INFLUENCE OF TEMPERATURE ON BUD BREAK, SHOOT GROWTH, FLOWER BUD ATROPHY AND WINTER PRODUCTION OF GLASSHOUSE ROSES

Promotor: dr.ir. J. Doorenbos, emeritus hoogleraar in de tuinbouwplantenteelt.

G.A. van den Berg

INFLUENCE OF TEMPERATURE ON BUD BREAK, SHOOT GROWTH, FLOWER BUD ATROPHY AND WINTER PRODUCTION OF GLASSHOUSE ROSES

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
in het openbaar te verdedigen
op woensdag 4 maart 1987
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen.

Aan mijn ouders

STELLINGEN

1.
De etmaaltemperatuur dient betrokken te worden bij de regeling van het kasklimaat (dit proefschrift).

2.
De temperatuursverdeling tussen dag en nacht beinvloedt de produktkwaliteit (dit proefschrift).

3.
Een hogere nacht- dan dagtemperatuur stimuleert de bloemknop-vorming (dit proefschrift).

4.
Het trage uitlopen van okselknoppen is naast de vorming van loze scheuten, onder gegeven lichtomstandigheden, de grootste belemmering voor de winterproduktie van kasrozen in Nederland (dit proefschrift).

5.
Het inbrengen van daglengtegevoeligheid in de roos zou de teelt-planning en de arbeidsproduktiviteit aanzienlijk verbeteren.

6.
De substraattemperatuur dient bij de kasklimaatregeling te worden betrokken.

7.
De teelt in kunstsubstraten is een fase tussen de teelt in de kasgrond en de teelt in voedingsfilm.

8.
Substraatteelt leidt via standaardisering en automatisering tot teeltvereenvoudiging.

9.
Bij de fytosanitaire eisen m.b.t. de export dient de eis „ vrij van schadelijke organismen" vervangen te worden door de eis „ vrij van reproductieve schadelijke organismen".

10.
De z.g. "nultolerantie" leidt tot milieu-onvriendelijke produktiemethoden.

11.
Ter verhoging van de effectiviteit van de toepassing van gewas-beschermingsmiddelen in de kasteelt dient de relatie tussen microklimaat en aktiviteit c.q. mobiliteit van het plaagorganisme te worden bestudeerd.

12.
Het opzetten en aktualiseren van een voor de teler, via een eigen terminal, direkt toegankelijke databank met teeltinformatie dient een belangrijk produkt te zijn van een moderne voorlichtingsdienst.

13.
Hoewel individueel bedrijfsbezoek geen overheidstaak is, is individueel bedrijfsbezoek noodzakelijk voor een overheidsvoorlichter om goed te kunnen funktioneren.

14.
Voor het goed funktioneren van een Proefstation is evenwicht tussen fundamenteel gerichte en praktijk gerichte onderzoekers noodzakelijk.

15.
Stellingen zijn vaak net als degenen die ze maken, er zit van alles tussen.

G.A. van den Berg
Influence of temperature on bud break, shoot growth, flowerbud atrophy and winter production of glasshouse roses
Wageningen, 4 maart 1987.

VOORWOORD

Bij het verschijnen van dit proefschrift wil ik allen bedanken die aan het tot stand komen ervan hebben bijgedragen.
Allereerst wil ik mijn ouders noemen, mijn broer en beide zusters, omdat zij met elkaar het mij hebben mogelijk gemaakt aan de Landbouwhogeschool te studeren.

Prof.dr.ir. J. Doorenbos ben ik dankbaar voor zijn bereidheid om als promotor op te treden. Zijn belangstelling in mijn onderzoek, zijn suggesties als ook het beschikbaar stellen van het Fytotron van het Laboratorium voor Tuinbouwplantenteelt te Wageningen, hebben het verloop van het onderzoek duidelijk positief beinvloed. Wat de proeven in het Fytotron betreft ben ik veel dank verschuldigd aan de medewerkers van Tuinbouwplantenteelt voor de verzorging van mijn proeven. In het bijzonder geldt dit Karel Steensma.

Het bestuur en de directie van het Proefstation voor de Bloemisterij in Nederland ben ik erkentelijk voor de vrijheid en tijd die mij gegeven zijn voor het schrijven van het proefschrift.

Mijn dank geldt ook de vele medewerkers van het Proefstation die mij geassisteerd hebben met het verzorgen van de proeven en het doen van de zeer vele waarnemingen. In het bijzonder geldt dit mijn oud assistenten Jos Valentin en Ria van Schoonhoven. De heren Theo de Haas, Wim van Marsbergen en Jacques Stammes dank ik voor hun waardevolle adviezen en hulp.

De dames Lidy Leffring en Adrie Verlind wil ik hier graag bedanken voor hun inbreng bij de bespreking van de proefresultaten en voor wat de laatste betreft ook voor haar ondersteuning bij het verwerken van de gegevens en de statistiek.

Annette Leighton-van Leeuwen dank ik voor haar hulp bij het engels en Wim van de Maat van de Technisch Fysische Dienst voor de Landbouw voor het tekenen van de vele grafieken met behulp van de computer. Mariet de Geus dank ik voor de fraaie omslagtekening.

In dankbare herinnering wil ik twee personen noemen die door hun vroegtijdig overlijden de voltooing van dit proefschrift niet mochten beleven, namelijk Prof.dr.ir. J.F. Bierhuizen die als co-promotor zou optreden en ir. P.J.J. Jakobs, die mij op enthausiaste wijze inwijdde in de mogelijkheden van de Exploratory Date Analysis.

Mijn vrouw Onny wil ik bedanken voor haar steun in de periode waarin dit proefschrift geschreven is.

Tot slot wil ik belijden: "Soli Deo Gloria".

CONTENTS

1. INTRODUCTION AND OBJECTIVES

The glasshouse cut rose (Rosa hybrida) is the most important cut flower of the Dutch floricultural industry. In 1985 the total auction turnover was 483 million Dutch Guilders. The total glasshouse area planted with roses was 758 ha, spread over about 1000 nurseries (VBN 1985). According to the auction turnover the 5 most important cultivars were: Motrea, Sweet Promise, Ruimeva, Merko and Varlon. In the Netherlands roses are commonly grown on root stock of Rosa canina selections and planted in glasshouse soil with a plant density of 6-9 shrubs per gross meter glasshouse soil surface. In 1976 experiments to grow roses on own roots in a thin layer of rockwool were started at the the experimental station in Aalsmeer (Van den Berg 1978). Since then this method has been spreading gradually in commercial rose growing. At the start of 1986 about 20 ha of roses were grown in rockwool, for the greater part on their own roots. The switch from soil to rockwool is encouraged by the prevalence of soil diseases. The use of movable benches has opened up the possibility of increasing the net productive soil surface, automatically reducing fuel costs per rose (Van den Berg 1984). The use of thin layers of an artificial substrate enable more possibilities for control of the root environment, and attracts more and more attention.

In the Netherlands cut roses are commonly produced all year round. If a cultivar is not adapted to this way of cultivation and produces flowers of a bad quality or too many flowerless ('blind') shoots in winter, the canopy is given a rest period of 4-6 weeks in December and January at 2-5^{o}C.

The glasshouses are commonly heated by warm water via steel pipes with a diameter of 51 mm. Nowadays pipes with a smaller diameter made of steel or finned alluminium are also installed. Thin pipes have a lower water content which make them more suitable for climate control. The reaction time is much shorter than with thicker pipes with a larger water content and offer a more stable temperature in the glasshouses, with less over and under shoot.

Two thirds or more of the pipes are installed at or about 20 cm above soil level inside or alongside the beds. The rest of the pipes belong to a separate heating system and are situated above the crop. Soil heating is not usual for soil grown roses. For roses grown in rockwool, heating of the substrate is given more and more attention. This is due to the good results obtained in commercial glasshouses with substrate heating during last winter (Breuering 1986).
Moveable thermal screens for the purpose of energy conservation are widely used in rose growing. For the same purpose tens of hectares of new glasshouses have been built with a double glass or acrylic cover. The average energy use for Dutch glasshouse roses per gross m^2 is 40-45 m^3 natural gas.
The glasshouse climate in modern glasshouses is controlled mainly by digital process computers. The introduction of the climate computer has widened the possibilities for climate control. Controlling on a basis of the mean daily temperature or on temperature sums has become a possibility.
In mid-winter the low light intensities reduce production. Supplementary lighting to overcome this problem is not widely used in Dutch rose growing. The high cost of electricity make supplementary lighting hardly profitable. The use of total energy systems in combination with artificial substrates on movable benches might change this situation. The very high production of more than 400 blooms per m^2 gross soil surface (Van den Berg 1984) may make supplementary lighting profitable.

Glasshouse air temperature is a climate factor that can be relatively easily controlled by the grower. This factor has a direct influence on the development time of the rose and indirectly affects the amount of light a rose shoot receives during its growth.

The object of the research covered by this thesis was to study the influence of temperature on production, quality and flower bud atrophy of cut roses during winter in Dutch glasshouses and to make this influence visible in graphs or simple 'models' which can be used

for planning and decision making in rose growing.
Special attention was paid to the influence of the distribution of temperature between day and night on production and quality.
Thermal screens are usually closed at night; this means that heating in the night needs less energy than heating in the daytime when the screens are open. This makes it possible to save energy without further investments.
The cultivars 'Sweet Promise' and 'Varlon' were chosen because these are widely used by the Duch growers. At the moment the research was started in 1976, these cultivars belonged to the leading ones and were expected to remain so for many years. These cultivars as required for the research can be produced all year round, and do not need a rest period during winter.
In this thesis each result chapter ends with a discussion, which gives some advice for commercial rose growing. At the end of all result chapters a final discussion is given.

2. MATERIALS, METHODS AND CONDITIONS

2.1. GENERAL

In this chapter the different growth facilities, the plant materials and the climate conditions of the experiments are described. In the experiments different rose cultivars were used. The main cultivars however were Sweet promise (Sonia^{R}) and Varlon (Ilona^{R}). In some experiments also the cultivars Merko (Mercedes^{R}) and Motrea^{R} were used and in one experiment, dealing with the sprouting of the lateral buds, also the cultivars: Ruimeva (Madelon^{R}), Tanatesil (Ilseta^{R}), Jelparaco (Carte Rose^{R}), Korenlo (Lorena^{R}) and Jeldanira (Mimi Rose^{R}). The experiments can be dividid into three groups:

(1) Roses on rootstock in glasshouse soil under natural light conditions.
(2) Roses on their own roots grown in containers filled with potting compost in the glasshouse under natural light conditions.
(3) Roses on their own roots grown in containers filled with potting compost in growth rooms under artificial climate conditions.

2.2. EXPERIMENTS WITH SOIL GROWN ROSES IN THE GLASSHOUSE

These experiments are coded by: **GSnr** (**G**lasshouse **S**oil).
For these experiments which formed the bulk of the research, the cvs. Sweet Promise and Varlon on the rootstock Rosa canina 'Inermis' were used. The rootstock 'Inermis' (Leemans and Laar 1977, Krussmann 1986) is widely used in the Netherlands. The experiments lasted 6 continuous winter seasons.
The roses were grown in glasshouse compartments of 12.0 by 9.6

meters. These were part of a newly built glasshouse with 30 compartments. The glasshouse climate was computer controlled by means of a Siemens 300-330 minicomputer system. This computer was also used for data logging and data processing.

During the first three years of the research 9 compartments were in use for the experiments and during the last three years 4 compartments. In each compartment 6 beds with three rows of grafts were planted in February 1977. The planting distance of the beds was: 30 cm in the rows and 35 cm between the rows. This resulted in a planting density of 6.4 plants per gross square meter glasshouse soil surface.

From the 6 beds only the center parts of the 4 middle beds, each part with a length of 6 meters, were used in the experiments. The two side beds and the front and back part of the middle beds had a fringe function and fell outside the experiments. The 4 middle beds were alternately planted with roses of the cv. Sweet Promise and Varlon. Thus in total there were 4 plots per compartment, two planted with 'Sweet Promise' and two with 'Varlon'. The center of a plot was not automatically the center of the glasshouse compartment.

A Chrysanthemum crop preceded the rose experiments. With this crop the most effective situation for the plots had been determined in such a way that the growth conditions of the plots in the nine compartments were as equal as possible.

Each of the 4 plots per compartment held 63 shrubs (3*21). From these plots the roses were harvested 3-6 times a week depending on the weather. During all the experiments the roses were cut upward above the first five-leaflet leaf. The 'blind' shoots however were cut downward beneath the stem joint on a thicker stem to reduce the chance that the shoot of the next growth cycle would grow blind too. Of the cut roses, number, average length and fresh weight were measured.

At the start of the experiments, from the 36 shrubs that formed the center of a plot, one shoot per shrub was selected for uniformity and labeled. These labeled shoots and their daughter shoots were

monitored on a weekly basis during the whole experiment. During harvest the roses produced by these labeled shoots were segregated from the rest and measured individually. These measurements involved length, fresh weight, diameter of the stem at the cut and at the center of the neck, diameter of the ovary, fresh weight of the flower bud, the number of internodes and leaves. For some years length and width of the flower bud and length of the neck were also measured.

In each compartment, in the centre of the four experimental plots, an isolated and ventilated psychometer box was placed containing a dry and a wet bulb temperature sensor (Pt 100). The sampling time was 1 minute. From these data the computer calculated the mean 24 hours temperature (from 00.00 hr-24.00 hrs), the mean daily irradiance and the relative air humidity. The irradiance was measured per compartment at shoot top level by means of a solarimeter (Kipp & Son), sensitive to radiation between 300-3000 nano meter. The sensors for radiation and temperature were calibrated before and during the experiments. The experiments started in the first or the second week of October and lasted until the first day of May the next year.

From the first of May until the start of the next experiment in the autumn, the treatments in all compartments were the same and aimed at banishing any variation between the compartments.

Out of the more than 90 rose cultivars sold at the Dutch auctions the cvs. Sweet Promise and Varlon were chosen for the experiments for the following reasons:

- From experience in practice one could suppose that both cultivars show a difference in sensitivity to temperature. 'Sweet Promise' is grown at a lower temperature level than 'Varlon'.
- The cultivars are usually kept in production during winter and do not need a rest period.
- The cultivars belong to the most important cut roses produced in the Netherlands and are well known by all Dutch rose growers.

The glasshouse compartments were heated by warm water via two pipe

heating systems. One low laying system, a string of poly-ethelene tubes with a cross-section of 17mm and restricted at 50°C, running over the beds at a height of 15 cm. The other system made of steel pipes with a cross-section of 51 mm and restricted at 95°C, running over the canopy at a height of 240cm above soil level. If heating was necessary the lower heating system was used first. If this system had reached its installed maximum temperature of 50°C and the air temperature was still below the setpoint, the upper heating system was also used.

Irrigation of the crop was performed by a permanent line of low pressure sprinklers set at soil level in the middle of each bed, as is commonly used for rose growing in Dutch glasshouses. Adding fertilisers was applied according to the standard scheme used at the Experimental Station. The same can be said for pest and disease control.

One of the problems encountered when starting the experiments with roses in the glasshouse soil was that it takes half a year from planting in February until a shrub of reasonable size has developped which is suitable for experiments. If an experiment stops in May, it is too late to replant in order to have a well developed shrub in October when the next experiment starts. The only way to avoid the situation that only one experiment per two years was possible in the same glasshouse, was to use the summer period to bring the shrubs in the different compartments back to the same conditions. This was done by pruning back to thick wood, that had been formed the year before in the same period under the same conditions. Of course this did not mean that this wood was physiologically totally identical in all plants, but it was the only way to deal with the problem.

The summer cultural practices and those in preparation for the next experiment were similar for all years and for all compartments.

After pruning, the temperature was kept at a moderate level; heating at 16°C and ventilating at 18°C for 5 months in all compartments. The first grown flush following pruning was left for flowering and cut downward afterwards to three, five-leaflet leaves. The next flush was

soft topped on three five-leaflet leaves above the joint. At the start of the new experiments in October all compartments were 'on flush'. Most of the differences caused by experiments in the previous season had disappeared. For the remaining differences, correction factors concerning quantity and fresh weight, were calculated for each compartment.

One can never be certain that these correction factors are one hundred percent accurate however. A small deviation remains a possibility. On logical grounds however, one may expect that if making corrections based on the differences present at the start of the experiments is omitted, an even bigger mistake is made when interpretating the results.

During the experimental periods from October until May the daily average relative humidity was in the range: 70-90%. The daylength was the natural daylength of the latitude at which the Experimental Station is located: 52°15' northern hemisphere. The main conditions of the experiments are given in underlying section. Where necessary extra information is given in the results section.

GS1:From 1 October 1977 until 1 May 1978

In use were 8 compartments in which 4 temperature treatments were performed, each in 2 replications. Cultivars: Sweet Promise and Varlon.

Imposed treatments; setpoints for heating :

1. night 12°C, day 20-22°C
2. " 15°C, " "
3. " 18°C, " "
4. " 21°C, " "

Set points for day and night both 12 hours per 24 hours. The setpoint for night started at sunset. The setpoint for ventilation was 1-2 °C above that for heating. During the daytime CO_2 was supplied up to a level of 1000-1200 vpm. If the window ventilators were opened more than 10 %, CO_2 suppletion stopped.

GS2: From 9 October 1978 until 1 May 1979

In use were 9 compartments in which 9 temperature treatments were performed; 3 night temperatures, each combined with 3 day temperatures. Cultivars: Sweet Promise and Varlon. One of the 9 compartments was planted with 'Sweet Promise' only. Imposed treatments, setpoints for heating:

1,2,3. night 12°C day 18°C, 20°C, 22°C
4,5,6. " 15°C " idem
7,8,9. " 18°C " idem

Further conditions: see GS1

GS3: From 9 October 1979 until 1 May 1980

In use were 9 compartments in which 7 temperature treatments were performed, one of them in 3 replications. Cultivars: Sweet Promise and Varlon. Imposed treatments, setpoints for heating:

1. night 18°C, day 18°C
2. " 17°C, " 19°C
3. " 16°C, " 20°C
4. " 6 hrs 18°C followed by 6 hrs 14°C, day 20°C
5. " 15°C, day 21°C (3 replications)
6. " 14°C, " 22°C
7. " 6 hrs 16°C followed by 6 hrs 12°C, day 22°C.

Installed daily (mean) temperature 18°C for all treatments.
Further conditions: see GS1.

GS4: From 10 October 1980 until 1 May 1981

In use were 4 compartments in which 4 temperature treatments were performed. Cultivars: Sweet Promise and Varlon. Imposed treatments, setpoints for heating:

1. night 16°C, day 22°C
2. " 18°C, " 20°C
3. " 20°C, " 18°C
4. " 22°C, " 16°C

Installed daily (mean) temperature 19°C for all treatments.

