia development at the same rate of assimilate production may also decrease FPS when assimilate levels in the plant are critical.

8.3. Flowering of individual stems

8.3.1. Time to flower primordia initiation

Main stem. Generally, flowering is initiated after the photoperiod has been 'perceived' by the leaves, a stimulus ('florigen') has been produced and transported to the apex (cf. Vince-Prue, 1975). However, in potato plants grown from (sprouted) seed tubers reproductive development may start earlier: FPI has been observed in potato plants grown in complete darkness (Jones & Borthwick, 1938; Clarke & Lombard, 1942; Leopold, 1949), and in sprouts during storage or before emergence (Wiersema, 1944; Krijthe, 1962; Firman et al., 1991; C.J.M. Almekinders, unpubl.). Apparently, fully developed leaves are not an absolute requirement and with artificial or diffuse light during (part of) the storage period sufficient flowering stimulus is produced to initiate flowering. A stimulus from the mother tuber may also be involved in the flower initiation of sprouts.

Firman et al. (1991) showed that in storage 20 to 40 leaf primordia are produced before the start of flower initiation. Sprouts on tubers of cv. Maris Piper even initiated as many as 46 leaf primordia in storage without having started FPI. While the number of leaf primordia preceding the first inflorescence can show large variation, the number of above-ground nodes is noted to be a fairly conservative, albeit genotype-specific character (Krijthe, 1962; Firman et al., 1991; Vos, 1995), although some variation due to the effect of environment has been reported (Jones & Borthwick, 1938; Jefferies & Lawson, 1991; Almekinders & Struik, 1994). In the presence of fully developed leaves and/or normal light, there is apparently little variation in time needed to start reproductive development. When FPI starts before planting, the number of above-ground leaves preceding the first inflorescence is, however, entirely determined by sprout elongation.

Lateral stems. Similar to the main stem, the onset of reproductive development of stems of higher levels of growth can be measured by the number of leaves preceding the inflorescence. This number decreases from lower to higher levels of growth (Almekinders & Struik, 1994). The reason for this decreasing leaf number remains speculative. Possibly, requirements for the apex to become reproductive are fulfilled earlier as the plant becomes physiologically older. However, like in indeterminate-type tomatoes and in contrast with determinate-types (Atherton & Harris 1986), the apex of a potato stem always initiates some leaf primordia before the flowering stimulus arrives and becomes effective. This means that all stems produce vegetative buds which can continue

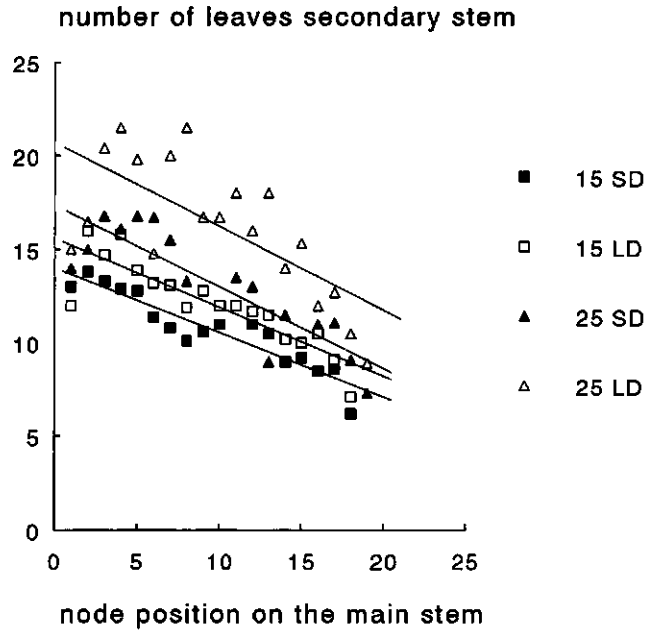


Figure 8.3. The effect of (node) position on the main stem from which secondary stems develop (counting from the ground level upward) on the number of leaves produced up to the secondary inflorescence at two temperature (15 and 25 °C, 24-h average) and two photoperiod (SD = short days, LD = long days) regimes. Data from the cv. Atzimba in an experiment described by Almekinders & Struik (1994).

sympodial growth.

The number of leaves is also influenced by the position of the node from which a lateral stem develops: the number of leaves of secondary stems increases from the highest node position on the main stem downwards (see Figure 8.3), as in tobacco (McDaniel & Hsu, 1976). This position effect on LP_j of secondary stems may be explained by differences in number of leaf primordia initiated by secondary stems on the moment they become 'determined' to flower, like in tobacco (McDaniel et al., 1987). Tertiary stems developing from the highest node on a secondary stem in potato also produce fewer leaves before forming an inflorescence than tertiary stems from lower nodes of the same stem, as is illustrated in Figure 8.1 for shoots of the cv. Atzimba.

8.3.2. Number of flowers per inflorescence

Inflorescences on stems from lower node-positions and on stems of higher levels of growth usually produce fewer flowers (Almekinders & Wiersema, 1991; Almekinders & Struik, 1994). These effects are a function of effects on initiation and on realisation of flower primordia. However,

information on these two effects and their interactions with inflorescence position is scarce.

Almekinders & Struik (1994) reported that secondary inflorescences initiated fewer flower primordia than primary inflorescences. Fewer flower primordia by stems of higher levels of growth is in line with the fewer leaves of those stems. The effect of level of growth on the number of leaf and flower primordia may be associated with increased rates of development as the plant ages or with a smaller apex.

The development of flower primordia into mature flowers is probably dominated by assimilate availability. Since flower primordia are weak sinks, their development is readily arrested by competition from other plant organs. Kinet (1977) showed for tomato that flower primordia are particularly sensitive during the stage of macroscopic appearance of the inflorescence: low light intensity or low rates of dry matter accumulation in this period results in extensive flower bud abortion in tomato.

The availability of assimilates to flower primordia depends on the position of the inflorescence as well as on the position of the flower in the inflorescence. In tomato, development of young inflorescences is affected by the presence of older inflorescences on the plant with fruits and seeds, and adjacent young expanding leaves (Marré & Murneek, 1954; De Zeeuw, 1954; Leopold & Lam, 1960; Hussey, 1963). The situation within the above-ground shoot of potato is probably very similar, although the berries and seeds in potato represent a smaller sink in terms of dry matter weight than in tomato. Furthermore, in potato, there is a change in assimilate production and partitioning in the plant, associated with the development of additional sinks in the form of tubers.

Availability of assimilates probably varies for different inflorescence positions. Assimilate availability is not necessarily largest for flower primordia of the first (primary) inflorescence position, because leaf and lateral stem growth may still be vigorous in that stage of shoot development. Moreover, competition between the flower primordia within a primary inflorescence may be stronger than in other ones because it usually initiates a larger number of flower primordia.

Later-produced inflorescences, on the other hand, develop when tubers as well as developing berries and seeds at lower inflorescence positions are stronger sinks and when photosynthesis decreases. In a final stage, when all assimilates are partitioned to the tubers (Van Heemst, 1986; Kooman, 1995), the development of latest produced inflorescences is likely to be seriously limited by a lack of assimilates in the shoot. This may reduce the number of flower primordia initiated or flower primordia survival, or limit berry and seed development, depending on the stage of development of these inflorescences.

Also the position of the flower (primordium) within the inflorescence affects flower primordia survival. The flower primordium on the last (distal) position in an inflorescence shows a lower flower primordium survival than the ones on more proximal positions (C.J.M. Almekinders, unpubl.). If not aborted before anthesis, the flower primordium on this position develops into a smaller flower, which usually produces fewer and smaller seeds (Almekinders et al., 1995). Because in absolute terms the amount of assimilates involved is small, it is conceivable that the flower-position effect within an inflorescence is largely hormonally regulated and (partly) caused by differences in age of

the primordia.

In potato plants which have more than one above-ground shoot, the number of flowers of an inflorescence also depends on the 'earliness' of the shoot. Later emerging shoots produce inflorescences with fewer flowers, probably as a result of decreased light interception (Almekinders, 1993).

8.4. Responses of flowering in potato

8.4.1. Effect of environment and crop husbandry

The work of Western-European and Northern-American breeders, particularly that in heated glasshouses during winter seasons in the 1940's and 1950's, showed the importance of photoperiod for flowering in potato, but did not produce conclusive information on the photoperiodic response of flowering (see Burton, 1989). A reason for this may be that only few reports clearly distinguish between flower initiation and realisation. Flowering responses in potato are mostly reported as 'more' or 'less successful', 'abundant' or 'improved', without further specification of the effects on the different components determining flower production. When potato plants are not flowering, it is usually not reported whether plants failed to produce inflorescences or whether all flowers had aborted.

Potato plants are reported to flower earlier under SD than under LD conditions, or at the same time (Garner & Allard, 1923;Driver & Hawkes, 1943). This classifies the photoperiod response of *Solanum tuberosum* for the time to flowering as (facultative) short-day and day-neutral (see Roberts & Summerfield, 1987). However, also (facultative) long-day type responses have been reported (cf. Salisbury, 1963).

LD generally improves flower primordia initiation and realisation (Werner, 1942; Bodlaender, 1963; Turner & Ewing, 1988; Burton, 1989; Almekinders, 1992; Almekinders & Struik, 1994), but also reduced flowering under LD conditions has been reported (Lundegårdh, 1966; Sadik, 1983).

Increasing temperature up to 28 °C usually improves flower production under natural light conditions (Marinus & Bodlaender, 1975; see Burton, 1989). Turner & Ewing (1988) found that improved flower production with higher temperature under LD was a result of increased flower primordia initiation as well as reduced flower bud abortion (i.e. improved flower primordia survival). Pronounced effects of temperature and photoperiod on number of flower primordia initiated or realised are however mostly referring to the last and/or only produced inflorescence of a potato shoot.

Information regarding the effect of agronomic practices on flowering responses is vague and scarce. High nutrient levels, especially of potassium, phosphorus and nitrogen (Werner, 1934; Bolle-Jones, 1954; S. Villagarcia, unpubl.) are reported to favour flowering, although at supra-optimal levels vegetative growth may take place at the cost of flowering (Wiersema, 1944). The reports on the influence of moderate levels of water stress on flowering in potato are contradictory (Wiersema, 1944; McIntosh, 1927; Ahmad, 1977, last two both cited by Burton, 1989). High stem density

reduces the number of inflorescences per shoot and the number of flowers per inflorescence (Almekinders & Wiersema, 1991). Practices such as not hilling potato plants, removal of tubers, and 'girdling' of stems improve flowering (Patterson, 1953; McClean & Stevenson, 1952; Thijn, 1954; Mok, 1985; Upadhya et al., 1985), although the success of the treatment is not guaranteed (East, 1908; Abdel-Wahab & Miller, 1963; Sadik, 1983). A positive effect of environmental factors and of agronomic practices on flowering is generally associated with improving assimilate supply to the inflorescences as a result of delayed tuberization or reduced tuber growth.

Based on the quantitative analysis of shoot development described in II.3, flowering responses can be catagorised as responses of individual stems, of an entire shoot system and responses of a whole plant, which can consist of more than one shoot system.

The response of 'time to FPI' of an individual stem is reflected in the number of leaf primordia produced by the stem (LP_j). The response of time to FPI for the shoot system is a function of the response of the main stem, which produces the first inflorescence of the shoot system. The response in flower production of an individual stem is the product of responses of FP_j and FPS_j, whereas the response of the number of flowers of the entire shoot system (F_{tot}) is a function of the total of responses of individual stems for FP_j, FPS_j and of the number of stems per shoot (k).

8.4.2. Individual stems

8.4.2.1. Temperature

Time to flower primordia initiation. Increasing temperature decreases the number of days from emergence to flower primordia initiation (FPI), but increases the number of leaves produced before FPI of main stems and lateral stems (Jones & Borthwick, 1938; Almekinders & Struik, 1994). This effect is also illustrated in Figure 8.3 for secondary stems in the cv. Atzimba. It means that with increasing temperature, flower initiation is delayed in terms of thermal time. This response to temperature seems considerable only at temperatures above 23 °C (24-h average); at lower temperatures the effect of temperature is not significant (Almekinders & Struik, 1994). Also in tomato, flower primordia initiation is delayed by increasing temperature (Dieleman & Heuvelink, 1992). Hussey (1963) attributes this temperature effect to slower enlargement of the apex as a consequence of increased competition with leaf growth.

Flower primordia initiation. Increasing temperature increases FP_j in potato (Turner & Ewing, 1988; Almekinders & Struik, 1994). However, temperature effects on FP_j reported by Almekinders & Struik (1994) were relatively small for individual inflorescences at temperatures below 23 °C, whereas the effect reported by Turner & Ewing (1988) was consistently significant only for the last-produced inflorescence of the sympodial shoot. This indicates that significant temperature effects on FP_j may be often a result of delayed cessation of shoot growth, i.e. increased D_{SP}. Increased temperature could allow the last-initiated inflorescences to complete D_{FP}, whereas with a shorter D_{SP}, the D_{FP} of the last inflorescences may be cut short.

Increasing temperature above the optimum temperature for the R_{FP_j} may reduce FP_j.

Flower primordia survival. Turner & Ewing (1988) and Almekinders & Struik (1994) reported a positive effect of increasing temperature on flower primordia survival (FPS). This effect can be explained by the temperature effect on assimilate production and partitioning. The rate of dry matter accumulation has an optimum temperature in potato at 18-25 °C (Winkler, 1971; Ku et al., 1977; Dwelle et al., 1981; Tibbits et al. 1994). However, because increasing temperature increases the partitioning to the shoot, the temperature for maximum rate of shoot-dry matter production is usually higher (Steward et al., 1981; Wolf et al., 1990; Van Dam et al., 1995; Struik & Ewing, 1995). Temperature also affects assimilate partitioning within the shoot, as is evident from effects on leaf/stem-weight ratios (Steward et al., 1981; Struik et al., 1989; Wolf et al., 1990). In tomato, conditions associated with low assimilate availability in the shoot favour the diversion of assimilates to the vegetative structures at the cost of the reproductive ones (Calvert, 1969; Kinet, 1977; Morris & Newell, 1987). The similarity of potato and tomato suggests that in potato too, partitioning of the assimilates within the shoot may shift away from the inflorescences when assimilates become limiting, such as under high temperature conditions. As a result of the temperature effects on dry matter production and partitioning, assimilate availability for inflorescence development may show a clear maximum at a relatively high optimum temperature. This could explain the good flower primordia survival at temperatures regimes up to 30 °C as a 24-h average (Turner & Ewing, 1988; Almekinders & Struik, 1994).

At supra-optimal temperatures the realisation of flower primordia is not only limited by assimilate availability, but also by the enhanced degeneration and ageing of flower primordia (Addicott & Addicott, 1982) and their reduced capacity to utilize the available assimilates, as is suggested for tomato (Dinar & Rudich, 1985).

An increased FP_j with increasing temperature may reduce FPS as a result of increased competition between flower primordia. Because of this internal regulatory mechanism, the temperature at which the maximum number of flowers is realised may be different from either the temperature at which the maximum number of FP_j is produced or the temperature of maximum FPS_j.

8.4.2.2. Photoperiod

Time to flower primordia initiation. Jones & Borthwick (1938) found that with a photoperiod of 11 hours or more, main stems produced fewer (22.3) leaves up to the inflorescence than with 9 hours (22.8). Contrary to this, Almekinders & Struik (1994) found that in growth chambers under LD conditions, stems produced a similar number or more leaves than under SD conditions, depending on the temperature and the cultivar (see also Figure 8.3). The effect of photoperiod at temperatures below 25 °C (24-h average) was in the order of 1-2 leaves over the entire range of photoperiods of 10 -18 h, whereas the effects were larger at higher temperatures.

Although the number of above-ground leaves per stem varies relatively little, Firman et al. (1991) showed that total number of nodes produced before initiation of the first inflorescence

varied considerably (see 8.3.1). Differences in pre-planting history, possibly including the condition of the mother tuber and genotype interaction, may explain contradicting effects of photoperiod on the number of above-ground leaves of the main stem. For insight into the effect of storage conditions on the flower initiation, more research is needed.

Because of the possibility that the pre-planting history affects the flowering response and that FPI starts before planting, it may be more appropriate to classify the photothermal response of 'time to FPI' on the basis of the response of lateral stems. Data from Almekinders & Struik (1994) showed that the responses of secondary and later formed lateral stems were also of a (facultative) SD or daylength-neutral type, but they could be different from the response of the main stem.

Flower primordia initiation. The reported increase in FP_j under LD (Clarke & Lombard, 1939; Werner, 1942; Turner & Ewing, 1988; Almekinders & Struik, 1994) can be explained as the result of an increased D_{FPj}. Data of Almekinders & Struik (1994) clearly showed that this effect is not only an effect of delayed cessation of shoot growth, which could explain the effect on FP_j of the last produced inflorescence. They found that also earlier initiated inflorescences formed significantly more flower primordia with LD.

Flower primordia survival. Similar to the effect of higher temperatures, increased FPS_j with LD may be explained by the effect of photoperiod on assimilate partitioning (Steward et al., 1981; Wolf et al, 1989; Van Dam et al., 1995). The effect on FPS_j is probably more pronounced for later formed, higher-position inflorescences, which develop when dry matter production and partitioning of assimilates to the shoot decrease.

LD favours the partitioning of assimilates to the shoot, but also affects the partitioning within the shoot (Bodlaender, 1963; Steward et al., 1981; Wolf et al., 1990; W.J.M. Lommen, unpubl.). If the analogy between potato and tomato holds true, as well as the similarity of photoperiod and temperature effects on dry matter partitioning within the shoot, then increasing daylength may favour vegetative over generative growth and reduce assimilate partitioning to the inflorescences. This suggests that when dry matter production is limited (low light intensity or high temperature), increased photoperiod could reduce FPS_j. Data and observations under high temperature support this theory. Van Dam et al. (1995) found that with a PAR < 150 W m^{-2}, at high temperature (24-h average >19 °C), shoot and total dry matter production were lower under LD than under SD. In the same treatments, flower primordia development was apparently more and earlier suppressed with LD (Almekinders & Struik, 1994). However, important genetic variation exists for the interaction between temperature and photoperiod effects on dry matter production and partitioning. As a consequence, temperature and photoperiod for maximum FPS_j may show large variation between genotypes. The range of conditions in which the combination of temperature and photoperiod is optimal for flower primordia survival seems relatively small.