Further conditions: see GS1.

GS5: From 5 October 1981 until 1 May 1982

In use were 4 compartments in which 4 temperature treatments were realised. Cultivars: Sweet Promise and Varlon. Imposed treatments, setpoints for heating:

1. 24 hours 19.0°C.
2. 22 " 18.5°C and 2 hours 24°C (from 18.00h until 20.00h).
3. 20 " 18.0°C " 4 " " (" 18.00h " 22.00h).
4. 18 " 17.3°C " 6 " " (" 18.00h " 24.00h).

Installed daily (mean) temperature 19°C for all treatments.
Further conditions : see GS1.

GS6: From 10 October 1982 until 1 April 1983

In use were 4 compartments in which 4 temperature treatments were realised. Cultivars: Sweet Promise and Varlon. Imposed treatments, setpoints for heating:

(1). From 10 October until 4 January the same as in **GS5**

(2). From 4 January until 1 April:

1. 24 hours 19.0°C.
2. 21 " 18.3°C and 3 hours 24°C (from 18.00h until 21.00h).
3. 18 " 17.3°C " 6 " " (" 18.00h " 24.00h).
4. 15 " 16.0°C " 9 " " (" 18.00h " 03.00h).

Installed daily (mean) temperature 19°C for all treatments.
Further conditions :see GS1

GS7: From 1 September 1983 until 1 January 1984

In use were 4 compartments in which 4 temperature treatments were performed. Cultivars: Sweet Promise, Ruimeva, Tanatesil, Jeldanira, Jelparaco and Korenlo. These cultivars had been planted in February 1983. The treatments and other conditions were the same as in experiment:**GS1**.

2.3. EXPERIMENTS WITH CONTAINER GROWN ROSES IN THE GLASSHOUSE

These experiments are coded by:**GCnr** (**G**lasshouse **C**ontainer)
Cultivars: Sweet Promise, Motrea and Merko.
In these experiments container grown roses on their own roots raised from cuttings were used. Working with containers made it possible to transfer the shrubs from one compartment to another in order to apply different temperature combinations depending on the stage of shoot development. Up to a maximum of 27 different combinations per experiment were used.
The plastic containers with a volume of 6-8 liters were filled with standard 'Rhijnbeek' potting compost. The containers were planted with rooted cuttings, one plant per container. Shrubs of at least half a year old were used in the experiments. 20-25 containers were used per temperature treatment. At the start of an experiment the branches were upper cut at two five-leaflet leaves and visually uniform branches were labeled. The new shoots sprouting from the terminal buds of the labeled branches were used for performing measurements.

The experiments took place in glasshouse compartments of 9.60m by 6.00m, adjacent to the compartments with the soil-grown roses. Climate control and registration were performed with the same process computer. The containers were placed on the glasshouse soil and watered and fertilised by hand.

Some experiments were done in small glasshouse compartments (5.00m by 3.00m) which were airconditioned. In these compartments the containers were placed on concrete tables.
By using cuttings it was possible to produce year round plant material for the experiments. A large stock of sometimes more than a thousand containers with roses was continuously available. All experiments were done with 2-9 replications and most of them were repeated in time.

GC1: From October 1980 until January 1981

In the middle of October 675 containers planted with rose cv. Sweet Promise were upper cut at two five-leaflet leaves above the joint. After bud break at a temperature of 20°C the containers were divided at random over 27 groups of 25 containers each. These groups were distributed equally over three compartments in which the following night/day-temperature treatments were imposed: 12/22, 15/22 and 18/22 (°C). The setpoints for night started at 18.00 hrs and lasted until 06.00 hrs in the morning. At the start there were thus 3 treatments. When the sprouts in a compartment had reached a length of 4-5 cm (this is the stage just before the strong elongation growth) two lots with each 3 groups were transferred to the other two compartments. This means there were now 3*3=9 treatments. After a lot of three groups had ended elongation growth, the moment was taken on which the sepals just gave way, two of the groups were transferred to the other two compartments. Thus at the end there were 3*3*3=27 different temperature treatments, depending on the stage of development of the shoot. The realised temperature range was: 16.2-19.6 °C.

GC2: From May 1981 until July 1981

The setup was the same as for GC1, but the experiment started in the first week of May. The imposed night/day-temperature treatments were: 14/16, 18/20 and 22/24 (°C). The realised temperature range was: 18.3 - 26.4 °C.

GC3: From October 1981 until December 1981

In the last week of October 250 containers were divided at random over two compartments after having been trimmed at two five-leaflet leaves above the stem joint. Visually uniform stems were labeled. In the compartments the next night/day-temperatures were imposed: 16/24 and 24/16 (°C). The setpoints for night started at 18.00h and lasted until 06.00h in the morning. From the time of trimming until harvest of the new shoot from the uppermost lateral bud, 25 containers were transferred at 4 different times between the compartments. The

shoot-stages at which transfer took place were:

1. terminal lateral buds just broken (=1 cm).
2. new sprouts 4-5 cm long.
3. flower buds clearly visible to the naked eye (2-3mm).
4. sepals give way.

Together with the two groups that were not transferred this means 10 different temperature treatments depending on the stage of development of the shoots.

The realised temperatures of the compartments were monitored daily and, if necessary, flower bud setpoints were adjusted to keep the temperature sum equal between the compartments. The realised temperatures for all 10 treatments fell within the range of: 19.6-20.0 (^{o}C). This experiment was repeted three times:

GC4: In the period: December 1981 until March 1982.
GC5: " " " : November 1982 " March 1983.
GC6: " " " : February 1984 " April 1984.

2.4. EXPERIMENTS WITH CONTAINER GROWN ROSES IN GROWTH ROOMS

These experiments were performed in the growth rooms of the Phytotron of the Laboratory for Horticulture of the Agricultural University in Wageningen. Dimensions of the rooms 4m x 6m.

Cultivar: Sweet Promise.

In the Phytotron plants were grown under artificial climate conditions. In the growth rooms of the Phytotron temperatures could be reached that were not possible in the glasshouses. The roses grew under artificial light with an irradiance of 20000-35000 mW/m2 (5000 -9000 lux) dependance of shoot heigth and shoot position (Philips TL 57 fluorescent tubes). The relative humidity was set at 70%. The plants used in these experiments originated from the 'plant stock' described earlier in 2.3. Twelve to fifteen containers were placed on one trolley. It was possible to make different temperature combinations by transferring the trolleys from one compartment to another. At the start of each experiment the branches of the rose

shrubs were upper cut at two five-leaflet leaves above the joint. The length of the light (day) and dark (night) period in the fototron experiments were respectively 8 and 16 hours, unless others mentionned.
More details of the individual experiments are given in the result sections of the next chapters.

2.5. EXPERIMENTS WITH SOIL HEATING

The influence of soil heating in relation to air temperature was studied during the first experimental year (1977-1978) for glasshouse grown roses cv. 'Sweet Promise'.
In each of 3 compartments belonging to experiment GS1, 4 plots planted with roses of the cv. 'Sweet Promise' were extended.
A plot measured about $2m^2$ bed surface. In two of the four plots an electric soil heating system made of electric wires was installed. The wires lay on a depth of 15 and 30 cm below the soil surface. The heating system was day and night controlled at $20^{\circ}C$ by means of a thermostate. The sensor was installed about 10 cm below the soil surface. The plots made no part of the experiment GS1, nor influenced the soil temperature in these experiments. The last two plots served as control plots.
The air temperature in the three compartments was controlled during the night at 12°, 15° and $18^{\circ}C$, respectively. The day temperatures were controlled between 20°-$22^{\circ}C$ in all three compartments. The other circumstances were the same as those in experiment GS1.

2.6. EXPERIMENTS WITH A 12% LIGHT REDUCTION WITH SOIL GROWN ROSES

During two successive years the influence of a permanent 12% light reduction on production and quality of 'Sweet Promise' was studied.
For this experiment one glasshouse compartment was glazed by special (so called) coated glass. The metaloxide coating of this glass reduced light transmission by 12%. Another compartment, with standard

transparent glass, served for control. The two compartments belonged to the same complex as the compartments from the experiments coded by GSnr. In the first experiment the night/day temperatures were controlled at 15/18°C and in the second experiment on 15/21°C. The other conditions were the same as in the experiments coded by GSnr.

2.7. LIST OF USED DEFINITIONS

-**Bud break** (sprouting) is the process in which the inhibition preventing a lateral bud meristem from developing is removed causing the bud to grow out into a new shoot. A bud is considered being broken if it has reached a length of at least one cm and continues to grow.

-**Sprout or shoot**: a broken bud with a length of at least 1 cm.

-**Week group**: a collection of roses of which the lateral buds had broken in the same week.

-**Growth cycle**: the period, in days, between two harvests and includes bud break and the development of the shoot until harvest.

-**Development time** of a shoot (DT) = the time, in days, between bud break and harvest.

-**Middle time** of a shoot (MT) = Time from bud break until the flower bud is clearly visible with the naked eye, without opening up the surrounding leaves. This is just halfway in the development time.

-**Daily (mean) temperature = average day and night temperature = 24 hours temperature** is the arithmetic mean of 1440 temperature measurements (one per minute from 00.00hr- 24.00hrs).

-**Mean (daily) temperature during a certain period** is the arithmetic mean of the 24 hours temperatures during that period.

-**Phytotron** = growth rooms with artificial climate conditions.

2.8. LIST OF USED ABBREVIATIONS

ABA = Abscisic acid.

ADR = average daily irradiance inside the glasshouse at shoot top

level during the development of a shoot ($Jcm^{-2}day^{-1}$).

BA = Benzyladenine.

BL = length of the flower bud exclusive the ovary (0.1 mm).

BW = Width of the flower bud (0.1 mm).

CCC = 2-chloroethyl trimethyl ammonium chloride

cv. = cultivar

DL = Average daylength during shoot development in minutes.

DS = Diameter of the shoot at the cut (0.1 mm).

DT = Development time from bud break until harvest (days).

FBW = Fresh flower bud weight (0.1 g).

FSW = Fresh shoot weight at harvest stage (g).

GA = Gibberellins.

GSnr= Code of the experiments with soil grown roses in glasshouses.

GCnr= Code of experiments with container grown roses in glasshouses.

IBA = Indole butyric acid.

IAA = Auxin (Indole acetic acid).

K = Cytokinins.

PBA = Benzylamino tetrahydropyranyl purine.

RH = Relative humidity of the air = (actuel VP/saturated VP)*100%.

R^2* = % variation accounted for by the regression equation.

RSUM= radiation sum in the glasshouse during shoot development $Jcm^{-2}day^{-1}$.

SP = 'Sweet Promise'.

SL = Total shoot length at harvest stage (mm).

T = Mean temperature during shoot development (^{o}C).

TIBA= Triiodobenzoic acid.

V = 'Varlon'.

VP = Vapour pressure of the water in the air (0.1mm Hg).

VPD = Vapour pressure deficit of the air (0.1mm Hg).

WPS = Fresh weight of the parent shoot (0.1 g).

a,b = Unlike letters indicate significant differences at the 5% level (Tukey's Yardstick).

* = if used below colums: treatments do not differ at the 0.05 level of significance (Tukey's Yardstick).

3. BUD BREAK

3.1. INTRODUCTION

The growing apex of a rose shoot inhibits the outgrowth of the lateral axillary buds lower on the shoot and the subtending stems. This inhibition by the apex is under hormonal control and called apical dominance. For the hormonal background of apical dominance see Appendix 1. When a shoot approaches the flowering stage the activity of the apical meristem decreases and so does the inhibition of the lateral buds. Depending on the cultivar and growth conditions, one or more of the uppermost lateral buds break and new sprouts are formed. In the practice of rose growing these sprouts are removed to ensure a maximal outgrowth of the top flower bud.

After removing the apex by cutting the marketable flower or by decapitation or pinching of the shoot, the dominance of the apex over the remaining part of the shoot disappears. In general the lateral bud now in uppermost position breaks to form a new flowering shoot. If the bud does not break, the bud is called 'dormant'. If the conditions for growth are unfavourable it may take weeks or even months until dormancy is removed and the lateral bud breaks. The phenomenon of dormancy as it occurs in higher plants was among others reviewed by Doorenbos (1953), Vegis (1964) and by Lyons (1973).

If after removing apical dominance more than one lateral bud breaks on the same stem, it is common that the sprout from the terminal bud, which mostly breaks first, shows the most vigorous growth and dominates over the lower one(s). This domination can be so severe that the lower sprouts stop growing, the flower bud atrophies or the lower sprouts even die. In our experiments this happened to most of the sprouts from the second uppermost buds when growing conditions were unfavourable in wintertime. In spring however, the growth of these lower sprouts was normally so strong that the

dominance of the uppermost one was unable to prevent the second sprout from reaching the flowering stage. Also, under the most favourable growing conditions in summer however, growth inhibition and flower bud atrophy of lower sprouts occurred and mostly of sprouts emerging from the third lateral bud.

A weakening of the dominant apex reduces its inhibitory effect on lower buds. Such a weakening can be a slow-down of growth. This may be caused by bending a vertical growing shoot horizontally. This is a cultivation method often effectuated in practice to stimulate bud break of a low situated lateral bud on a thin stem without removing the top of the shoot. The advantage of this so called 'lay back' pruning over 'cut back' pruning (the method in which the top is removed) is that more stem and leaf area remain so that the plant has more reserves to draw from. The effect of horizontal bud orientation on bud break and growth was studied by different research workers (Wareing and Nasr 1961, Palmer 1964, Zieslin and Halevy 1978).

The ageing of the apex also reduces its inhibitory effect. This may be related to flowering. Flowering shoots produce less inhibitory hormones than shoots with a strong vegetative growth (Laibach and Kribben 1953).

The nutrient status of the plant also has its influence on bud break. Early investigators developed the 'nutritive theory', a hypothesis involving starvation of buds through the monopolisation of nutrients by the apical bud (see review by Phillips 1975). Although this theory has slipped into the background, nutrients and water status of the plant play a role by influencing the hormone levels and the total 'growth vigour' of the plant; many reports on this subject have been published (McIntyre 1964,1971; Phillips 1964, Wakhloo 1970, Simpson and Saunders 1972, Hoad 1973, Hiron and Wright 1973).

Stimulating growth vigour in winter by supplementary lighting also results in better bud break (Carpenter and Anderson 1972, Vonk Noordegraaf 1976, Moe 1973, Cockshull 1975, Kosh-Khui and George 1977). Growth vigour is a simple expression for a process with a very

complicated physiological background and controlled by many factors in and around the plant. It may be considered as the fresh or dry weight production of a canopy per square meter per day.

The properties of the substrate in which the roses grow and the type of roots of the plant, rootstock or own roots, may also influence bud break via the growth vigour. The positive production results, obtained during the last few years by growing in rockwool, may partly be explained by a quicker bud break as a result of the favourable root environment (Van den Berg 1984, 1986).

One has also to consider the position of the terminal bud which is expected to break. A higher position on the shoot leads to a faster bud break (Moe 1973, Byrne and Doss 1981). Bud position inside the canopy determines the light level and the red light/far-red light ratio (Kaspenbauer 1971, Nederhoff 1984), which in its turn influences the hormone balance (Appendix 1). Also inhibition within the plant from already developing shoots on a recently terminated bud can delay bud break (this chapter).

Daylength also has an influence on bud break of roses. A positive effect of short days was reported by Moe (1972) and Cockshull (1975).

An effect of temperature on bud break is to be expected. All physical and biochemical processes in the plant are influenced by temperature. Rootzone warming in hydroponics are reported to stimulate bud break (Moss 1983, 1984, Moss and Daglesh 1984). Zeroni and Gale (1982) found for roses, an optimum soil temperature under their conditions of 18 ^{o}C. Air temperature has a strong influence on bud break (Van den Berg 1981). The air temperature inside the glasshouse is the climatic factor that can be influenced relatively easily by the grower. It gives the grower a tool to plan and control rose production. The influence of the air temperature on bud breakis the main subject of the research covered by following chapter.

At last; it is a well known fact in the practice of rose growing that high (> 90%) air humidities stimulate bud break while low (<60%) delay it. In former days, blowing steam into the glasshouse was a method to stimulate bud break.

3.2. MATERIALS AND METHODS

3.2.1. EXPERIMENTS ON TEMPERATURE AND BUD BREAK

Bud break of soil grown roses was monitored during 7 successive winter seasons in the glasshouse.

In the experiments: GS1-GS6, the influence of the temperature on bud break of 'Sweet Promise' and 'Varlon' roses was studied. An axillary bud was considered broken if it had a length of 1 cm and continued growing. This last provision is important as in the winter it often occurs at low temperatures, that a bud starts to break but stops when it has reached a length of about 1 cm. Then it goes into dormancy and remains dormant for weeks or even months before it definitely breaks and growths out in the spring.

In order to collect information about more cultivars an experiment (GS7) was set up with the cultivars: Sweet Promise, Ruimeva, Tanatesil, Jelparaco, Jeldanira and Korenlo.

Whether the daily distribution of the temperature at a given mean temperature had any influence on bud break, was studied in a the experiments GS3-GS6. These studies were performed with the cultivars: Sweet Promise and Varlon. At a constant daily mean temperature different combinations between day and night temperatures were made, even with higher night than day temperatures, which is a reversal of the common situation.

In experiments done in the Phytotron bud break of roses cv. Sweet Promise was studied in the temperature range 10^{o}C through 25^{o}C and a daily photoperiod of 8 hours. These experiments were repeated several times.

3.2.2. BUD BREAK AND SHOOT COMPETITION WITHIN A PLANT

To study shoot competition the influence of growing shoots on the breaking of the uppermost lateral bud of a neighbouring stem of the

same plant was examined. In this experiment container grown roses were used of the cultivars Sweet Promise and Merko (GC).
Bud break was compared between uppermost buds of plants of which all shoots had been cut at the first five leaflet-leaf and plants of which only one shoot had been cut.

Plant materials, methods, conditions, definitions, abbreviations and codes of the experiments have been described in chapter 2. If necessary supplementary information is given in the results section.

3.3. RESULTS

3.3.1. BUD BREAK AND THE MEAN DAILY TEMPERATURE

In the experiments GS1 and GS2 the influence of the mean daily temperature on breaking of the uppermost lateral bud after cutting the previous flower was studied in the period October until March. The results are shown in Figure 1 for cv. Sweet Promise and in Figure 2 for cv. Varlon. The vertical axis shows the percentage of broken buds and the horizontal axis the realised mean daily temperature during bud break. The different lines, lying above each other, represent the time in weeks after cutting. Both 'Sweet Promise' and 'Varlon' show the same overall effect. The rate for 'Sweet Promise' is higher than for 'Varlon'. In the Figures 3 and 4 bud break is presented in another way. The vertical axis again represents the percentage of broken buds, but the horizontal axis shows the number of weeks after cutting. The seven lines represent seven temperature ranges. The lowest two lines for 'Sweet Promise' display another pattern than those for 'Varlon'. Bud break stops for some weeks for 'Sweet Promise' while it continues for 'Varlon'.
The influence of harvest time on bud break is shown in Figure 5 for the cv. Sweet Promise. This figure displays the percentage of the uppermost lateral buds broken three weeks after being cut in the period October until April, for 5 temperatures. Because in spring the lower temperatures could not be realised, the corresponding lines are

shorter than those of the higher temperatures. The lines are nearly horizontal with a slight drop in December. 'Varlon' reacts qualitatively in the same way as 'Sweet Promise ', and is not shown separately.