Reported failure of *Solanum tuberosum* ssp. *andigena* to flower under European conditions and scarce flowering of potato in the northern Scandinavian summer (Hawkes, 1943; Lundegårdh, 1966) may well be explained by the above described effects of temperature and photoperiod on assimilate production and partitioning within the shoot.

When flower abortion occurs very early, the rudimentary inflorescence can hardly be distinguished or is invisible, creating the impression that the apex did not become generative at all and continued leaf primordia production. The sympodial branching may in such case be the only macroscopically visible indication that the apex formed a terminal inflorescence.

For the effect of photoperiod on the internal feed-back mechanism between the number of initiated flower primordia and flower primordia survival, a similar reasoning can be followed as for temperature (see 8.4.2.1).

8.4.2.3. Genotype

There appears to be some correlation between 'earliness' of genotype and earliness of flowering of individual stems: early maturing genotypes tend to have fewer stems per shoot, i.e. an earlier cessation of shoot growth. They also tend to have earlier onset of FPI_j (i.e. produce fewer leaves per stem) than late genotypes and to produce fewer flowers per inflorescence. However, there is no indication that the correlation between number of stems, LP_j and FP_j is the result of a feed-back mechanism.

The photothermal responses of 'time to onset of FPI', FP_j and FPS are similar for all cultivars on which information is available: increasing temperature and photoperiod tend to increase all three characters (Turner & Ewing, 1988; Almekinders & Struik, 1994). However, there is large genotypic variation for the magnitude of the various responses and for the interactions of temperature and photoperiod effects. As a consequence, the possibilities to control the number of flowers per stems (as a function of flower primordia initiation and survival) varies between genotypes.

The maximum FP_j is probably genotype dependent and may vary considerably.

8.4.3. Shoot system

8.4.3.1. Flowering responses

The response of the time till flowering of the shoot is determined by the response of the main stem, which is discussed earlier (8.4.2).

The photothermal response of flower production of the entire shoot is a function of the effect on number of completed stems (i.e. inflorescence positions) and the effects on F_j of individual stems.

Higher temperature and longer photoperiod increase the number of stems per shoot by increasing the (thermal) duration of stem production (D_{SP}) and reducing apical dominance. This increases the number of levels of growth and the proportion of nodes forming a completed stem (see Ewing & Struik, 1992; Almekinders & Struik, 1994), and thereby the number of inflorescence positions. These effects are illustrated for temperature in Figure 8.1.

Number of flowers per inflorescence depends on the position of the inflorescence in the

shoot (see 8.2.1, Figure 8.3), but data on the response of flower production at different inflorescence positions in the shoot are scarce. Interactions between inflorescence position, temperature and photoperiod for FP_j and FPS_j are likely since temperature and photoperiod affect the production of inflorescences as well as the pattern of assimilate partitioning. For example, with increasing photoperiod, the onset and the rate of the shift in assimilate partitioning are delayed (Kooman, 1995). Therefore, with increasing photoperiod, the limitation of assimilate availability may increase more gradually, i.e. over a longer period of time. Consequently, more inflorescences develop during a period of decreasing assimilate availability and FPS_j probably shows a more gradual decrease. Because increasing temperature and photoperiod also stimulate leaf and stem production, competition for assimilates within the shoot may increase and FPS_j may decrease with increasing temperature and photoperiod (see also 8.4.2.1 and 8.4.2.2). Similarly, increased nitrogen applications may stimulate leaf and stem growth at the cost of flower primordia realisation, with a possible negative effect on FPS_j. Observations that flowering is improved under (mild) stress conditions probably refer in most cases to improved FPS_j and may be explained by reduced competition from vegetative growth.

8.4.3.2. Genotype

Early maturing cultivars are characterised by early cessation of shoot growth, i.e. a short D_{SP}. They produce few stems per shoot and, consequently, few inflorescence positions. Typically, an early cultivar produces a main stem which ceases growth before, during or after initiating a (primary) inflorescence. Improved flower production of this only inflorescence with increasing temperature and photoperiods can often be explained by an increased D_{SP}, giving the primary inflorescence more time and assimilates to fully develop.

In contrast, late cultivars continue shoot growth for a longer period, thus producing more stems and inflorescence positions. Increasing temperature and photoperiod in late cultivars also increase D_{SP}, which can result in the production of an additional number of higher-position inflorescence positions. The effect of increasing temperature and photoperiod on the primary and other lower-position inflorescences is not always very clear.

There is large genotypic variation for the effects of temperature and photoperiod on stem and inflorescence production, and therefore large variation in the possibilities to control flower production via stem production.

In conditions that allow shoot growth to continue, inflorescence production of the shoot system is theoretically unlimited. However, not all cultivars may know such conditions.

8.5. Reconsidering flowering and tuberization in potato

8.5.1. The signal for flower and tuber initiation, and the time to initiation

There has been much speculation on the relation between the onset of flower primordia and tuber

initiation. Both for flowering and tuberization it is generally assumed that the photoperiod is 'perceived' by phytochromes in the leaves. Upon induction by appropriate daylength, a signal for flowering and tuberization is synthetised (or made transportable) and transported to the stem and stolon apices where it triggers the changes required for flower primordia and tuber initiation (Gregory, 1956; Salisbury, 1963). In many plant species, the hypothetical stimulus for flowering has to 'accumulate' and/or exceed a threshold value to become effective; photoperiod may influence the amount produced or transported. In most genotypes of *S. tuberosum*, SD apparently shortens the time to onset of FPI (see Driver & Hawkes, 1943; Almekinders & Struik, 1994). Normally, SD also results in earlier tuber initiation (Bodlaender, 1963; Ewing & Struik, 1992). Figure 8.4 demonstrates the two responses as found for two cultivars.

Because of the similarity of the mechanisms and responses, it is speculated that signals which trigger flower and tuber initiation are similar (see Ewing, 1885; Helder, 1993). This is further supported by the experimental results from Chailakhyan et al. (1981) and Martin et al. (1982). They showed that *Solanum tuberosum* ssp. *andigena*, which normally does not form tubers under LD, was able to tuberize when a shoot of *Nicotiana sylvestris* L. (which requires LD for flowering) was grafted onto it and exposed to long-days.

The assumption that the signals for flower initiation and tuberization are similar, implies that daylength requirements for the production of a flowering and tuberization stimulus in the leaves are similar. Initiation of flower primordia thus indicates that some of the tuberization signal is produced as well. However, plants that initiate flower primordia do not necessarily tuberize. H. Helder (pers. comm.) observed inflorescence formation in plants of *Solanum demissum* under SD and LD, but plants under LD did not form tubers. Also *Solanum tuberosum* ssp. *andigena* initiates flower

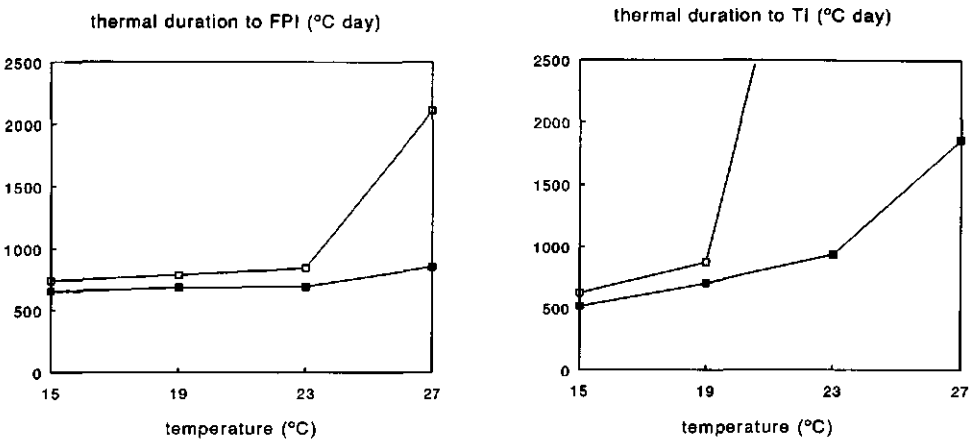


Figure 8.4. Photothermal effect on the time to flower primordia and tuber initiation, expressed in thermal durations (means of cvs Spunta and Désirée). The thermal duration from planting till flower primordia initiation (FPI) was calculated as the temperature sum needed to initiate the total number of above-ground leaves preceding the inflorescence, using as the rate of leaf initiation 0.02 leaves per °C day. Data of leaf production and the thermal time to tuberization were taken from Almekinders & Struik (1994) and from Van Dam et al. (subm.), respectively. Photoperiods: —o— 18 h, —■— 12 h.

primordia, shows abundant stolon formation, but does not tuberize under European-summer conditions (Ewing & Struik, 1992).