3.3.2. BUD BREAK AND THE TEMPERATURE DISTRIBUTION BETWEEN DAY AND NIGHT

In the experiments GS3-GS6, different combinations of day temperatures in the range 16 °C to 24 °C and night temperatures in the range 14 °C to 24 °C were given but the imposed daily mean temperature was the same for all treatments. No significant variations in rate of bud break were found at the .05 level of significance. Even reversing day and night temperature, resulting in a higher night than day temperature, did not influence bud break.

3.3.3. BUD BREAK AND DIFFERENCES BETWEEN CULTIVARS

In experiment GS7 the difference in bud break was studied for 6 cultivars.
The percentages of buds that had broken three weeks after cutting are given in Figure 6. Each line represents a cultivar. The line representing the cv. Varlon is taken from the experiments GS1 and GS2. On the vertical axis the percentage of buds is shown and on the horizontal axis the mean temperature. No differences were recorded in the rate of bud break at temperatures above 21 °C. If the temperature drops differences between the cultivars are clearly visible.

3.3.4. BUD BREAK AND INTERSHOOT COMPETITION

Intershoot competition and bud break was studied in an experiment with container grown roses cv. Sweet Promise.
The percentage of uppermost lateral buds that had broken 2 and 4 weeks after cutting, was calculated for buds on plants with only one

shoot cut, and for buds on plants of which all shoots had been cut at the same time. The mean temperature during bud break was 20°C. The results are listed in Table 1.

Table 1. Container grown roses cvs. Sweet Promise and Merko. Percentages of the terminated lateral buds broken 2 and 4 weeks after cutting all shoots (a) or only one shoot (b) of the shrub.

	Percentage broken lateral buds			
	'Sweet Promise'		'Merko'	
	2 weeks	4 weeks	2 weeks	4 weeks
a. All shoots cut	87a	93a	97a	97a
b. One shoot cut	46b	46b	42b	42b

The table clearly shows that if all shoots are cut, the lateral buds break sooner than when only one shoot is cut. This holds true for both cultivars.

3.3.5. BUD BREAK IN GROWTH ROOMS

Bud break of the cv. Sweet Promise was also studied in air conditioned growth rooms under artificial light conditions. The results recorded in the temperature range of 11°C to 25 °C and a light period of 8 hours are shown in Figure 7. The results show a strong positive correlation between temperature and bud break.

3.4. DISCUSSION

Bud break is positively correlated with the mean temperature in all experiments. This result could be expected because all processes involving bud break are sensitive to temperature. As soon as the inhibition of the apex over the lateral buds stops, the processes involving bud break start. If temperature is reduced bud break slows down until the buds go into dormancy. In this stage the buds can stay for weeks or months. With the exeption of some buds which stay dormant, even for years, all buds sprout in spring.
For bud break is not important how the mean temperature is realised. Within the limits of the experiments it made no difference how temperature was distributed over the night and the day, only the mean daily temperature was important. This has a consequence for commercial rose growing. With respect to energy saving it is advisable to give the highest temperature during the night when the thermal screen(s) are closed.

A subordinate effect of a closed screen is that the wanted air temperature can be realised with rather low pipe temperatures. This means that the relative air humidity stays on a higher level which improves bud break. Also the screen itself can, depending on its structure and material, attribute to a raise in air humidity.
The response to air temperature is not equally strong for all cultivars. Under the same glasshouse conditions there are considerable differences in response (Figure 6). Two groups can be distinguished: a fast and a slow group. The differences between these groups and also those within a group, can explain a large part of the variation in production as found in variety trials with these cultivars (Van Gelder 1984).
The cultivars Sweet Promise and Varlon, both belonging to the slow group, show a difference in behaviour. Above 17^{o}C 'Sweet Promise' shows a quicker bud break than 'Varlon'. If temperature decreases, the percentage of buds that break within 3 weeks after cut is higher for 'Sweet Promise' than for 'Varlon'. The lateral buds of 'Sweet

Promise' that do not break within 3 weeks are more inhibited than those of 'Varlon', however. While bud break of 'Varlon' continues at a reduced level, the 'Sweet Promise' buds go into dormancy for some weeks. The lateral buds of 'Varlon' that fall into dormancy however, remain much longer in this stage than the lateral buds of 'Sweet Promise'. It takes about 20 weeks for all 'Varlon' buds to break and about 14 weeks for all the 'Sweet Promise' buds.

For 'Sweet Promise' one can speak about a 'critical' temperature for bud break at $17^{o}C$-$18^{o}C$ below which the buds go from a state of inhibition by apical dominance into a state of leaf imposed dormancy, as is normal for outdoor roses in autumn. This temperature is within the range of $16^{o}C$ to $19^{o}C$ maintained in commercial glasshouses with this cultivar (Van Rijssel 1979). A reaction like that of 'Sweet Promise' has a practical implication. If a glasshouse is kept at the right temperature to secure a quick bud break and there are horizontal temperature differences in that glasshouse, there will be problems with bud break in the parts with a temperature below the critical value. Horizontal temperature differences are a common phenomenon in practice (Holsteijn and Vogel 1984, Holsteijn 1985, Koop 1984, Van den Berg 1986).

Problems with bud break automatically lead to a lower production and an increase in fuel costs per produced rose. Another negative point is that it hampers good planning.

The time of cutting showed no influence on the rate of bud break for cv. Sweet Promise at temperatures higher than $19^{o}C$. At lower temperatures a slight drop around the shortest day could be seen (Figure 5). The reaction of 'Varlon' was qualitatively the same as that of 'Sweet Promise' and is not shown separately.

Such a drop in bud break is to be expected. In the middle of winter growth vigour is at its lowest point. The stimulating effect of short days on bud break as reported for roses by Moe (1972) and Cockshull (1975), was probably not enough to offset the effect of this lack of growth vigour.

High temperatures clearly stimulated breaking of the second upper bud

after January. Starting in February, 75% of the second buds of 'Sweet Promise' broke if the temperature was higher than 20°C. If broken before March however, most of the sprouts from these second buds produced flowerless ('blind') shoots. Later on in the season these sprouts reached the flowering stage but their length and fresh weight were always less than those from shoots emerging from the uppermost bud. This inhibitory effect of shoots of the uppermost bud on those from lower buds is common in plant growth as was mentioned in the introduction.

The inhibitory effect that growing shoots exercise on the terminal bud of a sister shoot on the same plant was clearly demonstrated for 'Sweet Promise' and 'Merko' (Table 1). This phenomenon may be an explanation for the fact that in all experiments performed in growth rooms (Phytotron), bud break was faster than for plants in full soil in the glasshouse at the same temperature. The reasoning may be that when all tops of the plants have been removed the whole production of inhibitors stops and the active sinks are gone until the new uppermost meristems become active. At the start of the experiments in the Phytotron we cut all shoots. In this way intershoot inhibition was prevented. Figure 7 shows the fast bud break in the Phytotron. Even at a temperature of about 12°C, 50 % of the buds had broken within two weeks. This implies that it is possible to reduce the time needed for bud break and as a consequence, the time between two growth cycles without using extra energy by raising temperature.

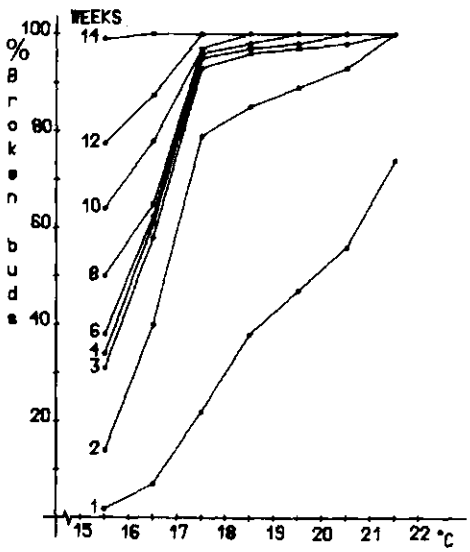


Fig.1 'Sweet Promise'

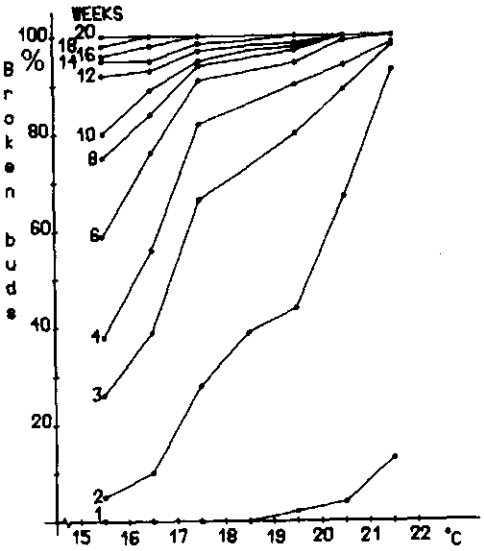


Fig.2 'Varlon'

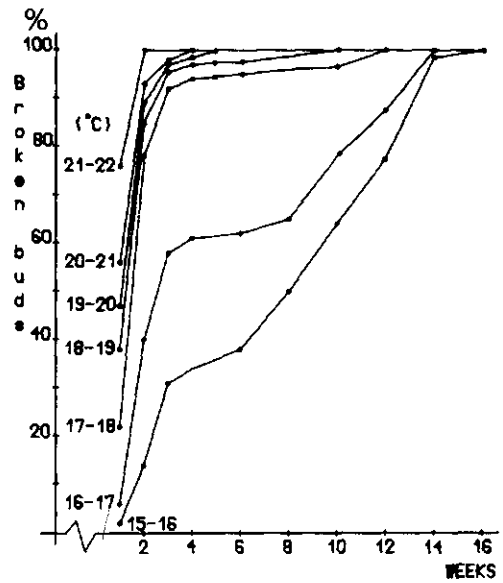


Fig.3 'Sweet Promise'

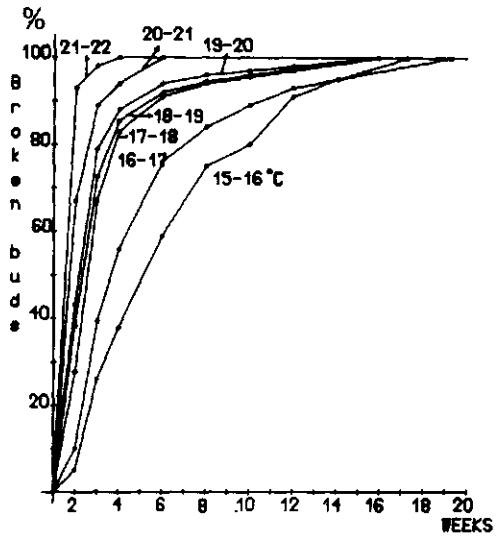


Fig.4 'Varlon'

'Sweet Promise' and 'Varlon', grown in glasshouse soil. Percentage of uppermost lateral buds broken at different points of time (weeks) after cut of the previous flower, in relation to the mean air temperature (^{o}C). Period: October untill May.

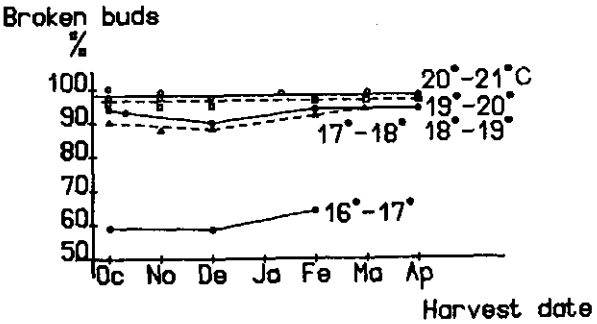


Fig.5 'Sweet Promise' grown in glasshouse soil. Percentage of uppermost lateral buds, broken three weeks after cut of the previous flower. For five temperature levels.

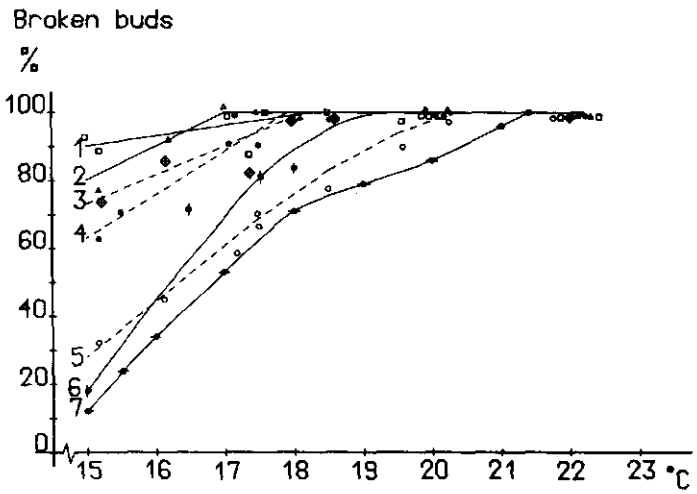


Fig.6 Rate of bud break in 7 cultivars, grown in the glasshouse soil. Percentage of uppermost lateral buds, broken within three weeks after cut of the previous flower in relation to the air temperature. Tanatesi (1), Korenlo (2), Jelparaco (3), Jeldanira (4), Ruimeva (5), Sweet Promise (6), Varlon (7).

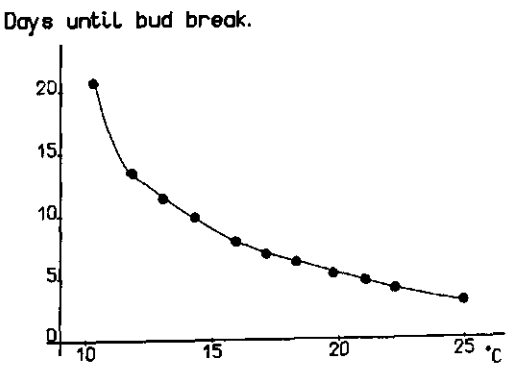


Fig.7 'Sweet Promise', container grown in growth rooms. Number of days to bud break of the uppermost lateral bud after cut of the previous flower in relation to the mean temperature.

4. DEVELOPMENT TIME OF A SHOOT FROM BUD BREAK UNTIL HARVEST

4.1. INTRODUCTION

Relatively few papers have been published on the effect of temperature on the growth cycle of roses in glasshouses. The length of the growth cycle was studied in growth rooms by Moe and Kristofferson (1969), and Moe (1972a,b, 1973). De Vries and Smeets (1979) and De Vries (1982) studied the influence of temperature on rose seedlings in growth rooms as a part of his breeding work.
The growth cycle in glasshouses was studied by Byrne (1978), Van den Berg (1980) and Schrock (1981). Van Rijssel followed the growth in 40 commercial nurseries with roses cv. Sweet Promise and 40 nurseries with the cv. Motrea (Van Rijssel 1979, 1982).
In general higher temperatures resulted in a shortening of the growth cycle, while lower temperatures led to the opposite. In the papers published on this subject the growth cycle from harvest to harvest is mostly taken as a unit and includes the time needed for bud break. In the present research the growth cycle was split into two parts. The first part included the time needed for bud break and the second part included the development time of the sprout from bud break (=1 cm long) until harvest. This split was made because it was observed in glasshouses that the time needed for bud break showed much more variation than the time for development from bud break until harvest. Taking the two parts as a unit made the whole subject more confusing than keeping them separate.
In the preceding chapter bud break was discussed and the following chapter will deal with the time for development from bud break until harvest. The length of the latter period is important; together with the time needed for bud break it determines the length of the growth

cycle, which is the base of the yearly production. The aim of the study of the development time of the shoot was fourfold:

(1) To study the relation between the daily mean temperature and the development time of a shoot.
(2) To study if, and if so how, the temperature distribution between day and night influences the development time.
(3) To study the interaction between temperature and stage of development of a shoot on its total development time.
(4) To construct a 'model' that can be used for production planning.

4.2. MATERIALS AND METHODS

Plant materials, methods, conditions, definitions, abbreviations and codes of the experiments have been described in Chapter 2.If necessary supplementary information is given in the result section.

4.2.1. EXPERIMENTS ON TEMPERATURE AND DEVELOPMENT TIME

To acquire the basic material for a model on development time, the experiments GS1 and GS2 were performed. The influence of the daily temperature distribution on the development time was studied in the experiments: GS3,GS4,GS5 and GS6. Interaction between temperature and stage of shoot development with respect to the development time was studied in the experiments: GC1, GC2, GC3 and GC4.

4.2.2. THE CONSTRUCTION OF A 'MODEL' FOR THE DEVELOPMEN TIME OF A SHOOT

A description will now be given of the method used to construct the model for the development time of a shoot, which is shown in its end form for the cv. Sweet Promise in Figure 10 and for cv. Varlon in Figure 14. The same method as described for this 'model' was also

used for the other 'models' in this thesis.
In experiment GS1 four night temperatures, 12^{o}, 15^{o}, 18^{o} and 21^{o} (C) were imposed combined with one day temperature of $20^{o}C$-$22^{o}C$. Every treatment was replicated once. In each of the 8 compartments of both cultivars 72 labelled shoots were monitored cut after cut. The date of cut and bud break was monitored for each flower. The lateral buds that sprouted in the same week were taken as one group, called: 'week group'. Of these groups the median of the development time of the shoots was calculated. The smoothed medians from each of the four temperature treatments are shown in Figure 8. Smoothing was done by taking running medians of 3, followed by skip means and hanning as described by Tukey (1977) in his book Exploratory Data Analysis (See Appendix 2).
The horizontal axis in Figure 8 shows the date of bud break. A lateral bud was considered having broken if its length was 1 cm and growth had continued. The vertical axis records the development time of the shoot from bud break until harvest in days. The four lines represent the four temperature treatments. The figure covers the period from August until April of the following year. From the four graphs we recorded for each week and for each treatment, the development time from bud break until harvest. As the computer registered daily the realised climate per treatment, it was possible to calculate for each 'week group' the mean daily temperature during the growing period. This meant that for each point of the four lines three important data were known:
(1) The date of bud break.
(2) The development time in days.
(3) The mean daily temperature during the growth period.