These observations support the opinion of Levy & Kedar (1985). They claim that the two events are not related, because tuberization is limited by temperature and photoperiod conditions, whereas flowering occurs under a very wide range of conditions. However, the range of photoperiods under which tuberization takes place is probably much wider than what is generally assumed. Most observations on tuberization refer to a relatively short time-span. When increasing this time-span, Helder (1993) found that cultivars of *Solanum tuberosum* do produce tubers under 24-hour photoperiods. Also Tibbitts et al. (1994) found that plants tuberize under 24-hour photoperiods when light intensity was sufficiently high. The capacity to tuberize under 24-hour photoperiods probably depends on the interaction between light intensity, temperature and genotype.

To the best of our knowledge, FPI always precedes tuber initiation. This does not contradict with the fact that early maturing cultivars may tuberize and mature without reaching the stage of flowering. Early cultivars presumably have initiated flower primordia, but their realisation is probably curtailed by the abrupt cessation of shoot growth.

The observed synchronisation of the macroscopic appearance of flowers (of primary inflorescences) and tuber initiation which is used in keys to describe stages of growth and development in potato (Anonymus, 1987; Griess, 1987; Griess, 1989), also suggests that flower primordia initiation takes place much earlier than tuber initiation. However, the synchronisation of tuberization and anthesis of the first flowers is coincidental. Moreover, increasing temperature and prolonging photoperiod delay tuber initiation much stronger than flower primordia initiation. This increases the time difference between the start of flower primordia initiation and tuber initiation. Since the first inflorescence of a shoot is formed after a rather constant number of leaves, flowering may be more useful as an indication for the rate of leaf production than for tuberization. In both cases, however, abortion of inflorescences in early stages of development limits the usefulness of appearance of flower buds or anthesis as an indication for other physiological events or processes in the plant.

Similarity of flowering and tuberization signals also suggests a possible relation between the development of different types of shoots of the potato plant. However, in contrast wiht the production of inflorescence positions, there is no clear pattern in the position of stolon tips that tuberize, and the time of tuberization varies between individual stolon tips (Svensson, 1962; Helder et al., 1993).

Although flower primordia and tuber initiation are not related in time, this does not exclude the possibility that the events are triggered by a similar signal from the leaves. The asynchrony of flower primordia initiation and tuber initiation may be explained by differences in the transport or distribution of the signal, or differences in the active form of the signals in stolon and stem meristems. Also the sensitivity of stem and stolon meristems for the signal may differ, as flower primordia initiation and tuberization are different events, involving completely different reactions. Moreover, environmental conditions to which the responding plant organs are exposed are different.

Finally, initiation indicates the completion of induction of the meristem, but does not provide information on the moment that the stem and stolon meristems attain the induced stage. The

difficulty to assess flower and tuber induction makes it impossible to prove the similarity of the signals and the possible relation between attaining the stage of induction of stem and stolon meristems.

8.5.2. Competition between flowering and tuberization, and assimilate partitioning

Shoot and tuber growth are generally considered as competing processes in the potato plant. However, the relation between the two sinks is not well understood, while the place of inflorescences as sinks within the shoot has not received much attention.

It is shown that the rate of assimilate production increases with tuber initiation (Bremner & Taha, 1966; Gifford & Moorby, 1967; Moll & Henninger, 1978), an effect that is probably associated with the 'induction' of the plant. After elimination of the tuber sink by pruning of tubers or artificial obstruction of downward transportation of assimilates, photosynthesis decreases (Burt, 1964; Nösberger & Humphries, 1965). This behaviour is typical for a sink-limited plant (Ewing & Struik, 1992) and means that tubers not necessarily (strongly) compete for assimilates with the shoot-sinks, as has been speculated in the past (East, 1908; Krantz, 1939; Thijn, 1954; Jessup, 1958). Cessation of shoot growth may therefore not be a consequence of strong tuber growth.

The theory that shoot growth does not stop as a result of competition for assimilates from the tubers, is supported by the observed cessation of shoot growth in plants or cuttings which are strongly 'induced to tuberize', but in which downward movement of assimilates is obstructed or tuberization inhibited (see Ewing & Struik, 1992). In such conditions even tuber-like structures can develop in inflorescences or above-ground leaf-axils (Marinus, 1987).

Whereas the shift in assimilate partitioning and tuber growth can thus be considered as separately controlled processes, cessation of shoot growth and (completion of the) shift of assimilate partitioning seem to be inevitably linked; cessation of shoot growth without a shift in partitioning of assimilates to storage organs has not been documented so far for stress-free conditions. Since, however, the shift of assimilate partitioning may take place without tuber formation, it may be more appropriate to speak of 'induction to shift assimilate partitioning' instead of 'induction to tuberize'.

The time needed to realize the complete shift may be short or very long (see 8.2.2, 8.4.3). During this period, the shift in the partitioning may apparently be reversed, as is shown by the phenomenon of 'secondary growth' (Ewing & Struik, 1992). A faster rate of shifting the assimilate partitioning could be associated with a stronger induction of the plant.

Although the assimilate partitioning to the different sinks may be controlled by an environmentally regulated (hormonal) mechanism, some direct assimilate competition between the different sinks is apparent. Pruning of flowers and/or berries sometimes increased tuber yields (Proudfoot, 1965; CIP, 1977; Jansky & Thompson, 1991), whereas artificial prevention of assimilate transport to the underground structures may improve flowering, but not necessarily so (see 8.4.1). The improved flowering by girdling, cutting of flowering stems, pruning of tubers and grafting on tomato, seems in many cases the result of delayed cessation of shoot growth. This allows more leaf and flower

primordia to fully develop, but may under certain conditions also result in initiation of more leaf and flower primordia. Obstruction of downwards assimilate transport probably interferes with the (hormonal) control of the assimilate partitioning in the plant. Interaction between assimilate status of the plant and hormonally regulated processes is a well-known phenomenon in flowering (Kinet & Sachs, 1984). Possibly, the assimilate status of the plant only interferes with the hormonal regulation when the plant has not yet realised the complete shift of assimilates partitioning. This could explain why these techniques to improve flowering are not always successful.

8.6. Overview

Flower production. Time to onset of flower primordia initiation and flower production in potato, and their responses to environmental factors can be described quantitatively by considering the shoot as a system composed of individual stems with terminal inflorescences.

Time till flower primordia initiation of each individual stem shows a photothermal response which is reflected in the number of leaves produced by the stem. This response confirms earlier reports that potato is a short-day (SD) or day-neutral (DN) plant for this character. The SD-type reactions are apparently of a 'facultative' nature, as there is no evidence that flower primordia initiation is completely inhibited under long day conditions. The variation in the response of main and lateral stems, and the influence of storage conditions are not fully understood.

The size of the photothermal effects on the different components for total flower production varies. In the range of natural temperature and daylength conditions, photothermal effects on flower primordia initiation seem relatively small compared to those on flower primordia survival. Especially in the higher temperature range ($>25°C$), flower production per stem seems mostly a function of flower primordia survival.

The photothermal effects on flower primordia survival are not very clear. Increasing temperature and photoperiod favours partitioning of assimilates to the shoot, but the resulting assimilate availability for the inflorescences is not independent of changes in partitioning within the shoot and in total dry matter production. Possibilities and relevance of manipulating the number of flowers per inflorescence for improving flower production may therefore be limited.

There is no evidence that the feed-back mechanism between number of flower primordia initiated and flower primordia survival plays an important role in potato. On the contrary, in the range of natural growing conditions, increased flower primordia initiation per stem seems to be often correlated with increased flower primordia survival. Exceeding a 24-h average temperature of 25 °C, however, flower primordia survival sharply reduces and becomes a limiting factor in flower production.

In the same range of natural photothermal conditions (average temperature <25 °C), the effects of temperature and photoperiod on leaf and flower production of individual stems are relatively small compared to the effect on stem and inflorescence production. Since increasing inflorescence production has no negative effect on flower primordia initiation and survival of individual inflorescences, flower production of the potato shoot is most effectively regulated by (photothermal) control of stem production.

Although there are no apparent interactions between duration of leaf primordia initiation, duration of flower primordia initiation and duration of stem production, these phases respond similarly to photoperiod: shorter photoperiods reduce the duration of these three different phases and thus increase rates of development. This suggests that there is a common physiological basis determining the end of the different phases. Short durations of the three phases are also genotypically correlated. In early genotypes this is expressed in early flower primordia initiation, few flower primordia per stem and early cessation of shoot growth, respectively.

From the analysis of flower production in this paper it is concluded that a number of characteristics have to be distinguished to explain flowering responses: time till flower primordia initiation, flower primordia production, realisation of flower primordia of individual inflorescences and inflorescence production. For example, the fact that higher temperature accelerates the start of flower primordia initiation (measured in chronological time), does not necessarily result in earlier flowering because inflorescences may abort. Also, increased inflorescence or flower primordia production per inflorescence does not necessarily result in a higher flower production because of possible effects on flower primordia survival. Not distinguishing between these different characteristics explains the contradictions in literature on flowering behaviour of potato.

Relationships with whole plant development. Flower primordia initiation (of the main stem), tuber initiation, shift of assimilate partitioning and cessation of shoot growth are the events that link above- and underground development of the potato plant. These different events seem to be expressions of an integrated complex of processes which regulate the course of potato plant development. Time to flower primordia initiation (of the main stem), time to tuber initiation and time to the cessation of shoot growth can be considered as the periods determining the scenario of potato plant development. Increasing temperature and photoperiod seems to increase the duration of these phases. However, the magnitude of the response of the durations of these periods varies.

Where the variation in (thermal) time till flower primordia initiation seems relatively small (in the range of 1-3 leaves), tuber initiation is strongly delayed with increasing temperature. This means that (thermal) time to flower initiation is relatively constant, whereas the duration of (thermal) time to tuber initiation varies strongly. Flower primordia initiation probably always precedes tuber initiation. The cases of early cultivars in which shoot growth ceases before the main stem realises an inflorescence do not conflict with this hypothesis: such main stems possibly have initiated an inflorescence, but development of the inflorescence may have been curtailed by the fast completion of the shift of assimilate partitioning to the tubers. However, this hypothesis needs to be proven. Storage periods may also influence the timing of the different events.

In considering whole plant development in potato, the relationship between time to tuber initiation and time to cessation of shoot growth seems more relevant than that between tuber initiation and flower initiation. The link between the first two events is formed by the shift in assimilate partitioning. However, their (physiological and chronological) relationship is still not well understood. The responses of time to tuber initiation and cessation of shoot growth both show strong interactions for temperature, photoperiod and genotype, but they differ to a certain extent.

Possibly, therefore, (physiological and chronical) relationships between above- and underground development vary with photothermal conditions.

Although the relation between qualitative aspects of the generative and vegetative development in potato are still poorly understood, this understanding is of limited importance for the control of flower production. The most important components in the flower production, stem production and flower primordia realisation, are highly dependent on the genotype and the interaction with temperature and photoperiod. The importance of light intensity for these interactions deserves further attention.

Chapter 9

GENERAL DISCUSSION ON PRACTICES, CONDITIONS AND PLANT TYPES FOR TPS PRODUCTION

9 GENERAL DISCUSSION OF PRACTICES, CONDITIONS AND PLANT TYPES FOR TPS PRODUCTION

9.1. Seed production components

Practical seed production practices aim at maximising quantity and quality of seed produced.

This study analysed the quantity of TPS produced, as described by

$$Total\ no.seeds = \sum_{i=1}^{m} (berry\ set * no.\ seeds)_i$$

in which m represents the number of flowers produced. The 100-seed weight was used for comparing differences in seed quality, since this was the only factor that affected the performance (germination, emergence and seedling vigour) of seed harvested from different treatments of a particular genotype within an experiment. Maximising TPS production thereby implies maximising number of flowers, berry set, number of seeds per berry and seed weight.

The flower production component was further analysed and defined as

$$Total\ no.flowers = \sum_{j=1}^{k} (no.\ flower\ primordia * FPS)_j$$

in which k represents the number of inflorescences produced and FPS is the proportion of flower primordia survival in an inflorescence, i.e. the success of a flower primordium to develop into a mature flower. Inflorescence production can be expressed on a per shoot, on a per plant or on a per m^2 basis.

9.2. Inflorescence and flower position

A potato shoot can produce one or more inflorescences over time and each inflorescence can produce one or more flowers (Chapters 2, 3 and 8). The results from the experiments on seed production indicate that inflorescences which are formed higher on a shoot and flowers which are formed at more distal positions within an inflorescence, produce lower quality and quantity of seed (Chapters 2, 3, 4 and 5). The lower quantity was a result of lower berry set and fewer seeds per berry. The lower quality as expressed in a lower 100-seed weight was associated with a decrease in the proportion of large seeds in the total number of seeds per berry.

Berry set and number of seeds per berry decreased 10 to 30% from the first to the last inflorescence on a shoot, and from the first to the last flower in an inflorescence (see Table 9.1). The combination of reductions in berry set and seed set resulted in a reduction of number of seeds produced per pollination by 40% from the first to the last inflorescence in cv. Atzimba (see also Chapter 2).

Differences in 100-seed weight of early- and late-produced inflorescences, and first- and last-produced flowers within inflorescences varied in most cultivars and experiments from 0 to 10%, with the exception of one cultivar in one experiment (Chapter 3). In this particular case, the difference in 100-seed weight was 22%. In the experiments reported, the reductions in 100-seed weight were principally a result of a smaller proportion of large seeds per berry. For example, a 10% reduction of 100-seed weight in the cv. Atzimba was associated with a 15% reduction of the proportion of large seeds. Such reductions in number of seeds per berry and in 100-seed weight meant that the number of large seeds produced per flower was reduced by 40-50%. Combining reductions in berry set, number of seeds per berry and 100-seed weight, the production of large seeds per pollination could fall by 60% (see Table 9.1).

The reduction in 100-seed weight from the first to the last flower within an inforescence was genotype dependent: some genotypes showed no effect of flower position on seed quality (Chapter 3). The influence of environmental conditions on these effects of flower and inflorescence positions and the interaction with genotype needs further study.

Seed production of inflorescences from different shoots showed that differences in

Table 9.1. The relative reduction of individual seed production components and the accumulated effect on the production potential of large seeds per flower in various cultivars as a consequence of differences in inflorescence position, flower position, stem density and production site.

Treatment/cultivar	berry set	seed set	proportion large seeds	production large seeds per flower[a]	100-seed weight
Inflorescence position (Chpt. 2)					
Atzimba (Expt. 1)		0.92			0.97
Atzimba (Expt. 2)	0.69	0.88	0.62	0.38	0.96
CEX-69.1		0.91			0.94
Yungay		0.92			-
Flower position (Chpt. 3)					
Atzimba		0.81			0.88
R-128.6		0.74			0.78
Serrana		0.61			0.97
Shoot density (Chpt. 5)					
Atzimba	1.00	0.94			1.00
Yungay	0.88	0.89			0.97
Renacimiento	0.94	0.87			0.99
Location (San Ramon vs. Huancayo)					
Atzimba	0.65	0.52	0.21	0.07	0.94

[a] calculated as a function of relative berry set, seed set and proportion of large seeds.

inflorescence positions could be interpreted as differences between early- and late-produced inflorescences (Chapter 5). For practical TPS production this implies that later produced flowers (in an inflorescence, on a shoot, on a plant or in a field) are less productive for TPS production.

The possibility to manipulate berry set, number of seeds per berry and 100-seed weight by not using flowers for seed production seems limited. Not using (later-formed) inflorescences on a shoot for seed production significantly improved seed production on earlier formed ones (Chapter 2), and not using later-produced flowers in an inflorescence possibly improves seed production by earlier-produced flowers as well. However, the improvements are so small that they usually do not compensate for the unused production capacity from the later-produced flowers. This means that leaving inflorescences and flowers unused can improve the average production per flower (i.e. increases average berry set, number of seeds per berry and 100-seed weight), but does reduce the quantity of seeds produced. Whereas this reduction is not always significant for the large seeds, it is significant for the medium and small sized seeds (Figures 2.2 and 9.1).

For practical TPS production, the results on seed production from different positions of inflorescences and flowers mean that seed production from later flowers can be considered as an additional production which is increasingly lower in quantity and quality as the flowering period progresses, i.e. pollinations are less efficient when later-produced flowers are used. Which flowers to use for TPS production is thus an economical decision, which depends mainly on the (decrease of the) production capacity of the flowers, costs of production and prices of the (different grades of) seed. These considerations will determine a moment during the flowering period after which further pollinations are not economical anymore.

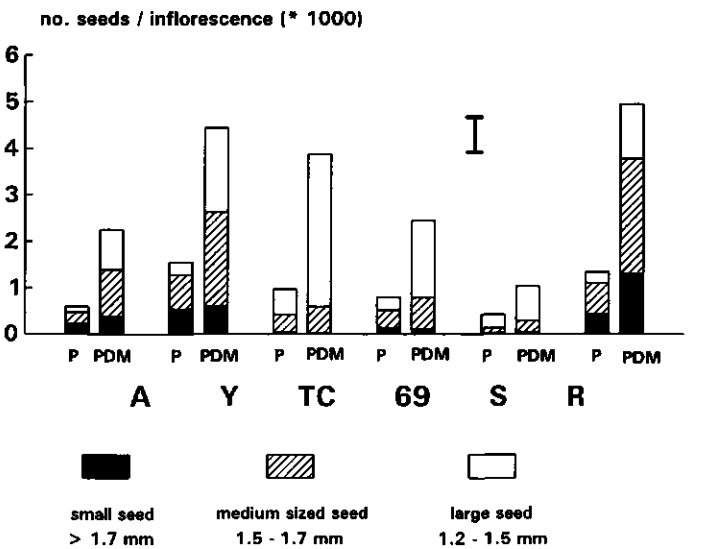


Figure 9.1. The effect of producing seeds from proximal (P) flower positions in inflorescences only, and from proximal, middle and distal flower positions (PDM) on the total production from primary inflorescences in six cultivars. Data from an experiment carried out in Huancayo (1985/86). Bar is LSD($0.01 < P < 0.05$) for comparisons of totals within cultivars (A = Atzimba, Y = Yungay, TC = Tomasa Condemayta, 69 = 69-47.2, S = Serrana, R = Renacimiento). Average of 12 flowers per inflorescence.