These three data were combined in one figure. This is illustrated for the first day of the months of October, December and April in Figure 9. In this figure the horizontal axis shows the realised mean daily temperature during development time, and the vertical axis the development time in days. The abbreviations refer to the

corresponding months. The four different marks represent the four imposed temperature treatments. In this figure one can fit two groups of lines. First a group of four lines (broken) fitted through the sets of identical marks showing for each temperature treatment the realised temperature during the period under consideration and the corresponding development time. Second a group of 3 lines (solid) showing the relation between date of bud break on the first of the corresponding month and the development time in relation to the realised mean daily temperature.

Figure 9 can be extended by adding more months and more points per month. For ease of survey this is not done here. From Figure 9 in an extended form to Figure 10 is a small step. This last figure presents on the horizontal axis the date of bud break and on the vertical axis the development time in days. The 8 isotherms show how this development time changes from September until April in relation to the mean temperature during growth. Figure 10 can be considered as being the 'model' we were looking for. It was constructed by using the data from the experiment GS1 and was verified and extended with the isotherm of 15°C by data from experiment GS2.

4.3. RESULTS

4.3.1. DEVELOPMENT TIME AND THE MEAN DAILY TEMPERATURE.

The influence of the mean daily temperature on the time a broken lateral bud needs to grow and develop until it is ready for harvest, is displayed in Figure 10 for the cv. Sweet Promise and in Figure 14 for cv. Varlon.

On the horizontal axis the date of bud break is shown, and on the vertical axis the development time in days.

When looking at these figures, two things strike:

(1) In the temperature range 22°C-17°C the distances between the isotherms are nearly the same, but at lower temperatures they increase.

(2) The isotherms are curved, but not fully symmetrical and follow the natural annual radiation cycle.

If the data of the Figures 10 and 14 are analysed, with the method of linear least square regression (see Appendix 3), the following regression equations, for abbreviations see **2.7.**, ensue:

'Sweet Promise': **DT**=103.74 -3.1992**T** -0.01224**ADR** (R^2* = 97.7).
'Varlon': **DT**=144.63 -5.0268**T** -0.01398**ADR** (R^2* = 98.6).

If Figure 10 is extended with another dimension, in such a way that the mean daily irradiance measured at shoot top level in the glasshouse during the development time is put on the horizontal axis, Figure 11 emerges. In this figure there are four dimensions: the three from Figure 3 and the irradiance inside the glasshouse. For ease of survey only four isotherms are shown. The letters alongside the isotherms refer to the first day of the corresponding month. They represent the day on which a bud had broken. The isotherms show a 'hysteresis' effect: at the same mean irradiance and the same mean temperature the development period is shorter in autumn than in spring. E.g., at a irradiance of 300 $Jcm^{-2}day^{-1}$ shoots develop about 7% quicker in autumn than in spring. This hysteresis disappears if on the horizontal axis, the mean irradiance during the whole development time is replaced by the irradiance during the period from bud break until visible flowerbud. This moment was monitored and appeared to be in the middle of the developing period. It is called the 'Middle Time'. Figure 12 shows the result of this transformation for 'Sweet Promise'. The figure displays all eight isotherms from 15°C to 22°C. The letters again refer to the corresponding months. Letters without a dot refer to the first day of the month and those with a dot to the middle of the month. The vertical axis shows the 'Middle Time'. Hysteresis has now disappeared and a linear relation emerges between the Middle Time - and of course also the Development Time- with the mean irradiance during the Middle Time. This result means that

hysteresis arises in the second half of the development period. In this period the visible flowerbud develops until it reaches the harvest stage. This is illustrated in Figure 13. The cv. Varlon behaves the same as 'Sweet Promise' and also shows hysteresis in the second half of the development time, which is not shown here separately.
The mean deviation from the model was less than two days. From Figure 12 it becomes also clear that if irradiance is more than circa 600 $Jcm^{-2}day^{-1}$ it no longer influences the development time.

Figure 15 shows the percentage development time is shortened if in the range 15°C to 21°C the air temperature is raised by 1 °C. Figures 10 and 14 show that the relation between the development time and temperature is not linear in the range 15°C to 22°C. Especially in the lower temperature range the data point towards an exponential relationship. In the glasshouse experiments the temperature range was between 15°C and 22°C. So no information was obtained about the higher and lower temperatures. In experiments in growth rooms however, a temperature range between 9°C and 25°C was realised. If the average development time in these experiments is put in a graph it gives insight into the course of the development time at lower and higher temperatures than realised in the glasshouse experiments. This course (drawn line) is shown in Figure 16. The broken line in this figure is the corresponding line from the glasshouse experiments with 'Sweet Promise' taken from a period with about the same light level. The exponential curve in the figure fits the data rather well (r=0.986). If a linear line is fitted over the range 17°C to 25°C the best equation is: y= 54.94-0.94x (r=-0.969). This fit is not bad but less satisfactory than the exponential fit.

4.3.2. DEVELOPMENT TIME AND TEMPERATURE DISTRIBUTION BETWEEN DAY AND NIGHT

The 'models' representing the development time (Figure 10 and 14) appeared to be of value not only for the data from the two

experiments GS1 and GS2, but also for those from GS3,4,5, and GS6. It appeared in these experiments that at a given daily mean temperature, temperature distribution between day and night was not important for the development time within the limits of the experiments (P=0.05). Even when the night temperature was higher than the day temperature, development time was not affected.
Regardless how the mean temperature was reached during the experiments, the models from Figure 10 and 14 held for all 6 experimental years.

4.3.3. DEVELOPMENT TIME AND INTERACTION WITH SHOOT STAGE AND TEMPERATURE

In the previous experiments given temperatures were not changed during the development of the shoots. To detect possible differences in sensitivity for temperature during shoot development, experiments were set up with container grown roses cv. Sweet Promise. (GC1,2,3 and 4). These roses were transferable, which made it possible to make different combinations between temperature and shoot stage.
In the experiments GC1 and GC2 a total of 27 combinations were made. In these experiments the day temperature was always higher than the night temperature, as is the common situation in practice. The number of days between bud break and harvest was monitored and the mean daily temperature calculated. The results are shown in Figure 17. This figure presents two groups of data points, each with the corresponding fitted straight line. The highest group refers to experiment GC1, performed in wintertime, the lowest group to GC2 performed in spring when temperatures and light intensities were much higher. The lines fit well. Some points can be considered as 'outliers'. Removing them improves the fits. No relation was found between residuals and treatments.

In each of the following experiments, GC3 and GC4, 10 combinations were made. Five with a higher day than night temperature and five with a higher night than day temperature, a situation

reverse as in practice. The results of these experiments are listed in Table 2. No significant difference at the .05 level was found. The small differences in growth time are due to accidental deviations and to small (< 0.5°C) in realised temperatures. Also experiments with container grown roses performed for other purposes, never showed a reliable interaction between shoot stage and temperature.

Table 2. Rose cv. Sweet Promise, container grown in the glasshouse. Development time in days from bud break until harvest for 2 different 12 hrs night/12 hrs day temperatures, imposed during different stages of shoot development. Realised mean temperatures 19.6-20.0 (°C).

Night/Day Temperature (°C)	Given from harvest until:	Night/Day Temperature during rest of the growth	Development time in days from bud break until harvest GC3	GC4	average
16/24	harvest	24/16	38	38	38
"	sepals give way	"	38	39	38.5
"	flower bud visible	"	38	38	38
"	shoot elongation(4cm)	"	38	40	39
"	bud break	"	38	39	38.5
24/16	harvest	16/24	39	39	39
"	sepals give way	"	38	39	38.5
"	flower bud visible	"	39	39	39
"	shoot elongation(4cm)	"	38	39	38.5
"	bud break	"	39	39	39
			*	*	*

4.4. DISCUSSION

In the construction of the 'models' for the development time from bud break until harvest (Figure 10 and 14), the medians were used instead of the means. The reason was that some of the 'week groups', which formed the basis of the calculations, showed in the middle of winter at low temperatures sometimes 'outliers'. These were shoots with a very low growth rate. In most cases such an outlier did not strongly influence the mean of a week group, but in cases of a small week group it did. To keep a uniform data handling it was decided, instead of removing outliers, to take medians instead of means.

In the 'models' some lines are partly dotted. These parts were obtained by extrapolation because of the absence of data. The reason was that the lowest temperatures could not always be realised because of the outside climate conditions. With some calculations the 'models' can be transformed to show the date of harvest on the horizontal or on the vertical axis. This can be useful for commercial growers, but is not shown here. Because of the more than two dimensions (variables) in some of the figures, the figures can be transformed by placing other variables on the axis. This can sometimes give a better view on a specific variable.
In summer all treatments were the same and all glasshouses were ventilated to the maximum. As a logic result the realised temperatures were nearly equal and fell in the range $19^{o}C$-$21^{o}C$. Within this temperature range the isotherms ran horizontally in summer.

The development time in the 'models' follows the annual natural radiation cycle. A clear relation between the annual radiation cycle and development time was o.a. demonstrated by Klapwijk and De Lint (1975) for tomato seedlings. Van der Hoeven and Groenewegen (1970) and Van Esch (1976) found also such a type of relation for lettuce from data sampled at commercial holdings.

A linear relationship between the Middle Time and the mean daily irradiance was found. This is shown in Figure 12 for cv. Sweet

Promise. Because the Middle Time is just halfway of the development time, the last also shows a linear relation with the irradiance during the Middle Time. During the second half of the development time also a linear relation was found, but at a higher level in autumn than in spring, with a connection in November (Figure 13). The irradiance during the first half of the development determines the whole development time. This means that during the second half of shoot development, the light intensity prevalent under natural light conditions does not influence development time. This phenomenon has also been reported by Pieters (1985) who worked with sunflower.
Klapwijk (1979) plotted the crop cycle of lettuce from planting out until harvest against a date midway between sowing and planting out (middle date) and found that the longest time from planting to harvest practically coincides with the middle date on the shortest day. He also found no influence of the natural light level on development time between April and September. Treating our rose data on the same way, he got qualitatively the same results (Klapwijk 1980). The graphs Klapwijk obtained look very much like those in Figure 12.

Because light is the driving force of photosynthesis, which in itself is the basis of plantlife, a positive relation between irradiance and development time is to be expected. If the mean irradiance inside the glasshouse rises above circa 600 $Jcm^{-2}day^{-1}$ for cv. Sweet Promise and circa 500 $Jcm^{-2}day^{-1}$ for cv. Varlon, no further reduction in development time was found; the isotherms in Figure 12 run horizontally. In the Netherlands on a latitude of about 52^{o} this light situation occurs in the glasshouse between April and September. In that period of the year light is no longer a restriction for development time of the individual shoot unless it is situated inside the canopy, shaded by other shoots. This means that the light level above which the development time is no longer reduced, can be higher for a crop as a whole, than for a individual shoot.
Decreasing development time by increasing light intensity has also been found in experiments done in growth rooms (Moe 1972a, Moe and

Kristofferson 1969, De Vries and Smeets 1978, De Vries and Du Bois 1982). A practical application is the use of supplementary lighting in winter. This method to reduce the development time has been reported by several authors (Carpenter and Anderson 1972, Wiseley and Lindstrom 1972, Khosh-khui and George 1977, Armitage and Tsujita 1979). Because of the high electricity costs, supplementary lighting is only used on a small scale in the Netherlands.

The relation between development time and temperature is exponential (Figure 16). In the most important temperature range (17^{o}-21^{o}C) for winter production in Dutch glasshouses it is very close to linearity, however.

Within the limits of the experiments no significantly interaction was found between the development time with temperature and shoot stage. The mean daily temperature during the whole growth period accounts for about 99% of the variation in the data of the experiments done on this subject (Figure 17). This implies that it is possible to decrease the setpoint for heating at certain times, and compensate for this later on, to reach a predecided mean daily temperature or temperature sum during shoot growth, without delaying harvest time. This means that within certain limits, a period with a low temperature can be compensated by a period with a high temperature.

The distribution of temperature over day and night did not influence growth time either. Such a reaction to temperature was also reported by Cockshull et al. (1982) for some Chrysanthemum species and by Hurd and Groves (1984) for tomatoes.

Even a higher night than day temperature showed no effect on the development time. With respect to energy conservation this opens up the possibility to raise the night temperature when thermal screens are closed and decrease the setpoint for heating in daytime when the screens are open. The fuel saved in this way do not need extra investments.

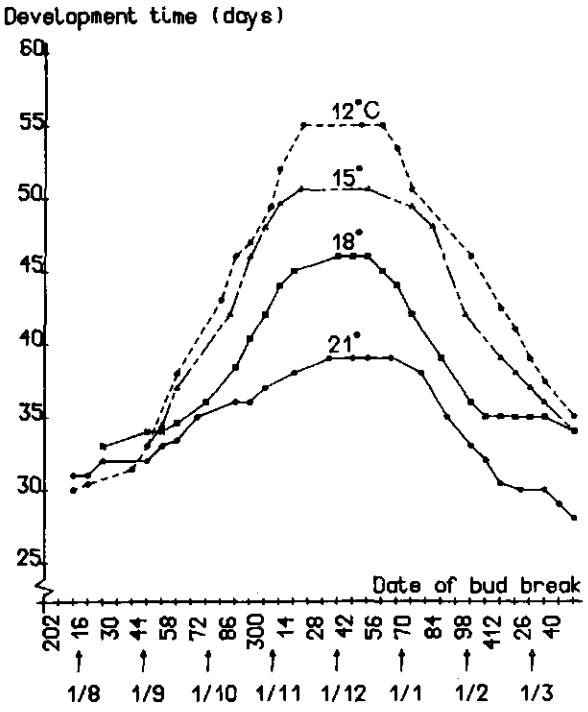
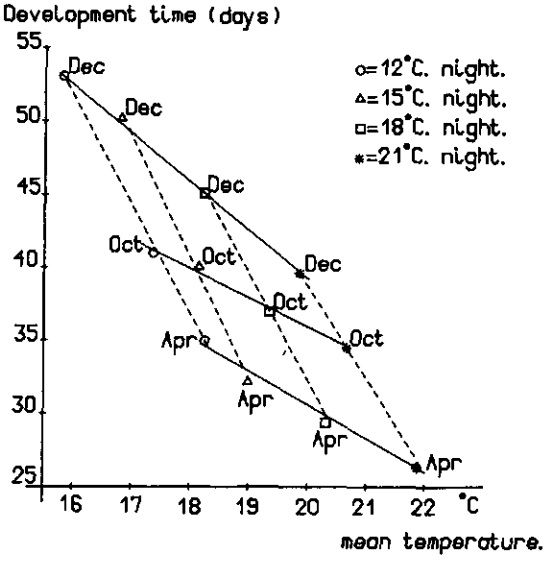


Fig.8 'Sweet Promise', grown in glasshouse soil. Development time of broken lateral buds for 4 night temperatures (12°, 15°, 18° and 21°C) at one day temperature 20-22°C.

Fig.9 'Sweet Promise', grown in glasshouse soil. Development time for lateral buds, broken on the first day of October, December and April; for 4 night temperatures in relation to the mean temperature.



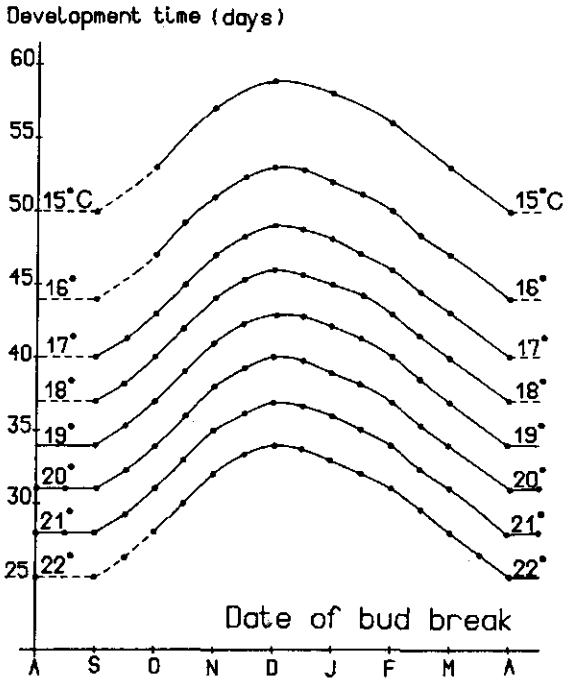


Fig.10 'Sweet Promise', grown in glasshouse soil. 'Model' for the development time in days from bud break until harvest in relation to the mean temperature and the date of bud break.

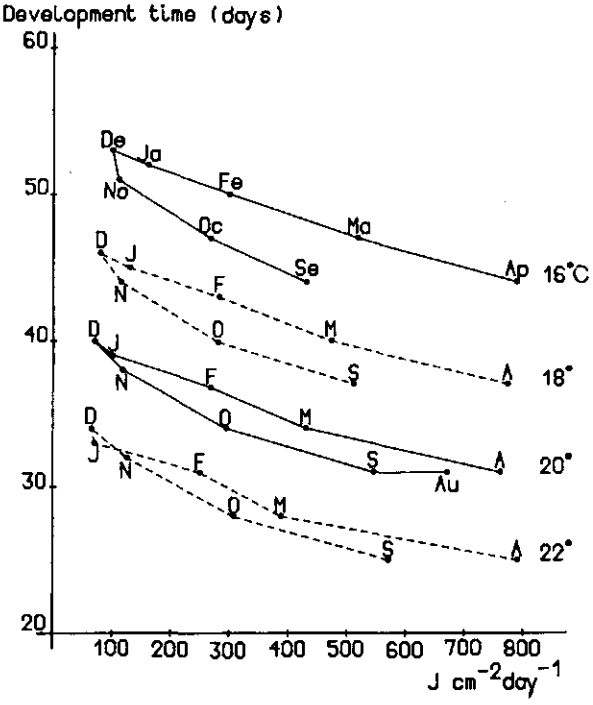
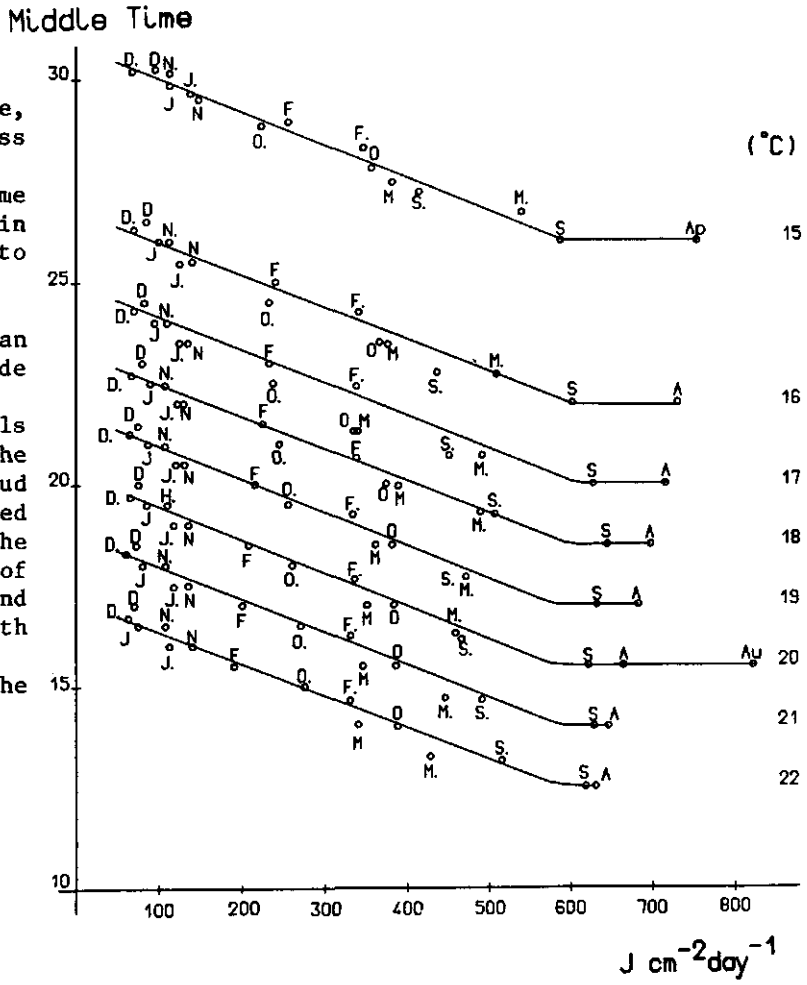


Fig.11 'Sweet Promise', grown in glasshouse soil. Development time in relation to the mean daily inside irradiance, date of bud break and the mean temperature. The capitals alongside the lines represent the first day of the corresponding month.