9.3. Environmental factors

Studies of environmental effects on flower and seed production components were limited to effects of temperature and photoperiod, the principal factors determining differences in growing conditions between seasons and locations.

Photothermal conditions had strong effects on flower production (Chapters 6, 7 and 8). Increasing temperature and photoperiod at temperatures below approximately 25 °C (24-h average) usually increased each of the components determining flower production per shoot: number of flower primordia per inflorescence, flower primordia survival and number of inflorescences per shoot (Chapters 6, 7 and 8). Effects of increasing temperature and photoperiod on inflorescences and flower primordia production is explained by an increased thermal duration of inflorescence and flower primordia production (Chapter 8). The positive effects of increasing photoperiod and temperature on flower primordia survival in this temperature range can be explained by the effects on assimilate production and partitioning. Increasing temperature and photoperiod increase the assimilate supply to all shoot structures because they delay the shift of assimilate partitioning to the tubers. Increasing temperature and photoperiod may also increase the rate of assimilate production.

The (magnitude) of photothermal effects on the different components determining flower production vary. These effects also strongly interact with genotype and probably with light intensity. However, the effects of temperature and photoperiod on flower production per inflorescence are relatively small in comparison with the effects on inflorescence production. This means that at temperatures below approximately 25 °C (24-h average), flower production is principally a function of inflorescence production. Further increase in temperature increases inflorescence production and possibly also enhances flower primordia production per inflorescence. However, because such increase in temperature sharply decreases flower primordia survival, flower primordia survival is the principal component determining flower production at temperatures above 25 °C (Chapters 7, 8). Increasing photoperiods at supra-optimal temperature possibly has similar effects, but this may be compensated by a higher assimilate production when increased photoperiods are associated with a larger light interception integral. Reduced flower primordia survival with increasing temperatures and photoperiods may be explained by effects on the assimilate production and its partitioning within the shoot (Chapter 8). Increasing temperature and photoperiod possibly favour the partitioning of assimilates to leaves and stems over that to inflorescences. When assimilate production becomes a limiting factor at higher temperatures, this shift in partitioning within the shoot may result in flower bud abortion.

These temperature and photoperiod effects on partitioning between above-ground shoot and below-ground structures, and on the partitioning between vegetative and generative structures within the shoot, imply that an optimum temperature for flower primordia survival is probable; this optimum temperature is likely to be photoperiod and genotype dependent.

Analysis of effects of temperature and photoperiod on berry set, number of seeds per berry and 100-seed weight) was not part of this study. However, since the experiments were carried out in the different locations (at approximately similar latitudes), over various seasons, using similar

production practices and involving the same cultivar(s), the results provided some indications of environmental effects on these seed production components.

Comparison of the results reported in Chapters 2, 3, 4 and 6 shows that berry set, seed set and 100-seed weight were reduced in the warmer location. The pollen production from the male parent was also reduced in quantity, and of lower quality. These reductions appear to become a limitation for TPS production with increasing temperatures before flower primordia survival seriously limits the flower production (Chapter 6).

Within a seed lot from one production field, lower weight or smaller size of seeds usually means a lower potential of germination, emergence and seedling growth. In an exploratory comparison of seed performance, seeds produced in the warm temperature location showed little difference with seed of similar size produced under moderate temperature conditions (C.J.M. Almekinders, unpublished). This suggests that seed production in warmer environments is of lower quality because of the smaller size of the seeds produced.

Although prolonging the photoperiod could have a negative affect on seed production as a result of stimulating vegetative shoot growth at the cost of assimilate supply to flowers and seeds, in the experiments with dim-light extension of the photoperiod (Chapter 6) such effect was not observed. Under natural light conditions such effects are more unlikely as longer photoperiods are usually associated with a larger light interception integral, which could compensate for an effect.

9.4. Crop husbandry

When comparing inflorescences at similar positions on the shoot, increasing stem density reduced the efficiency of pollinations by reducing berry set, seed set and seed size. However, these effects were relatively small for the total seed production (Chapter 4). The effect of stem density on seed production is thereby principally a function of the effect on flower production. In some cultivars, increasing stem density can increase flower production per m^2, whereas in others the increased number of stems per m^2 is off-set by the reduction of flower production per stem. For practical seed production, the advantage of increasing seed production per m^2 by increasing plant density has to be weighed against a reduced production per mother plant.

Applications of high rates of nitrogen fertilizer decreased number of seeds per berry (Chapter 2), but other effects of nitrogen fertilization and effects of pruning of lateral branches on berry set, number of seeds per berry and 100-seed weight were mostly not significant in this study and not of practical importance (Chapters 2 and 4). Pruning of basal secondary stems improved the flower production on the main axis by increasing the inflorescence production. Pruning also increased the number of flowers per inflorescence, probably by improving flower primordia survival. However, the total flower production of the shoot systems was reduced by the pruning. The effects of cultural practices on flower production can be explained by their effect on the (shift in) partitioning of assimilates from the shoot to the tubers. For example, N fertilization may act by delaying the shift in partitioning to the tubers, whereas pruning of lateral stems or tubers probably interferes more directly with assimilate partitioning. However, the potential of crop husbandry practices (fertilization, irrigation, pruning of stems, etc.) to increase flower production seems relatively small

in comparison with the effects of variation in temperature and photoperiod.

In conclusion, the results of the study show that variation in the quantity of seed produced is mostly a function of variation in flower production. Increasing the quantity of seed produced is thus best achieved through an increase of flower production. At temperatures below app. 25 °C (24-h average), there is a positive correlation between number of inflorescences per shoot and number of flowers per inflorescence. However, variation in flower production is mostly a function of variation in number of inflorescences per shoot. Therefore, for regulation of flower production, photothermal control of this component appears most relevant. Since temperature is a rather uncontrollable environmental factor, inflorescence production can be best controlled by prolonging the photoperiod.

9.5. Location

The selection of the production site determines natural photoperiods and to a certain extent the temperature conditions. Within a production site, daylength and temperature conditions vary between seasons, years, and with planting dates within seasons. Locations and growing seasons with moderately high temperatures and long photoperiods are favourable for flower and seed production in potato. Photoperiods may also be artificially extended or nights may be interrupted with light treatments to improve flower production. Cool short-day winter seasons in the tropics are unfavourable for flower production. Genotypes that cease shoot growth early under those conditions may not produce any inflorescence positions with flowers. Warm environments (both with short and long photoperiods) limit TPS production through flower bud abortion and poor seed set.

9.6. Plant type

In the evaluation of genotypes for their suitability as parental material in TPS production, the number of seeds produced per flower, per m^2 and per plant are important factors, as well as the stability of the seed production. Therefore, a good TPS parent is characterised by a large number of flowers produced, a high percentage of berry set and a large number of seeds per berry. For a high flower production, a plant should form inflorescences with a large number of flowers and should have a favourable assimilate partitioning between reproductive and vegetative shoot structures to allow good flower and seed development.

A plant with a high inflorescence production is not necessarily the most favourable type of mother plant for practical, large-scale TPS production. A large number of inflorescences per shoot implies a long flowering and, consequently, a long production season. In long production seasons, maintaining the mother plants and risks of weather, pests and diseases become important factors. An advantage of a long flowering season may be the flexibility and distribution of labour requirements.

To produce large seeds, the ideal type of plant for TPS production may be a plant which

ceases leaf and stem production soon after full expansion of the first inflorescence and which thereafter continues assimilate partitioning to the shoot for some time. This would maintain a high level of assimilates available in the shoot for seed development, without vegetative growth competing for it. Such a situation is artificially created by pruning all basal lateral and apical lateral stem growth after realisation of the primary inflorescence. However, experiments reported in this study did not produce evidence that pruning of basal lateral stems only, favours the quality of seed produced (Chapter 4). Nor is there evidence that continued stem and leaf production as a result of artificial extension of the photoperiod reduces seed size (Chapter 6).

Most important however, a TPS parent should produce a progeny with a high seed viability and vigour, and with a high potential for tuber production. Genotypes of potato wich are well adapted to environmental conditions and the length of the growing season, as expressed in high and early tuber yields, are mostly producing few stems per shoot and, consequently, producing few inflorescence positions. Larger investment in shoot growth and development would reduce the harvest index of tuber production. Particularly early cultivars wich have a short growing season produce few inflorescence positions. For the objective of TPS production, flower production of these genotypes may be increased by increasing temperatures and prolonging photoperiods. This can be achieved by the selection of a suitable production site, i.e. with longer photoperiods and moderately high temperatures, or by artificial extension of the photoperiod. However, considerable photothermal response of inflorescence production probably also implies a considerable response of plant maturity and the harvest index. Such a large response would thus narrow the adaptation of the genotype for tuber production to a smaller range of agro-ecological conditions.

Furthermore, it is important to realise that appropriate seed handling and processing after harvest are a prerequisite for any positive effect on seed quality to be expressed in better performance of the seed.