Fig.12 Sweet Promise, grown in glass-house soil. Middle time (see text) in relation to the mean temperature and the mean daily inside irradiance. The capitals represent the months of bud break: naked capitals the first day of the month and capitals with a dot the middle of the month.



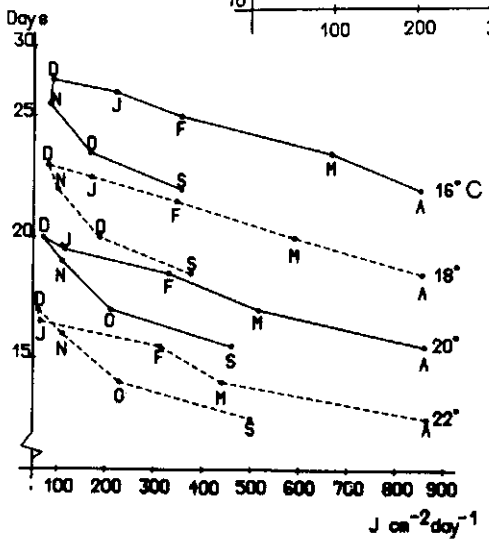


Fig.13 'Sweet Promise', grown in glasshouse soil. Time in days from the Middle Time until harvest in relation to the mean temperature and the mean daily inside irradiance. The capitals represent the date of bud break at the first day of the corresponding month.

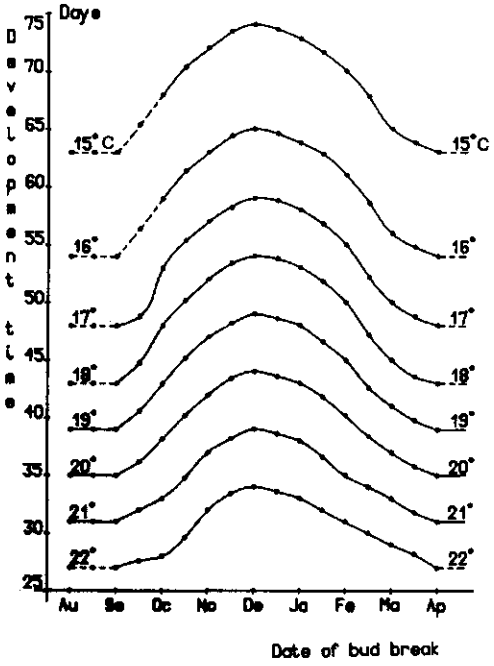


Fig.14 'Varlon', grown in glasshouse soil. 'Model' for the development time in days from bud break until harvest, in relation to the mean temperature and the date of bud break.

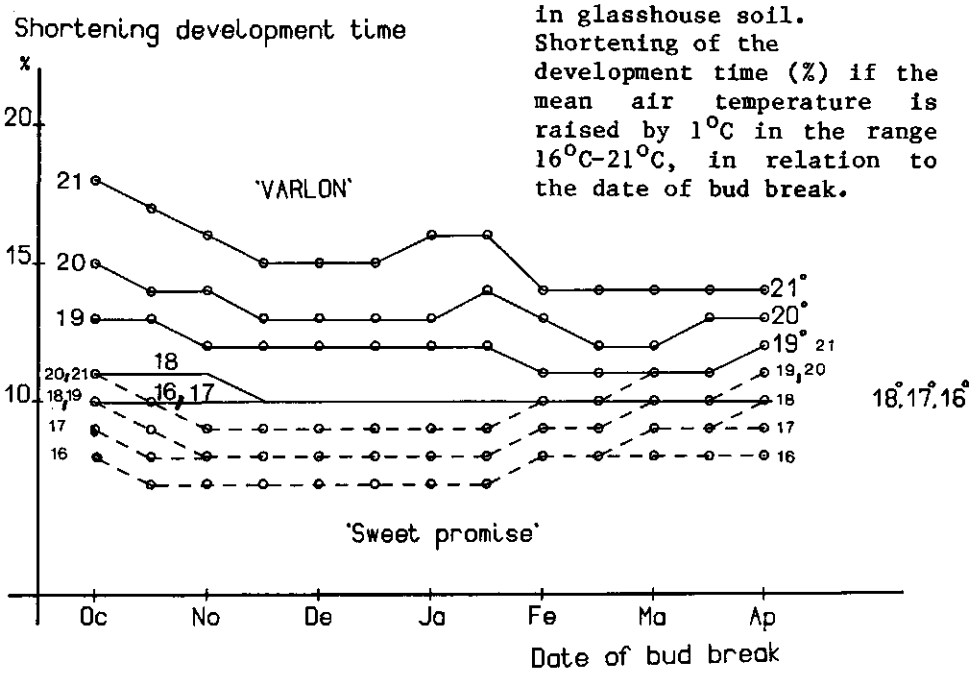
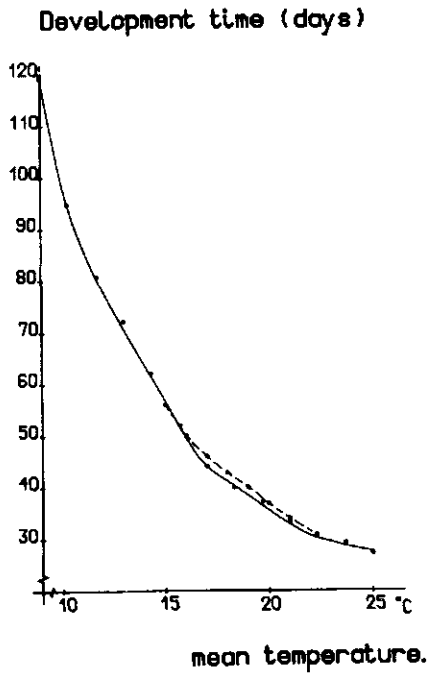


Fig.15 'Sweet Promise' (broken lines, small figures) and 'Varlon' (solid lines, large figures), grown in glasshouse soil. Shortening of the development time (%) if the mean air temperature is raised by 1°C in the range 16°C-21°C, in relation to the date of bud break.

Fig.16 'Sweet Promise', grown in glasshouse soil. Development time in days from bud break until harvest in relation to the mean air temperature. The solid line represents data from experiments with container grown roses in growth rooms and the broken line data from experiments with soil grown roses in the glasshouse.
$y=237.07e^{-.092x}$ ($r=-.987$).



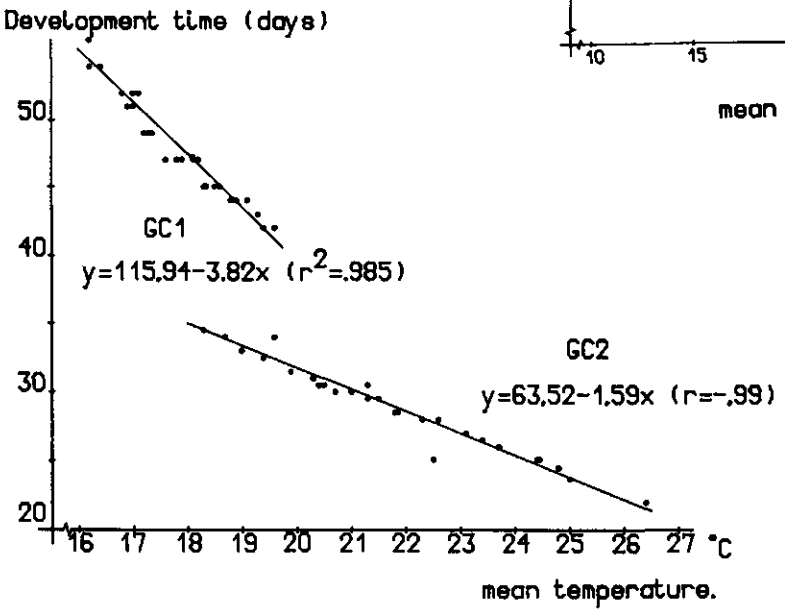


Fig.17 'Sweet Promise', container grown in the glasshouse. Development time in days from bud break until harvest in relation to the mean temperature. The 27 dots per line originate from 27 different combinations between temperature and stage of development. The two lines represent two experiments (GC1 and GC2, see text).

5. FRESH WEIGHT OF SHOOT AND FLOWER BUD

5.1. INTRODUCTION

In this chapter the influence of the temperature on fresh weight of shoot and flower bud is the subject. No special attention is paid to dry weight, which was between 25 % and 30 % of the fresh weight.
Fresh weight is of direct importance to the grower with respect to the market value of the rose. Besides the climate factors irradiation and air temperature already mentioned in previous chapter, the factor air humidity, also plays a role. Air humidity directly influences transpiration of the plant and thus its water balance (Bierhuizen and Slatyer 1965, Kramer 1983).
If it is assumed that the water potential at the evaporating surfaces in the leaves is zero, or close to zero, the transpiration flux of water vapour is proportional to the vapour pressure deficit (VPD) of the air outside the leaf at the same temperature (Kramer 1969, Aston 1973, Bunce 1984), and inversely proportional to leaf and air diffusion resistance (Bierhuizen and Slatyer 1965, Kramer 1983). Transpiration influences the water potential of the plant (Elfving et al. 1972). A high water potential (close to zero) stimulates cell enlargement and thus leaf and stem growth (Slatyer 1967, Boyer 1968, 1970) and, as a consequence, yield. This was reported for different plant species (Plant et al. 1974, Frenz and Lech 1981, Wiebe 1981.) The water potential of the leaves influences stomatal aperture which in its turn influences the carbon dioxide flux into the leaf, and successively photosynthesis and as a consequence growth and yield (Brix 1962, Boyer 1970, Morison 1983, Bunce 1984). Besides this indirect effect via the water balance, also a direct effect of air humidity on stomatal aperture has been reported for some species (Lange et al. 1971, Schulze et al. 1972, Sheriff et al. 1975).
If a low air humidity causes too high a transpiration, the plant runs

into problems with water stress and many aspects of plant growth can be affected (Boyer 1970, Hsiao 1973, Kramer 1983). Irreversible reduction in growth as a result of low water potentials caused by low air humidities, was reported by Boyer (1970). Such a negative effect on growth can sometimes be offset by a very rapid growth if the water status of the plant is brought back into balance (Gates 1955, Owen and Watson 1956).

Although the influence of air humidity on growth is imminent, there are contradictory reports in literature (see review by O'leary 1975). In general, low air humidities and high VPD's result in a decrease in fresh and dry weight and a decrease in stem length and leaf area, while high humidities and low VPD's lead to the opposite reaction (Kristofferson 1963, Cotter 1967, Krizek et al. 1971, Ford and Thorne 1974, Swalls and O'leary 1975, Tibbit and Bottenberg 1976). Other research however showed no clear influence of air humidity on growth (Hughes 1965, Nonnecke et al. 1971, O'leary and Knecht 1971, 1972, Sanden 1985).

If leaf and air temperature are close, the actual VPD between the saturated air at the intercellular evaporating surfaces inside the leaf and the surrounding air outside the leaf is close to the VPD of that outside air. Leaf and air temperature can differ however. This is especially the case in situations in which strong radiation from the sun or from heating pipes are involved, or in situations with strong leaf cooling by transpiration or heat losses by radiation to the cold glasshouse cover (Van den Berg 1986).

5.2. MATERIALS AND METHODS

In chapter 4 a 'model' was developed for the development time of a shoot. That 'model' was based on data from labeled shoots which were monitored on a weekly base. The same method was used to construct a 'model' on fresh shoot and flower bud weight at harvest. For the 'model' on fresh shoot weight the weekly means of all roses harvested

in the experimental plots were used, the labeled as well as the unlabeled ones. For the 'model' on bud weight the mean of the week groups of the labeled shoots was used. The 'models' were also analysed with the method of linear least square regression (see Appendix 3).
Plant materials, methods, conditions, definitions, abbreviations and codes of the experiments have been described in Chapter 2.

5.3. RESULTS

5.3.1. A 'MODEL' FOR FRESH SHOOT WEIGHT

The 'model' for fresh shoot weight is shown in Figure 18 for 'Sweet Promise' and in Figure 19 for 'Varlon'. These figures show the date of bud break on the horizontal axis and total fresh shoot weight, including the part of the shoot that remains on the shrub on the vertical axis (right scale) and also the weight of the cut rose (left scale). The remaining part that left on the shrub after cut was at average 10% of the total shoot weight. If a linear regression is fitted for both 'models', the following equations are found: (For abbreviations see **2.8.**).

Sweet Promise: **FSW** = -9.76 + 0.0008962**RSUM** + 0.4372**RH** - 0.5450**T**
(R^2* = 96.7%).

Varlon: **FSW** =-44.64 + 0.0004618**RSUM** + 0.7174**RH** + 0.5346**T**
(R^2* = 97.2%).

The proportional decrease in fresh weight, at a temperature increase of 1°C, compared to a given mean temperature in the range 16°C through 21°C, is shown in Figure 20.
The figure makes it clear that the decrease in weight is stronger for 'Sweet Promise' than for 'Varlon' and in midwinter it is bigger than in autumn and spring.

5.3.2. FRESH SHOOT WEIGHT AND INTERACTION WITH SHOOT STAGE AND TEMPERATURE

Interaction between temperature, stage of shoot development and shoot weight was studied for 'Sweet Promise' in the glasshouse. In this study, transferable container grown roses were used.
In the experiments 27 different combinations of temperature and developmental stage were imposed (GC1,GC2). The result of experiment GC1 is shown in Figure 21. This figure shows a negative linear relationship between shoot weight and temperature during development time. The linear relation accounts for nearly 95% of the variance in the data. A further analysis of the residuals did not show any structure. The experiment was repeated in May of the same year and showed qualitatively the same results, which are not shown separately (GC2). No significant interaction was found between temperature and shoot stage on fresh shoot weight.

5.3.3. FRESH SHOOT WEIGHT AND TEMPERATURE DISTRIBUTION BETWEEN DAY AND NIGHT

The experiments on this subject are divided into two groups:

5.3.3.1. DAY TEMPERATURE HIGHER THAN NIGHT TEMPERATURE

In practice the temperature is commonly higher during the day than during the night. In experiment (GS3) the influence of the diurnal temperature distribution on fresh shoot weight was studied. In this experiment, 7 combinations of day and night temperatures were made around the same mean temperature of 18 ^{o}C. The results of this experiment are listed in Table 3.

Table 3. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Average fresh shoot weight (g) at harvest for 7 night/day temperature combinations at the same daily mean of 18°C. Period November until May. All temperatures were realised between 18.2°C to 18.7°C. Treatments with the same letter do not differ at the 0.05 level of significance (Tukey's Yardstick).

	Fresh shoot weight at harvest (g).	
hrs night/hrs day (°C)	'Sweet P.'	'Varlon'
- 12 hrs 14 / 12 hrs 22	16.7 a	23.7 ab
- 6 hrs 16 followed by 6 hrs 12 and 12 hrs 22	16.4 a	21.9 a
- 12 hrs 15 / 12 hrs 21 (3 replications)	16.9 a	24.3 b
- 12 hrs 16 / 12 hrs 20	16.2 a	22.5 ab
- 6 hrs 18 followed by 6 hrs 14 and 12 hrs 20	17.0 a	24.7 b
- 12 hrs 17 / 12 hrs 19	17.2 a	22.8 ab
- 24 hrs 18	16.8 a	23.3 ab

Table 3 shows the average fresh shoot weight of the cut roses. No reliable differences between the treatments were found for 'Sweet Promise'. The results for 'Varlon' show some differences, but a pattern is absent. The deviations must be due to chance.

5.3.3.2. DAY TEMPERATURE LOWER THAN NIGHT TEMPERATURE

Compared with the situation in the practice this is a reversed condition. In the first experiment on this subject (GS4), four 12 hrs night/12 hrs day temperature treatments were performed: 16/22, 18/20, 20/18 and 22/16 (°C) respectively. The results are listed in Table 4,A and in the Figures 22 and 23.

Table 4. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Average fresh shoot weight (g) during harvest. For three winter seasons and four temperature treatments per season with the same daily mean of 19°C. Treatments with different letters differ at the 0.05 level of significance (Tukey's Yardstick).

Fresh shoot weight during harvest (g)

	'Sweet Promise'			'Varlon'		
	A	**B**	**C**	**A**	**B**	**C**
Treatment	**GS4**	**GS5**	**GS6**	**GS4**	**GS5**	**GS6**
1.	17.7 a	16.7 a	17.5 a	19.5 a	20.2 a	20.4 a
2.	15.8 b	17.8 b	17.8 a	18.9 a	19.7 a	20.7 a
3.	14.9 bc	17.0 ab	16.9 b	17.5 b	20.8 a	20.1 a
4.	14.2 c	16.7 a	17.7 a	14.7 c	21.2 a	20.2 a

Legend:

A. (GS4) *October 1980 until May 1981.*
12 hrs night/12 hrs day temperature (°C)
Installed daily mean is 19°C for all treatments.
1. = 16/22
2. = 18/20
3. = 20/18
4. = 22/16

B. (GS5) *October 1981 until May 1982.*
Installed daily mean is 19°C for all treatments.
1. = 24 hours 19°C
2. = 22 " 18.5°C and 2 hours 24°C (from 18.00h until 20.00h).
3. = 20 " 18.0°C " 4 " " (" " " 22.00h).
4. = 18 " 17.3°C " 6 " " (" " " 24.00h).

C. (GS6) *October 1982 until April 1983.*
Installed daily mean is 19°C for all treatments.
From November through 15 January the same treatments as B.
From 16 January
1. = 24 hours 19°C.
2. = 21 " 18.3°C and 3 hours 24°C (from 18.00h until 21.00h).
3. = 18 " 17.3°C " 6 " " (" " " 24.00h).
4. = 15 " 16.0°C " 9 " " (" " " 03.00h).

Table and figures both show a tendency for the weight to decrease when, at a given mean temperature, day temperature decreases and night temperature increases.

This effect of day and night temperature was studied further in airconditioned glasshouses with container grown roses cv. Sweet Promise (GC3 and GC4).

These experiments started with two groups of roses of which the lateral buds had just broken (= 1 cm). One group was installed at a 12 hrs 24^{o}C night/12 hrs 16^{o}C day temperature regime and the other group at the reversed temperature regime. Transferring containers between the two compartments resulted in 10 treatments. The growth cycle from cut to cut for all treatments was the same: 50 days. The influence on shoot weight is shown in Figure 24.

In this figure the horizontal axis represents the treatments and the vertical axis shows the mean fresh shoot weight at harvest. In the figure, two parallel straight lines can be seen. The upper line represents the results from the treatments that started with a higher day than night temperature, the lower line the treatments that started with the reversed temperatures. The figure shows that the more nights with a higher night than day temperature, the lesser the weight. It also makes a difference whether shoot development starts at a high or at a low night temperature. This implies an interaction of temperature with the stage of shoot development.

More experiments with higher night than day temperatures were performed in the Phytotron. In one experiment with a photoperiod of 8 hours, 15 different temperature treatments were realised. The effect on fresh shoot weight is shown in Figure 25. This figure shows the mean temperature on the horizontal axis and fresh shoot weight on the vertical axis. The treatments are written next to the dots which represent the results of the experiment.

The figure shows that:

(1) If at a given day temperature, night temperature decreases resulting in a decrease of the mean temperature, fresh shoot

weight increases (solid lines).

(2) If at a given night temperature, day temperature decreases resulting in a decrease of the mean temperature, fresh shoot weight decreases (broken lines "perpendicular" to the solid lines).

(3) At a given mean temperature, a constant temperature during day and night results in the heaviest shoots (uppermost broken line).

(4) At a given mean temperature, a bigger difference in temperature between day and night results in a lower shoot weight.

5.3.4. FRESH SHOOT WEIGHT AND LENGTH OF A DIURNAL PERIOD WITH A HIGHER NIGHT THAN DAY TEMPERATURE

Experiment GS4 showed that a 12 hours higher night than day temperature results in a decrease in shoot weight. The effect of a shorter night period with a higher than day temperature was studied in two experiments (GS5 and GS6). In these experiments 4 treatments were given, one with a constant temperature of 19^{o}C and three with a night period of 24^{o}C of different lengths. These periods with a high temperature started at sunset. The daily mean temperature was 19^{o}C for all treatments. The results of these two experiments are listed in Table 4B and 4C. This table shows no reliable difference between the treatments for the cv. Varlon (P=0.05). For the cv. Sweet Promise one of the four treatments differs significantly (P=0.05) in both years. A tendency cannot be seen in these differences, however. The deviations must be due to chance.

5.3.5. FRESH WEIGHT OF THE FLOWER BUD AT HARVEST AND ITS FRACTION OF TOTAL SHOOT WEIGHT

The relation between date of bud break and flower bud weight during

harvest is shown for 'Sweet Promise' in Figure 26 and for 'Varlon' in Figure 27. The corresponding linear regression equations are: (for abbreviations see **2.8.**).

'Sweet P.':**FBW** = 41.0- 3.29**T** + 0.0735**DL** + 0.26**RH**- 0.000266**RSUM**
(R^2*=92.4%)

'Varlon':**FBW** = 34.8 - 3.29**T** + 0.1143**DL** - 0.000310**RSUM** + 0.198**RH**
(R^2*=91.1%)

The proportion of total fresh shoot weight belonging to the flower bud was calculated too and the results are shown in Figure 28 for 'Sweet Promise' and in Figure 29 for 'Varlon'. In these figures the horizontal axis shows the date of bud break and the vertical axis the flower bud fraction in percentages. For both cultivars the isotherms show an optimum. The reaction to temperature during decreasing light intensities is opposite to that during increasing light intensities. On a distinct date of bud break a linear relation between the percentage of bud weight and temperature appears. Such a linear relation also appears in an experiment with 27 different temperature combinations (GC1) in the temperature range 16.2°C - 19.5°C (Figure 30). An experiment with 25 temperature combinations, performed in the Phytotron, also showed a linear relation in the same temperature range (Figure 31). For temperatures lower than about 13°C, the flower bud fraction increases very quickly, however.

If at a given daily mean temperature, night temperature increases and day temperature decreases, the flower bud fraction shows a tendency to increase slightly (Table 5). For 'Sweet Promise'this increase is not significant, however (P=0.05).

Table 5. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Flower bud fraction in percentages of total fresh shoot weight of the cut roses during harvest. Period November until May (GS3). Daily mean temperature is 18°C for all treatments. Day and night temperature both 12 hours.

Treatments Night/Day(°C)	Flower bud fraction of total fresh shoot weight (%) 'Sweet Promise'	'Varlon'
14/22 (mean of 2)	21.5 a	21.4 a
15/21 (mean of 3)	21.6 a	22.0 a
16/20 (mean of 2)	21.7 a	21.6 a
17/19	22.5 a	23.4 b
18/18	22.3 a	23.7 b

If on a diurnal base the night temperature is 12 hours higher than the day temperature, the increase in bud fraction becomes more pronounced (Table 6A). If the high night temperature lasts no longer than 6-9 hours the effect does not clear appears (Table 6B,C).

Table 6. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Flower bud fraction in percentages of total fresh shoot weight of the cut roses during harvest. Results from three experiments.
Legend: see Table 4.

	Flower bud fraction of total fresh shoot weight (%) 'Sweet Promise'			'Varlon'		
	A	B	C	A	B	C
Treatment	GS4	GS5	GS6	GS4	GS5	GS6
1.	20.2 a	24.0 a	24.7 a	20.4 a	21.6 a	22.0 a
2.	21.8 b	23.6 a	24.2 ab	21.4 ab	22.9 bc	23.8 abc
3.	24.2 c	25.0 a	22.8 bc	23.2 b	22.7 bc	21.4 ab
4.	24.2 c	24.3 a	23.3 ab	22.3 b	22.0 ac	24.2 c

In experiments with container grown roses in the glasshouse, which only lasted one flush, no clear influence of an increasing night temperature on the flower bud fraction could be seen.

5.3.6. AVERAGE INCREASE IN FRESH WEIGHT PER SHOOT PER DAY

The average daily increase in fresh weight of the shoot during its development can be taken as a measure for growth vigour or productivity. It was calculated by dividing total fresh shoot weight at harvest by its development time. The results are displayed in Figure 32 for 'Sweet Promise'and in Figure 33 for 'Varlon' . These figures show the date of bud break on the horizontal axis and the average daily increase in fresh weight per shoot on the vertical axis.
In the figure for 'Sweet Promise' (32) two turning-points appear. In the figure for 'Varlon' (33), this is not the case. During the whole period 'Varlon' shows a higher increase in fresh weight at a higher temperature.

5.3.7. MEAN IRRADIANCE DURING THE PRODUCTION OF ONE GRAM FRESH SHOOT WEIGHT

The mean irradiance inside the glasshouse during the production of one gram of fresh shoot weight was calculated by dividing the mean irradiance during shoot growth by the average shoot weight. For 'Sweet Promise' and 'Varlon' this level is shown in Figure 34 and 35 respectively. In these figures the horizontal axis shows the date of bud break and the vertical axis the mean daily irradiance in the glasshouse. The figure for 'Sweet Promise' (34) shows two turning-points which are missing in the figure for 'Varlon' (35). Both figures show that if the irradiance in the glasshouse decreases, less irradiance is needed to produce one gram of fresh weight.

If the mean daily irradiance inside the glasshouse during development is placed on the horizontal axis, a hysteresis effect emerges (Figure 36). At the same average light level, a higher efficiency appears in autumn under decreasing rather than in spring under increasing light conditions. The turning point lies in December.
A hysteresis effect also appears in the relation between fresh shoot weight and the mean daily irradiance inside the glasshouse (Figure 37). A similar graph for fresh weight of the flower bud however shows no hysteresis (Figure 38).

5.4. DISCUSSION

Between the mean temperature during development time and fresh shoot weight a negative linear relation exists (Figures 18 and 19). Such a negative relation for roses was reported earlier by Moe (1969), De Vries an Smeets (1979) and Van den Berg (1980). Shoot weight follows the natural radiation cycle. The lightest shoots emerge from lateral buds broken in December. If light conditions during shoot growth increase, shoot weight increases too. Both cultivars show qualitatively the same reaction. A positive reaction of shoot weight to light has been reported earlier by several authors (Chandler 1954, Carpenter 1972, White 1973, Armitage 1979). The average fresh weight production per shoot per day during shoot development shows differences between both cultivars. For 'Varlon' the average fresh weight production per shoot per day is positively correlated with temperature during the whole period from October until following May (Figure 33). 'Sweet Promise', however, shows two turning-points in its graphs (Figure 32). This difference in behaviour is due to the fact that shoot weight of 'Sweet Promise' shows a stronger decrease at higher temperatures and low light intensities than shoot weight of 'Varlon' (Figure 20). This results in thinner shoots with little growth vigour in winter and a low average daily fresh weight production. When growth increases in spring, average daily fresh

weight production is again positively correlated with temperature.

Final shoot weight is determined by the effect of temperature on the development time and on the average daily fresh weight production. As the effect of a higher temperature on the increase in the average daily fresh weight production is less than on the reduction in development time, shoots grow lighter.

The mean light level inside the glasshouse under which one gram of fresh shoot weight is produced shows, of course, the reversed view (Figure 34 and 35). At a lower light level less light is needed to produce one gram of fresh shoot weight, so 'light efficiency' becomes higher. This reaction to light can be explained by the course of the photosynthetic rate at increasing irradiance (Gaastra 1959, Incoll 1976).

If a linear regression equation is fit for shoot weight, up to about 97% of the variation in the 'models' can be explained in using the explanatory variables: total irradiation, relative humidity (RH) and mean temperature. Compared with the equation for the development time of a shoot this means one extra climate factor: the relative humidity of the air. Instead of the RH, the Vapor Pressure Deficit of the air (VPD) was also used in the regression equations. The percentages variation accounted for scarcely changed; only the coefficients did.

The three variables in the equations are not independent from each other and it is also well thinkable that the variables (RH) and (T) are highly correlated with an unknown variable which in its turn is highly correlated with fresh shoot weight. In this last situation (RH) and (T) are 'proxies' (see Appendix 3).

For these reasons the coefficients are likely to be unreliable indicators of the importance of the corresponding variable apart from the other ones and one can not use the equations to predict what will happen to fresh weight if one of the variables is changed neglecting the others. The method of linear least square regression was used for analysing and not for predicting the data. It shows that the three variables: RSUM, RH and T together, account for nearly 97% of the variation in the 'models' on fresh shoot weight, but says nothing

about the importance of each of them individualy.
A possible unknown variable correlated with RH and T may be the water potential of the shoot or its turgor. These entities influence cell volume and consequently fresh shoot weight.

In the experiments the average VPD was in the range of 1.36 - 5.82(mm Hg), corresponding to a relative humidity of 70% - 90% in a temperature range of 16°C - 22°C. According to literature, it is not to be expected that in this range there is a great influence on growth. Mortenson (1984) did not find any influence on fresh weight in this range for roses. During freezing weather however, when heating pipes were hot, low humidities at a level that can influence growth occured from time to time. Daily humidities as low as 40% were measured under those circumstances.

In six experiments performed in the Phytotron with the cv. Sweet Promise a negative 'Thermoperiodicity' on shoot weight was found. This means less growth under a diurnal change in temperature in comparison with the growth measured under constant temperature conditions with the same mean (Figure 25). The term 'Thermoperiodicity' was introduced by Went (1944) and is used for 'responses of plants to cyclic temperature variations' (Went 1953). The results for roses agree with reports on dry weight production of other species: beans (Dale 1964), tomatoes (Hussey 1965, Friend and Helson 1976), wheat, oats, corn, pea and cucumber (Friend and Helson 1976). Warrington et al.(1977) found a positive thermoperiodicity for dry weight production of Soybeans, however.

In the Phytotron experiments with 'Sweet Promise', shoot weight was on average 10% lower, compared with shoot weight at constant temperature, if day temperature was higher than night temperature. If night temperature was higher than day temperature this difference increased to about 30%. The deleterious effect of a higher night than day temperature is clearly demonstrated by Figure 25.

In the glasshouse experiments with soil-grown roses we only found a clear negative thermoperiodicity for shoot weight when night temperature was higher than day temperature during 12 hours at a

diurnal basis, but not if night temperature was lower than day temperature (Table 3). These results from soil grown roses in the glasshouse are contradictory to the results acquired in the Phytotron. The difference is probably caused by the fact that in the experiments with soil grown roses, average root temperatures were scarcely influenced by the diurnal switch between day and night temperature, but in the experiments in the Phytotron they were strongly influenced. Depending on the imposed night/day temperature combination, root temperatures decreased until 13°C or even 9°C. Such low root temperatures influence the water balance of the plants by enhancing the flow resistance for water in the roots (Kramer 1940, Cameron 1941, Kuiper 1964). If the plants are transferred from low to high temperature, the warming up of the roots stays behind the shoot. The transpiration suddenly increases and the high root resistance results in a low water potential and a stress situation of the shoot, which decreases growth. A decreasing effect of low root temperatures on shoot growth was reported a.o. by Abd el Rahman et al. (1959) for tomatoes, by Brouwer (1964) for beans and by Kleinendorst and Brouwer (1970, 1972) for maize. Cooper 1973 reviewed this subject. The effect of the higher night than day temperature on growth can be explained by the phenomenon that at night, growth in fresh weight is reported to be higher than at daytime (Kleinendorst and Brouwer 1970, Challa 1976). This can be explained by the generally high water potential at night, when transpiration is lower than in daytime. This high water potential makes it possible for the plant to reach a turgor far above the threshold value for cell elongation (Boyer 1968).

A reversed temperature regime resulting in a lower water potential at night might reduce growth in such a situation.

The graphs for shoot weight show a negative linear relation with the mean daily temperature (Figures 18, 19 and 21). A clear interaction between temperature, development stage of the shoot and shoot weight was only found when night temperature was higher than day temperature. When imposed directly after bud break, such a regime led to shoots of less weight than when imposed in a later stage of shoot

development (Figure 24). During the winter season, flower bud weight shows the same behaviour as shoot weight. The linear regression equation accounts for about 92% of the variation in the 'models'. In the equation daylength appears as a significant explanatory variable. Daylength influences the weight of the flower bud. The bud fraction moves opposite to total shoot weight and opposite to the natural radiation cycle. In autumn the flower bud fraction is negatively correlated with temperature, but in spring the correlation is positive. This behaviour of the flower bud was caused by the fact that the weight of the vegetative part of the shoot was more strongly influenced by the natural radiation cycle than the generative part, to which the flower bud belongs. This may be caused by a relatively stronger sink position of the flower bud during shortening days, compared to the leaves.

The bud fraction is mainly determined by the mean temperature and not clearly influenced by the temperature distribution during the development of the shoot (Figure 30) or by the diurnal temperature distribution (Figure 31). Very low temperatures, below 13^{o}C, strongly increase the flower bud fraction. Flower bud growth is less restrained at these temperatures than stem and leaf growth.

The difference in growth behaviour between flower bud and the generative part of the shoot is also clearly demonstrated by the relation between the flower bud and total shoot weight with the mean irradiance during shoot growth. Total shoot weight shows hysteresis with the time of the year (Figure 37), but the weight of the flower bud does not (Figure 38). Because the flower bud surface per gram is much lower than for the rest of the shoot, this difference in behaviour may be partly caused by a difference in evaporation in relation to air humidity.

At the same temperature and irradiance the average fresh weight production per shoot per day is higher in October/November than in January/February (Figure 36). This can be partly caused by a difference in the humidity of the air, which was higher in the first period. However internal factors in the plant, e.g. 'growth vigour'

may also play a role. In autumn reserves in the plant are higher than in the beginning of the year.

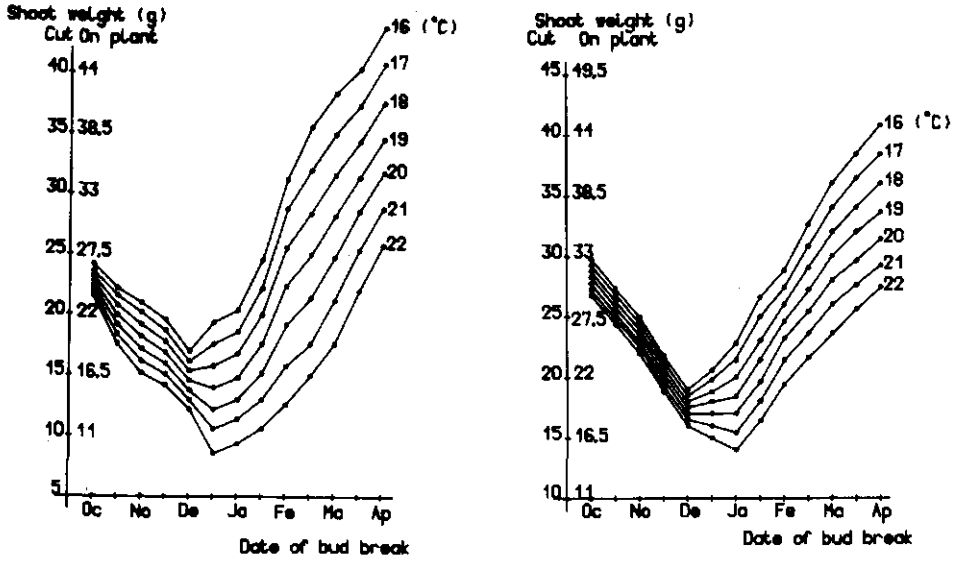


Fig.18 (l) 'Sweet promise' and **Fig.19** (r) 'Varlon', grown in glasshouse soil.'Model' for fresh shoot weight (g) in relation to date of bud break and the mean temperature.