In conclusion, the most important results of the study for practical TPS production are that the last flowers of an inflorescence and the last inflorescences produced by a plant or in a field have a strongly reduced potential for seed production. Competition for assimilates between flowers and between inflorescences is small and offers little potential for improving seed size. Genotypes which start tuber growth early and have a short growing season, usually produce few inflorescence positions, resulting in low seed production. The quantity of seed produced can be best increased by increasing flower production through longer photoperiods and higher temperatures.

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SUMMARY

I. Introduction

The use of botanical seeds of potato, i.e. True Potato Seeds (TPS), for potato tuber production has several advantages. The most important ones, reduced virus and disease transmission and reduced transport and storage costs, are particularly important for potato production in developing countries. For a technology to successfully grow potato tubers from TPS, the availability of good quality, low cost seed is of paramount importance.

Maximising quantity and quality of seed production requires optimising growth and development of above-ground, sexual reproductive structures, i.e. flowers and seeds. However, since potatoes are conventionally produced from and for the tubers, the knowledge of growth and development of above-ground reproductive structures is limited. The objectives of this study were to define practical methods of large-scale field production of high quality TPS, and to contribute to the understanding of above-ground development in potato.

Field experiments to determine practical methods of TPS production were carried out in three locations in Peru. Additionally, two experiments were carried out in controlled conditions to study the effects of temperature and photoperiod on shoot and flower development in potato.

II. Flowering and botanical seed production in potato

Because a potato shoot can produce various inflorescences, and seeds are formed while the shoot may still be producing new flowers, leaves and stems. For TPS production it was important to know which flowers and inflorescences were most productive and which flowers and inflorescences could best be used for TPS production. The productivity of a flower for seed production was defined by the quantity and quality of seed produced. The quantity was a function of berry set and the number of seeds per berry. The quality was measured by seed weight or seed size.

Analysis of the effect of inflorescence and flower position showed that later-produced inflorescences on a shoot and later-produced flowers within an inflorescence generally had a lower berry set, and produced smaller and fewer seeds per berry. However, the flower position within an inflorescence did not clearly affect seed size in all cultivars. These findings imply that later-produced flowers in a field are less efficient for TPS production.

Not using later-produced flowers for seed production was studied as a practice to increase the size of seeds from earlier-produced flowers. Not using flowers means for most cultivars which are presently used for hybrid-seed production that flowers are not pollinated. Although the 100-seed weight of the production from the first inflorescence was significantly higher when later-produced inflorescences were not used for TPS production, this did not compensate for the reduction in seed yield. The increase in 100-seed weight was associated with an increased proportion of large seeds in the total production, but the total number of large seeds produced per plant was similar or significantly reduced. Not using later-produced flowers within an inflorescence has a similar effect on the seed production per inflorescence.

In two experiments with different plant density treatments, increasing plant density reduced

average flower production per shoot and per inflorescence, and berry and seed production per flower from each inflorescence position. The effect on the total seed production, however, was small because the reduction in seed production was compensated by a shift in production from late- to early-formed fowers; earlier-formed flowers had better berry set and produced more and larger seeds. The effect of stem density on seed production was therefore principally determined by the effect of stem density on flower production. In one cultivar, the reduction of flower production per shoot with increasing plant density was compensated by the increased number of stems per m^2. In the other two cultivars the reduction of flower production per stem with increasing density was smaller, resulting in a higher flower production per m^2.

Late harvest of berries increased berry weight and number of seeds per berry from primary inflorescences. Application of additional nitrogen during the flowering period only significantly decreased the number of seeds per berry. Pruning lateral stems enhanced flower production of the main axis and decreased the total number of flowers per plant, but it did not affect berry or seed production from main-stem flowers.

Artificial increase of the daylength with a 5-hour photoperiod extension or a 3-hour night break increased inflorescence production in warm conditions. The photoperiod treatments significantly increased the number of flowers at the last produced inflorescence positions, but not at other positions. Pollen production and quality, berry set, seed set and 100-seed weight were not affected by the photoperiod treatments. The variation of TPS production over the three experiments was characterized by variation in flower production and low and variable seed production per flower.

III. Shoot development and flowering

A general description of shoot development and flowering in potato is based on results from two experiments in controlled conditions to study the effect of temperature and photoperiod on shoot development, and on a review and analysis of literature. In this description, the potato shoot is considered a system composed of a main stem and a series of lateral stems, each individual stem producing a number of leaves and a terminal inflorescence with one or more flower primordia. Flowering of individual stems is described by the 'time to flower primordia initiation' and 'flower production'. The 'time to flower primordia initiation' is expressed quantitatively in the number of leaves produced per stem. Flower production per stem is defined as a function of the number of flower primoridia initiated and flower primordia survival (i.e. the success of a flower primordium to develop into an open flower).

In two experiments under controlled conditions, with temperature treatments in the range from 15 to 27 °C (24-h average) and photoperiods from 12 (SD) to 18 h (LD), increasing temperatures and photoperiods increased the number of stems, which was associated with an increased number of inflorescences and leaves per shoot. In most treatments, increasing temperature and photoperiod increased the number of leaves and flower primordia of individual stems. These effects are explained as an increase of (thermal) duration of the phases corresponding with leaf primordia, flower primordia and stem production. At temperatures below 25 °C, flower primordia survival was generally favoured by increasing temperature and LD. Effects of temperature

and photoperiod on leaf and flower production was relatively small under these temperature conditions compared to the effect on stem and associated inflorescence production. Total leaf and flower production per shoot were therefore largely determined by the effects on stem production. At higher temperatures, flower primordia survival sharply decreased and became the principal factor determining flower production.

Finally, the similarity of signals leading to flower primoridia initiation and tuberisation is discussed. The relation between shoot and tuber growth is analysed on the basis of changes in assimilate partitioning to shoot and tubers and the responses of this partitioning to photothermal variation and genotype interactions.

IV. Conclusions

The most important results and conclusions from the study are used to discuss TPS production practices, conditions and plant types. It is concluded that the last-produced flowers in an inflorescence and the last-produced inflorescences in a field have a strongly reduced potential for seed production. The competition between inflorescences and between flowers is apparently small and reducing it offers little potential for improving seed size. Genotypes which start tuber growth early and have a short growing season, usually produce few inflorescence positions, resulting in low seed production per plant. The quantity of seed produced can be best increased by increasing flower production, which is best achieved by longer photoperiods and higher temperatures.

SAMENVATTING

I. Inleiding

Botanisch aardapppel zaad, ofwel TPS (True Potato Seed), kan goed worden gebruikt als uitgangsmateriaal voor de teelt van aardappelen in plaats van pootaardappelen. De belangrijkste voordelen van het gebruik van botanisch zaad in vergelijking met pootgoed zijn dat de meeste virussen en ziekten niet overgaan met het zaad en dat transport- en bewaarkosten lager zijn. Deze voordelen zijn met name belangrijk voor de aardappelteelt in ontwikkelingslanden. Voor een succesvolle technologie waarbij aardappelen worden geteeld uit botanisch zaad is de efficiënte produktie van kwalitatief hoogwaardig botanisch zaad een voorwaarde.

Bij de produktie van TPS betekent het maximaliseren van hoeveelheid en kwaliteit van het geproduceerde zaad dat de groei en ontwikkeling van bepaalde bovengrondse delen van de plant, namelijk die van bloemen en zaden, moet worden geoptimaliseerd. Omdat aardappelen in het algemeen worden geteeld uit pootgoed met als doel een hoge knolproduktie, is de kennis over groei en ontwikkeling van bovengrondse voortplantingsorganen van de aardappelplant beperkt.

Het eerste doel van de gepresenteerde studie was het definiëren van praktische methoden voor het produceren van hoge kwaliteit TPS, op grote schaal onder veldomstandigheden. Het tweede doel was bij te dragen aan een verbeterd inzicht in de bovengrondse ontwikkeling van de aardappelplant. Veldproeven welke dienden om praktische produktie methoden te definiëren werden uitgevoerd op drie locaties in Peru, met een vergelijkbare breedtegraad (11-12°C). De produktieomstandigheden verschilden sterk tussen de locaties, alsmede tussen de seizoenen. Aanvullend zijn twee experimenten uitgevoerd onder gecontroleerde omstandigheden in het fytotron van de vakgroep Agronomie van de Landbouwuniversiteit in Wageningen. Deze experimenten hadden tot doel het effect te bestuderen van temperatuur en daglengte op de stengelontwikkeling en de bloei van aardappel.

II. Bloei en productie van botanisch zaad

Een aardappelstengel kan verschillende bloeiwijzen vormen, en elke bloeiwijze bestaat uit één of meer bloemknoppen. Wanneer de bloemknoppen zich ontwikkelen tot open bloemen dan kunnen deze na bestuiving en bevruchting bessen met zaden vormen. Een deel van de bloemen en het zaad ontwikkelt zich aan de plant terwijl de stengel doorgaat met het produceren van nieuwe bloeiwijzen en bladeren. Voor TPS produktie is het belangrijk te weten welke bloeiwijzen en welke bloemen het meest geschikt zijn om te gebruiken. Het wel of niet gebruiken van bloemen betekent bij de meeste cultivars waarvan op dit moment hybride-zaad geproduceerd wordt, dat bloemen wel of niet worden (hand-)bestoven. De geschiktheid van een bloem voor zaadproductie werd bepaald op basis van de kans tot beszetting, de hoeveelheid zaden per bes en zaadgrootte of -gewicht.

Bestudering van de zaadproduktie van bloeiwijzen en bloemen met een verschillende positie op de stengel gaf aan dat later geproduceerde bloeiwijzen op een stengel en later geproduceerde

bloemen in een bloeiwijze een lagere kans tot beszetting hebben, en minder en kleinere zaden produceren. In sommige variëteiten had de positie van de bloem binnen een bloeiwijze echter geen effect op de zaadgrootte. Dit betekent dat later-gevormde bloemen minder produktief zijn voor TPS produktie.

Het niet gebruiken van later gevormde bloemen werd bestudeerd als mogelijkheid om het 100-zaad gewicht, en daarmee de kwaliteit van het geproduceerde zaad te verhogen. Het 100-zaad gewicht van de zaden geproduceerd door de eerste bloeiwijze was significant hoger wanneer later gevormde bloeiwijzen niet werden gebruikt. Echter, dit compenseerde niet de daling van de zaadproduktie. Weliswaar nam het aandeel grote zaden in de totale produktie toe, maar het geproduceerde aantal grote zaden was gelijk of significant lager. Het niet gebruiken van later gevormde bloemen in een bloeiwijze heeft een vergelijkbaar effect op de zaad productie per bloeiwijze.

In twee experimenten verlaagde een toenemende plantdichtheid het aantal bloeiwijzen per stengel, het aantal bloemen per bloeiwijze, de kans tot beszetting, het aantal zaden per bloem en het 100-zaad gewicht van alle bloeiwijze-posities. Het effect op de totale zaadproduktie was echter klein omdat deze reductie in zaadproduktie per bloem gecompenseerd werd door een verschuiving van de produktie van laat- naar vroeg-gevormde bloemen. Vroege bloemen hadden een hoger percentage beszetting, en produceerden meer en grotere zaden. Als gevolg hiervan kan worden gesteld dat het effect van plantdichtheid op de zaadproduktie grotendeels bepaald werd door het effect van plantdichtheid op de bloemproduktie. In één cultivar werd de daling van het aantal bloemen per stengel bij toenemende plantdichtheid gecompenseerd door het groter aantal stengels. Bij de andere twee cultivars was het effect van de plantdichtheid op het aantal bloemen per stengel geringer, hetgeen resulteerde in een toename van het aantal bloemen per m^2 met een toename van de plantdichtheid.

Door het uitstellen van het oogsten van bessen van de eerste bloeiwijze nam het besgewicht en het aantal zaden per bes van die bloeiwijzen toe. Het verhogen van de stikstofgift resulteerde enkel in een significante afname van het aantal zaden per bes. Het verwijderen van zijstengels verbeterde de bloemproductie van de hoofdstengel, maar verlaagde het aantal bloemen per plant. Deze maatregel had geen effect op de bes- en zaadproduktie per bloem op de hoofdas.

Het kunstmatig verlengen van de daglengte met 5 uur en het onderbreken van de nacht met een lichtperiode van 3 uur verhoogden het aantal bloeiwijzen per plant onder gematigd hoge temperatuur. De daglengtebehandelingen gaven een significante verhoging van het aantal bloemen van de laatst-gevormde bloeiwijze op een stengel, maar niet van eerder gevormden. Stuifmeelproduktie en kwaliteit, beszetting, zaadzetting en 100-zaadgewicht werden niet beïnvloed door de daglengtebehandelingen. De verschillen tussen de drie experimenten met daglengtebehandelingen in de warme omgeving werd vooral gekenmerkt door een grote variatie in bloemproduktie en in zaadproduktie per bloem.

III. Stengelontwikkeling en bloei

Een algemene beschrijving van bovengrondse ontwikkeling en bloei in aardappel is gebaseerd op de

gegevens uit de twee proeven onder gecontroleerde omstandigheden waarin het effect van temperatuur en daglengte op de stengel werd bestudeerd, en op analyse van de literatuur. In deze beschrijving wordt de aardappelstengel beschouwd als een systeem dat bestaat uit een hoofdstengel en een serie zijstengels, welke hier verder zullen worden aangeduid met de term 'stengelstukken'. Iedere individueel stengelstuk vormt een aantal bladeren en een terminale bloeiwijze met een aantal bloemprimordia. Bloei van een individueel stengelstuk wordt beschreven door de 'tijd tot aanvang van de bloemprimordia-initiatie' en door de 'bloemproduktie'. De 'tijd tot aanvang van de bloemprimordia-initiatie' komt kwantitatief tot uitdrukking in het aantal bladeren dat per stengelstuk wordt geproduceerd. De bloemproduktie per stengelstuk is gedefinieerd als een functie van het aantal bloemprimordia dat is geïnitieerd en de 'overlevingskans van bloemprimordia' (de kans van een bloemprimordium om te ontwikkelen tot een rijpe bloem).

In de twee experimenten onder gecontroleerde omstandigheden, met temperaturen variërend van 15 tot 27 °C (24-uurs gemiddelde) en daglengtes van 12 tot 18 uur, nam het aantal stengelstukken toe met het toenemen van de temperatuur en van de daglengte. Dit was gerelateerd aan een toename in het aantal bloeiwijzen en bladeren van de gehele stengel. In de meeste behandelingen nam met een toenemende temperatuur en daglengte ook het aantal bladeren en bloemprimordia van individuele stengelstukken toe. Deze effecten kunnen worden verklaard als gevolgen van een langere tijdsduur (gemeten in graaddagen) van de verschillende fasen die overeenkomen met de perioden bladprimordia-, bloemprimordia- en stengelproduktie. Bij temperaturen beneden de 25 °C nam de overlevingskans van bloemprimordia in het algemeen toe met de temperatuur en de daglengte. Bij temperaturen beneden de 25 °C waren de effecten van temperatuur en daglengte op blad- en bloemproduktie van de individuele stengelstukken relatief klein in vergelijking met de effecten op stengelproduktie en de daarmee gerelateerde produktie van bloeiwijzen. Het totaal aantal bladeren en bloemen van de gehele stengel werd daardoor voornamelijk bepaald door de effecten op de produktie van de stengelstukken. Bij verder verhoging van de temperatuur neemt de 'overlevingskans van bloemprimordia' sterk af en wordt dit de voornaamste factor die de bloemproduktie bepaalt.

De overeenkomst tussen de signalen die leiden tot bloei- en knolinitiatie worden besproken. Verder wordt geconcludeerd dat de verandering in de assimilatenverdeling in de aardappelplant het proces is dat het begin van ondergrondse groei en stoppen van de bovengrondse en met elkaar verbindt. Eenzijdige of wederzijdse beïnvloeding door concurrentie om assimilaten lijkt mindere mate de bovengrondse en ondergrondse ontwikkeling te bepalen dan wellicht algemeen wordt aangenomen.

IV. Conclusies

In het laatste hoofdstuk worden de belangrijkste implicaties van de resultaten van de studie voor praktische TPS-produktie besproken. Er kan worden geconcludeerd dat de laatst geproduceerde bloemen in een bloeiwijze en de laatst geproduceerde bloeiwijzen in een plant of in een veld een sterk gereduceerd vermogen tot zaadproduktie hebben. De concurrentie tussen bloeiwijzen en tussen bloemen in een bloeiwijze is blijkbaar klein en geeft ook weinig mogelijkheden om tot produktie van grotere zaden te komen. Genotypen die vroeg tot knolzetting overgaan en die vroeg afrijpen produceren in het algemeen weinig bloeiwijzen, hetgeen resulteert in een lage bloem- en

zaadproductie per plant. De produktie van zaad kan het best worden verhoogd door (kunstmatige) verlenging van de daglengte en hogere temperaturen. Dit betekent ook dat TPS-produktie het best kan plaatsvinden in gebieden en seizoenen met een gematigd hoge temperatuur en een lange dag.

CURRICULUM VITAE

Cornelia Janny Maatje (Conny) Almekinders was born on 13 December 1955 in Vlissingen, The Netherlands. After obtaining the Atheneum-B diploma at the Gemeentelijk Lyceum Dordrecht, she started her studies at the Wageningen Agricultural University in 1974. In 1983 she graduated with specializations in Field Crops from Temperate Climates, Plant Nutrition and Soil Fertility, Farm Management, and Development Economics. From 1983 till 1989, she was stationed as a DGIS associated scientist for the Centro Internacional de la Papa in Huancayo and San Ramon, Peru. The research carried out during these years forms the basis of this thesis. From 1990 till 1993, she worked for the IVO (Development Research Institute) in Tilburg and Central-America. In 1993 the author spent 5 months in Peru at CIP and as consultant. Since her return from Peru in 1989, she was affiliated to the Department of Agronomy, to carry out additional research on flowering in potato, prepare a thesis and publications on TPS and other topics.