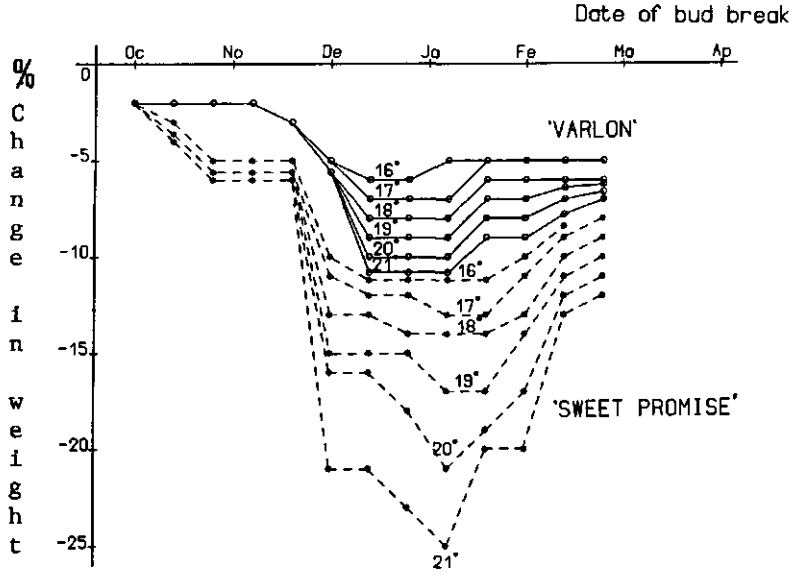


Fig.20 'Sweet Promise' (broken line) and 'Varlon' (solid line), grown in glasshouse soil. Change in fresh weight if the mean temperature is raised by $1^{o}C$ on the temperature range $16^{o}C$ - $21^{o}C$, in relation to the date of bud break

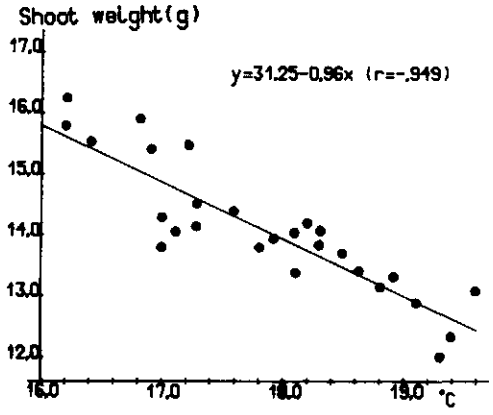
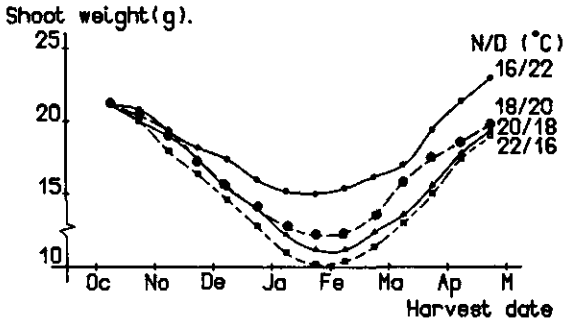


Fig.21 'Sweet Promise', container grown in glasshouse. Fresh shoot weight in relation to the mean temperature, for 27 temperature treatments depending on shoot stage (see text).

Fig.22 'Sweet Promise', grown in glasshouse soil. Fresh shoot weight of cut roses for four night/day temperature treatments at one daily mean of 19°C.



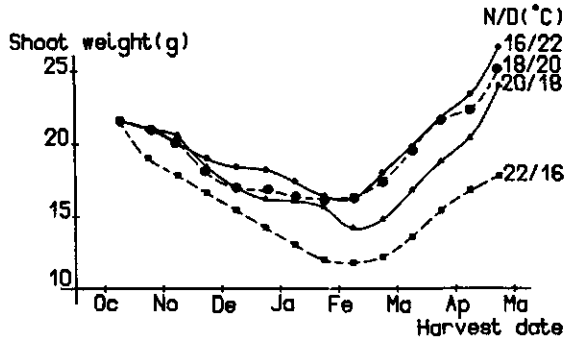


Fig.23 'Varlon', grown in glasshouse soil. Fresh shoot weight of cut roses for four night/day temperature treatments at one daily mean of 19°C.

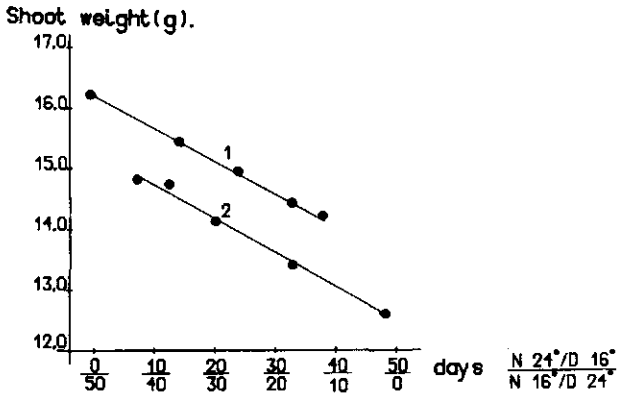


Fig.24 'Sweet Promise', container grown in the glasshouse. Relation between fresh shoot weight and number of nights with a higher (24°C) than day temperature (16°C). Daily mean is 20°C for all treatments. Growth cycle is 50 days for all combinations.
line 1. Shoots started after bud break with a lower night than day temperature, followed by nights with a higher than day temperature.
line 2. Shoots started after bud break with a higher night than day temperature, followed by nights with a lower than day temperature.

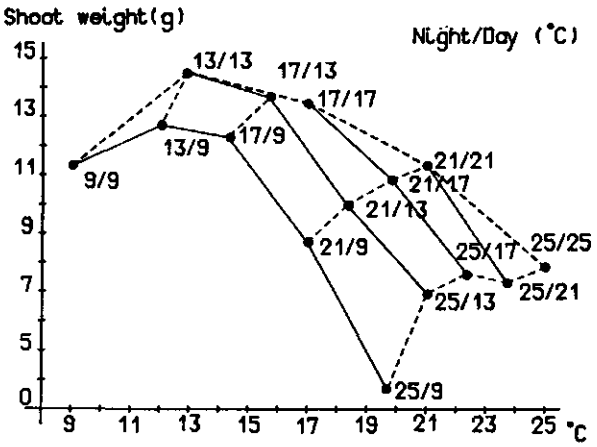
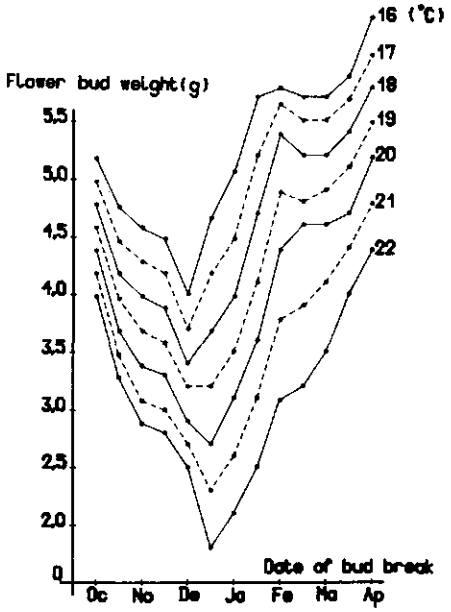


Fig.25 'Sweet Promise', container grown in growth rooms. Fresh shoot weight in relation to the mean temperature, for 15 different 16hrs dark/8hrs light temperature combinations.



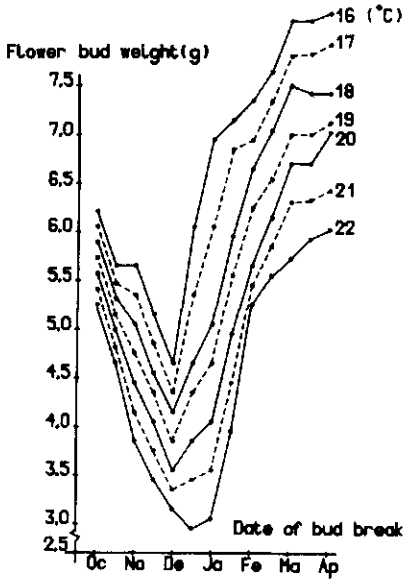
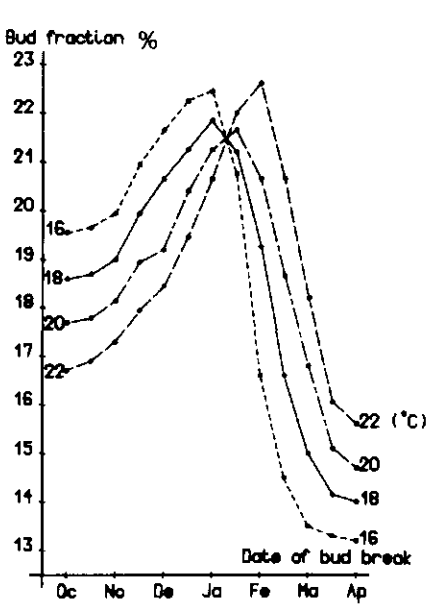


Fig.26 (l) 'Sweet Promise' and **Fig.27** (r) 'Varlon', grown in glasshouse soil. 'Model' for fresh flower bud weight (g) during harvest in relation to date of bud break, and the mean temperature.



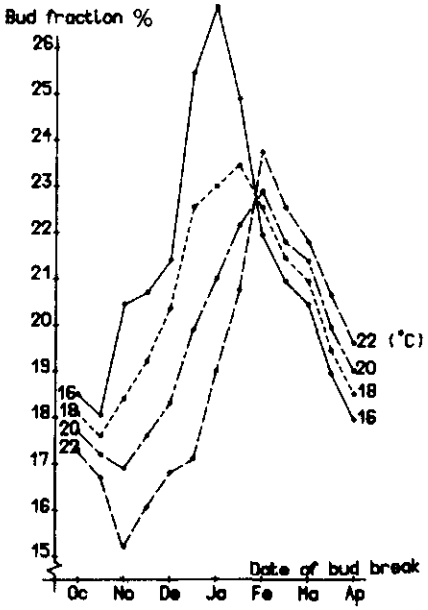


Fig.28 (l) 'Sweet Promise' and **Fig.29** (r) 'Varlon', grown in glasshouse soil. Flower bud as fraction of total fresh shoot weight, in relation to date of bud break and the mean temperature.

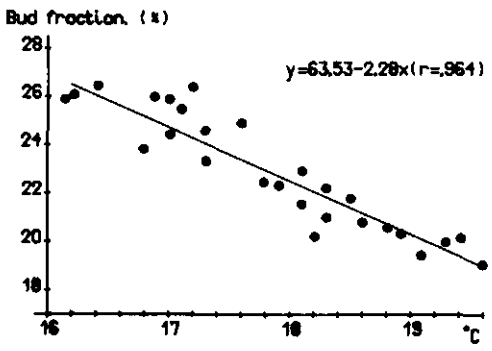


Fig.30 'Sweet Promise', container grown in the glasshouse. Flower bud as fraction of fresh shoot weight in relation to temperature.

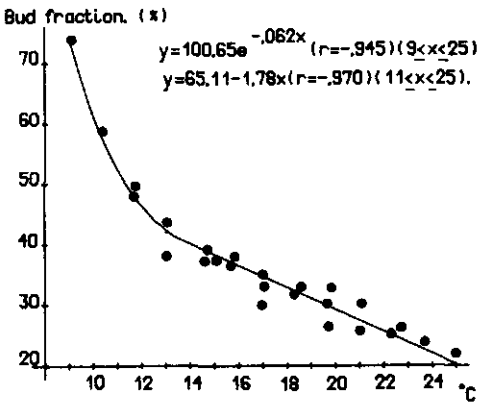
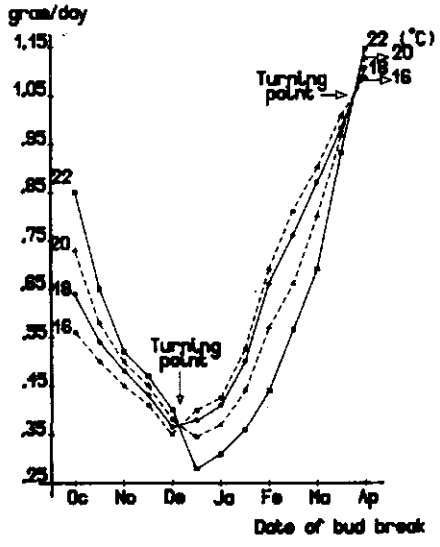


Fig.31 'Sweet Promise', container grown in growth rooms. Flower bud as fraction of fresh shoot weight, in relation to temperature.



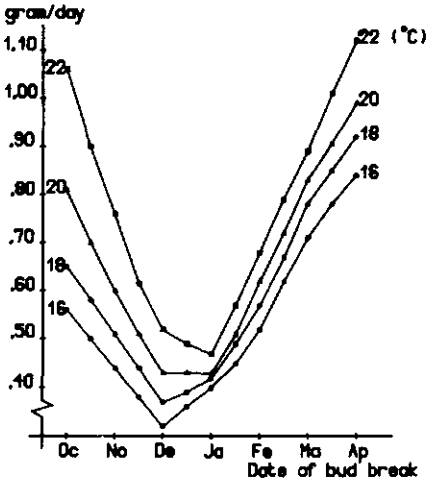
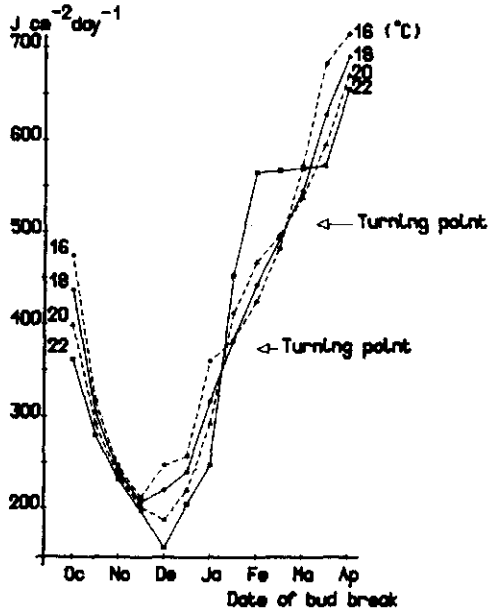


Fig.32 (l) 'Sweet Promise' and **Fig.33** (r) 'Varlon', grown in glasshouse soil. Relation between average daily increase in fresh weight per shoot with day of bud break and the mean temperature.



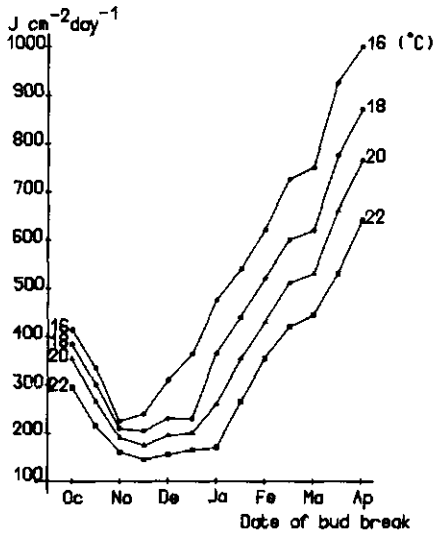


Fig.34 (l) 'Sweet Promise' and **Fig.35** (r) 'Varlon', grown in glasshouse soil. Relation between average inside irradiance during the production of one gram of fresh shoot weight with date of bud break and the mean temperature.

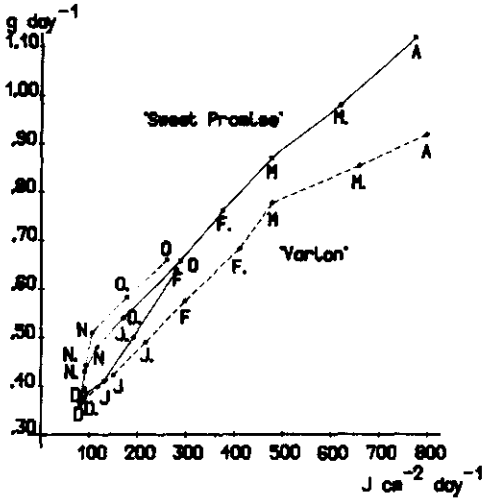


Fig.36 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between the fresh weight production in grams per shoot per day and the mean daily inside irradiance. Naked capitals refer to the date of bud break on the first day of the corresponding month and capitals with a dot to the middle of the month. Mean temperature 18°C.

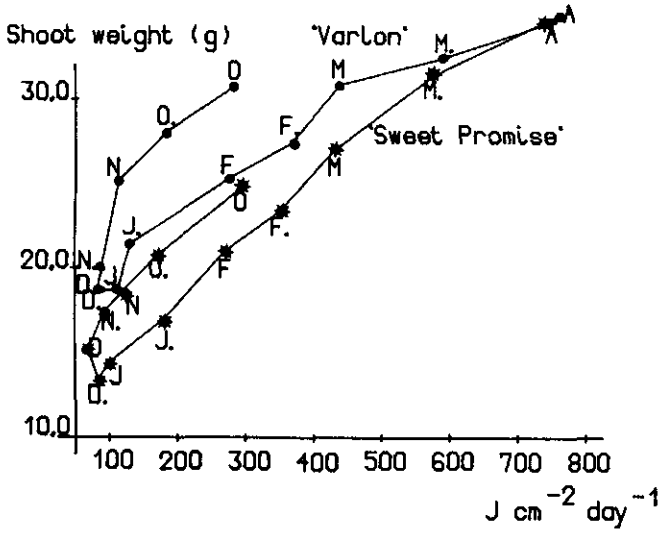


Fig.37 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between fresh shoot weight and the mean inside irradiance. For capitals:see Fig.36. Mean temperature 20°C.

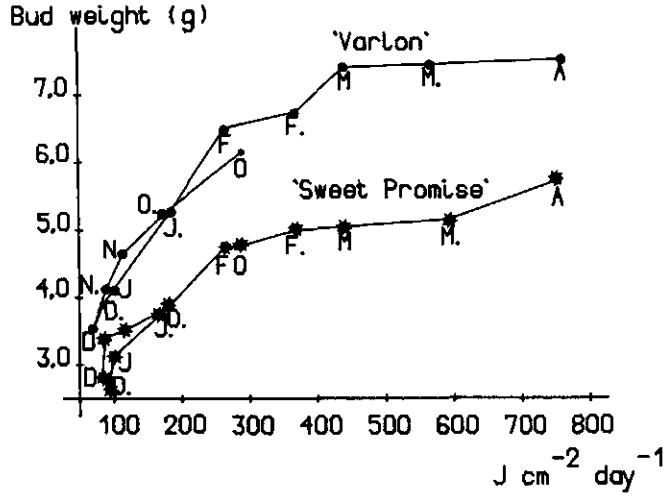


Fig.38 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between fresh flower bud weight and the mean inside irradiance. Capitals: see Fig.36. Mean temperature 20°C.

6. MEASUREMENTS OF THE SHOOT

6.1. INTRODUCTION

This chapter deals with the measurements of the rose shoot. Together with fresh weight, shoot size determines the market value of the rose. At the auction, long thick stems with big flower buds are considered being top quality.

The influence of the climate factors: temperature, irradiation and daylength on shoot length has been studied by several research workers. A decrease in shoot length if temperature increases was reported by a.o.: Moe and Kristofferson (1969), Moe (1972a,1973), De Vries et al. (1980,1982) and by Brown and Omrod (1980). In some experiments an optimum temperature for shoot length was found (Byrne et al.1978, Van den Berg 1981).

At low air temperatures, rootzone warming increased shoot length of soil grown roses (Brown and Omrod 1980), container grown roses (Zeroni and Gale 1982) and roses grown in nutrient film (Moss 1983, 1984, Moss and Dalgleish 1984).

A decrease in shoot length caused by short days was reported by Moe (1972a) for roses in growth rooms, and by Carpenter et al. (1972) for glasshouse roses. This reaction to daylength is not uncommon for woody plants. It was a.o. reported by Barrick et al. (1973) for Rhododendron.

Reports on the effect of the irradiance on shoot length are not unequivocal. In experiments in growth rooms, De Vries and Smeets (1978) and De Vries et al. (1982) found longer stems at higher irradiance. Moe (1972a) however, found a shortening effect of an increase in irradiance. Tsujita and Dutton (1983) found a lengthening effect of supplementary lighting in greenhouses in winter. Carpenter et al. (1972) and Cockshull (1975) however, reported a shortening effect.

Several authors found no significant effect of supplementary lighting on shoot length (Wiseley and Lindstrom 1972, White and Richter 1973,

Armitage and Tsujita 1979).

These sometimes contradictory results may partly be accounted for by a phenomenon reported by Carpenter and Rodriguez (1971b), who found that supplementary lighting reduced the formation of non flowering 'blind' shoots. This resulted in a higher number of small flowering shoots, that otherwise would have grown blind. These small shoots reduce average shoot length. Apart from this, the experiments reported in the literature were performed with different cultivars and plant material under different conditions, which may have influenced shoot length strongly.

Not only climate factors, but also the plant, or more precisely the subtending or parent shoot, is reported to have a clear influence on shoot length. Byrne and Doss (1981) reported that thicker parent shoots produced longer daughter shoots.

The subject of this chapter is not only shoot length, but also discussed are: neck length, the length and width of the flower bud, the diameter of shoot and neck and the number of leaves on the shoot. Their relation with temperature under natural light conditions was studied for soil grown roses of the cvs. Sweet Promise and Varlon sprouted in the glasshouse in the period October until April. Supplementary studies were performed with container grown 'Sweet Promise' roses in the glasshouse and in growth rooms (Phytotron).

6.2. MATERIALS AND METHODS

The methods used in this chapter do not deviate from those in the previous chapters. The 'models' of shoot length were based on the means of the weekgroups, which included all the roses harvested in an experimental plot, labeled and unlabeled ones. The 'models' on neck length, flower bud length and width, diameter of the shoot at the cut and at the middle of the neck and number of leaves of the cut roses were based on weekly means of the labeled shoots. The 'models' were also analysed by the method of linear least square regression (see Appendix 3).

Plant material, methods, conditions, definitions, abbreviations and codes of the experiments have been discussed in Chapter 2.

6.3. RESULTS

6.3.1. A 'MODEL' FOR SHOOT LENGTH

The 'models' for shoot length are shown in the Figures 39 and 40 for the cvs. Sweet Promise and Varlon respectively. On the horizontal axis the figures show the date of bud break and on the vertical axis total shoot length at harvest stage, measured from the joint. The shoot fraction that remained on the shrub after cut was known from the labeled ones. This information was used to calculate also for the non labeled shoot total shoot length. The regression equations that fit closest are for: (for abbreviations see 2.8.).

'Sweet P.': $SL = -879 + 0.680WPS + 121.6T - 2.9T^2 + 0.0696ADR + 2.66RH$
(R^2*= 86.2%).

'Varlon': $SL = -1478 + 0.969WPS + 223.7T - 6.0T^2 + 0.0460ADR$
(R^2*= 88.2%).

Figures 39 and 40 show an optimum temperature for shoot length for 'Sweet Promise' between 18°C and 19°C and for 'Varlon' between 17°C and 18°C.

6.3.2. SHOOT LENGTH AND INTERACTION WITH SHOOT STAGE AND TEMPERATURE

In two experiments each with 27 combinations between temperature and development stage of the shoot, interaction was studied for 'Sweet Promise' (GC1, GC2). When shoot length was plotted against the mean daily temperature during shoot growth, a negative correlation appeared (Figure 41). All shoots fell in the relatively small range

from 56.6 - 63.6 cm. No clear interaction with the stage of shoot development could be detected.

6.3.3. SHOOT LENGTH AND DISTRIBUTION OF TEMPERATURE BETWEEN DAY AND NIGHT

The experiments on this subject are divided into two groups:

6.3.3.1. DAY TEMPERATURE HIGHER THAN NIGHT TEMPERATURE

The influence of the common diurnal temperature distribution, with a higher day than night temperature on shoot length in the glasshouse is shown in Figure 42 for 'Sweet Promise' and in Figure 43 for 'Varlon' (GS3). These figures shows the harvest date on the horizontal axis and the average shoot length of the cut roses on the vertical axis. The roses were cut at the first five-leaflet leaf above the joint. The figures show an optimum night/day temperature combination for cv. Sweet Promise at 15/21(^{0}C) and for 'Varlon' at 15-16/20-21(^{0}C).

6.3.3.2. DAY TEMPERATURE LOWER THAN NIGHT TEMPERATURE

In three successive winter seasons experiments were performed on this subject with 'Sweet Promise' and 'Varlon' in the glasshouse. In the first experiment (GS4) four different night/day temperature combinations were made at one daily mean temperature of 19^{o}C. Two of the combinations had a higher night temperature than day temperature. Day and night temperature both lasted 12 hours per 24 hours. The results of these treatments on the length of the roses, cut at the first five-leaflet leaf, are shown in Figure 44 for 'Sweet Promise' and in Figure 45 for 'Varlon'. These two figures demonstrate that at the same daily mean temperature, an increase in night temperature results in a decrease in shoot length. The average length of all roses cut during the period November until May is shown in Table 7A. The results show the same tendency as in the former experiment (GS3);

an increase in night temperature, above the optimum, leads to a decrease in shoot length.

Table 7. Rose cvs. Sweet Promise (SP) and Varlon (V), grown in glasshouse soil. Average total shoot length (cm) of cut roses from three experiments with each four different temperature treatments.
Legend: see Table 4.

	Total shoot length (cm)					
	A		B		C	
	GS4		GS5		GS6	
Treatment	SP	V	SP	V	SP	V
1.	62.1 a	64.0 a	58.7 a	65.0 a	63.0 a	66.8 a
2.	57.8 b	60.5 a	58.8 a	65.7 a	61.2 a	65.9 a
3.	53.4 c	56.1 b	58.2 ab	62.6 a	62.6 a	67.1 a
4.	52.3 c	56.1 b	56.4 b	64.0 a	59.6 b	64.8 a

For 'Sweet Promise' the effect of a higher night than day temperature on shoot length was studied in the phytotron too. The results of 25 temperature combinations, ten of which with a higher night than day temperature and a diurnal photoperiod of 8 hours, are shown in Figure 46. In this figure the horizontal axis shows the mean temperature during the experiment and the vertical axis shoot length measured from the joint to the ovary, thus with the exclusion of the flower bud. A line is drawn throught the data points (dots) which belong to the combinations with a lower night than day temperature, the common situation in practice. The line shows an optimum at about 18°C. The treatments are written near the data points. The data points from the treatments with a higher night than day temperature all lie below the drawn line. These points deviate more from the line if the difference in temperature between night and day temperature increases. Figure 46

shows that:

(1) If at a given day temperature, night temperature decreases resulting in a decrease in the daily mean temperature, shoot length responds with an optimum curve with an optimum at about $18^{o}C$.

(2) If at a given night temperature, day temperature decreases resulting in a decrease in the daily mean temperature, shoot length decreases.

(3) At a given mean temperature an increase in night temperature combined with a decrease in day temperature, results in shorter shoots.

(4) At a certain mean temperature a constant temperature during day and night gives the longest shoots.

6.3.4. SHOOT LENGTH AND THE LENGTH OF A DIURNAL PERIOD WITH A HIGHER NIGHT THAN DAY TEMPERATURE

The length of the diurnal period with a higher night than day temperature necessary to decrease shoot length, was studied in two experiments (GS5 and GS6). In these experiments day and night temperatures were constant with the exception of a period of $24^{o}C$ beginning at sunset. The daily mean temperature was $19^{o}C$ for all treatments.

The results of these two experiments are listed in Table 7B and 7C. In both experiments, treatment number 4 shows the shortest roses for 'Sweet Promise'. This treatment differs significantly from the other one (P=0.05). The cv. Varlon however, shows no reliable differences.

6.3.5. SHOOT LENGTH AND THE NUMBER OF NIGHTS WITH A HIGHER THAN DAY TEMPERATURE

This study was performed in airconditioned glasshouse compartments with container grown roses cv. Sweet Promise. During shoot development, containers were transferred from a compartment with a high day (12 hrs 24°C) and a low night (12 hrs 16°C) temperature, to a compartment with the reversed temperature combination. This resulted in 8 different treatments with the same development time from bud break until harvest of 40 days, in which the number of nights with a higher night than day temperature increased from 0 until 40. The results from this experiment are shown in Figure 47. In this figure the horizontal axis shows the number of nights with a higher temperature than in day time and the vertical axis shoot length from joint to ovary. The graph shows a negative linear relation between shoot length and the number of nights with a higher than day temperature.

6.3.6. LENGTH GROWTH

The growth in length of the shoot from bud break until harvest was studied for the cv. Sweet Promise in the phytotron and also in the glasshouse. In the phytotron the length from joint to ovary was measured every second day. In the glasshouse, measurements were performed once a week.

The results from 11 different 8 hrs light/12 hrs dark temperature combinations are shown in Figure 48.

In this figure the horizontal axis shows the time in days after cut, and the vertical axis shoot length in cm's. The Figure shows that shoot elongation is nearly linear during the greater part of the developing period. Only the first part of the curve until a length of about 4 cm has been reached, and during the last week before harvest the lines differ from a straight one. The tops of the curves form a bell-shape with a maximum at about 18°C. Curve "i" totally differs from the other ones. This last curve originates from a treatment with a higher night than day temperature!

If the mean temperature decreases, the growth rate (the tangent of the angle between the straight part of a curve with the horizontal axis) decreases too.
When the average daily increase in length during the development time is calculated and plotted agaist the mean daily temperature, a positive linear relationship appears (Figure 49). This figure is the mean of two experiments in the Phytotron.

In the glasshouse experiments growth curves were made too, both for 'Sweet Promise' and 'Varlon'. The shape of these curves was the same as those in the phytotron experiment and are not shown separately. The average daily increase in length during the development is shown in the Figures 50 and 51 for 'Sweet Promise' and 'Varlon', respectively. In these figures the mean temperature is shown on the horizontal axis and the average increase in length on the vertical axis. The lines refer to shoots which had been broken on the first day of the corresponding month and show a linear relation between the average daily length growth and temperature.

Dividing shoot weight of the cut roses by their length gives fresh weight per cm, a quantity that can be considered as a measure for firmness (Figure 52 and 53). The figures show a decrease in firmness if the temperature increases. A difference between 'Sweet Promise' and 'Varlon' appears in the period October until December. In this period firmness for 'Sweet Promise' decreases at an increasing temperature but not for 'Varlon'.

6.3.7. NECK LENGTH

The relation between temperature and neck length is shown in Figure 54 for 'Sweet Promise'. In the figure two lines are to be seen. The long one shows the results from phytotron experiments with a diurnal light period of 8 hours. The short line is from an experiment with soil grown roses in the glasshouse and gives the average neck length over the period November until May (GS2). Both curves show an optimum

at about 19°C. The optimum for the short line is less pronounced than for the long one, however. If at a given 24 hours temperature night temperature increases, neck length decreases (Table 8A).

Table 8. Rose cvs. Sweet Promise (S) and Varlon (V), grown in glasshouse soil. Average neck length (mm) and ratio neck/total shoot length, of cut roses (%), for three experimental years with each four treatments. Legend: see Table 4.

	A GS4				B GS5				C GS6			
	neck (mm)		neck/shoot		neck (mm)		neck/shoot		neck (mm)		neck/shoot	
	S	V	S	V	S	V	S	V	S	V	S	V
1:	100a	76a	.15	.11	140	127	.22	.18	139	116	.21	.16
2:	92ab	74a	.14	.11	138	130	.21	.18	141	119	.21	.16
3:	87bc	69b	.16	.11	139	126	.22	.19	142	118	.21	.16
4:	86c	67b	.16	.11	135	135	.22	.19	142	117	.22	.17
			*	*	*	*	*	*	*	*	*	*

Experiments in the phytotron showed that the rate between neck length and total shoot length is not influenced by temperature in the range of 15°C until 25°C (Figure 55). Temperatures lower than 13°C showed a strong increase in this ratio, however.
The temperature distribution between day and night did not reliably influence the neck/shoot ratio. Also a higher night than day temperature did not affect it (Table 8B and 8C).

6.3.8. LENGTH, WIDTH AND VOLUME OF THE FLOWER BUD AT HARVEST

The length and the width of the flower bud were measured during the first experiment with soil grown roses (GS1). The measurements were

performed at harvest stage. The length was measured from the receptacle until the tip of the petals; thus with the exclusion of the ovary. The Figures 56 and 57 show the 'models' for flower bud length for 'Sweet Promise' and 'Varlon', respectively. The corresponding linear regression equations are: (for abbreviations see **2.8.**).

'Sweet P' **BL**= -332 + 0.1127**ADR** - 0.377**WPS** + 4.59**RH** + 50.4**T**- 1.68**T**^{2}
(R^2*=91.9%).

'Varlon' **BL**=229 + 0.0959**ADR** - 6.84**T** + 2.47**RH** - 0.0878**WPS**
(R^2*= 96.8%).

The 'models' for the width of the flower bud measured at the height of the receptacle are shown in Figure 58 for 'Sweet Promise' and in Figure 59 for 'Varlon'. The corresponding linear regression equations for the figures are: (for abbreviations see **2.8.**).

'Sweet P' **BW**=39.2 - 5.53**T** + 0.3673**DL** - 0.1363**ADR** + 0.66**RH**
(R^2*= 94.0%).

'Varlon' **BW**= -1.5 + 0.1270**DL** + 2.702**RH** - 4.499**T** (R^2*= 92.3%).

In the figures the horizontal axis represents the date of bud break and the vertical axis the length and width of the flower bud, respectively. The figures show a decrease in bud length and bud width during autumn followed by an increase in spring; a lower temperature leads to longer and broader flower buds.

If the flower bud is considered as a cylinder, which is close to reality at the moment it opens, it is simple to calculate its volume. The results of this calculation are shown in Figure 60 for 'Sweet Promise' and in Figure 61 for 'Varlon'.

6.3.9. DIAMETER OF THE STEM

The diameter, measured at the cut, is shown in Figure 62 for 'Sweet Promise' and in Figure 63 for 'Varlon'. The horizontal axis shows the date of bud break and the vertical axis the diameter. These figures clearly show that lower temperatures lead to thicker stems, and that lateral buds that break in the depth of winter produce the thinnest shoots. The influence of the temperature distribution between day and night at a given mean temperature on the diameter was also studied. Night temperatures in the range from 14°C until 18°C combined with day temperatures in the range of 18°C until 22°C, did not show a reliable influence on the diameter (Table 9).

Table 9. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Diameter of the shoot at the cut (0.1mm), diameter of the middle of the neck (0.1mm) and the ratio between both, for five 12hrs night/12hrs day temperature treatments. Period November until May (GS3).

GS3	'Sweet Promise'			'Varlon'		
Treatment	Diameter(0.1mm)			Diameter(0.1mm)		
N/D (°C)	shoot	neck	ratio	shoot	neck	ratio
1. 14/22	43	29	.67	55	33	.60
2. 15/21	44	30	.68	55	33	.60
3. 16/20	43	29	.67	56	33	.59
4. 17/19	44	29	.68	54	32	.59
5. 18/18	46	30	.65	56	33	.59
	*	*	*	*	*	*

If, however, the installed night temperature rises above the day temperature for 12 hours on a diurnal base, the diameter decreases reliably as is shown in Table 10.

Table 10. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Diameter of the shoot at the cut (0.1mm), diameter at the middle of the neck (0.1mm) and the ratio between both, for four 12hrs night/12hrs day temperature treatments. Period November until May (GS4).

GS4	'Sweet Promise'			'Varlon'		
Treatment	Diameter(0.1mm)			Diameter (0.1mm)		
N/D (^{o}C)	shoot	neck	ratio	shoot	neck	ratio
1. 16/22	50 a	33 a	.66 a	51 a	31 a	.61 a
2. 18/20	49 a	31 b	.63 a	51 a	30 b	.59 a
3. 20/18	46 b	30 bc	.65 a	49 b	30 ab	.61 a
4. 22/16	45 b	29 c	.64 a	48 b	29 b	.60 a

If the period with the higher night than day temperature lasts no longer than 6-9 hours per 24 hours the diameter is not influenced (Table 11 and 12).

Table 11. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Diameter of the shoot at the cut (0.1mm), diameter at the middle of the neck (0.1mm) and the ratio between both, for four night/day temperature treatments. Period November until May (GS5). For treatments see also: Table 4B.

GS5	'Sweet Promise'			'Varlon'		
Treatment	Diameter(0.1mm)			Diameter(0.1mm)		
Night/Day (^{o}C)	shoot	neck	ratio	shoot	neck	ratio
1. 19/19	45	30	.67	55	33	.60
2. 2 hrs 24/18.5	47	32	.68	56	33	.59
3. 4 hrs 24/18.0	45	30	.67	51	31	.61
4. 6 hrs 24/17.3	44	29	.66	57	33	.58
	*	*	*	*	*	*

Table 12. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Diameter of the shoot at the cut (0.1mm), diameter at the middle of the neck (0.1mm) and the ratio between both, for four night/day temperature treatments. Period November until April (GS6). For treatments see also Table 4C.

GS6		'Sweet Promise'			'Varlon'		
Treatment		Diameter(0.1mm)			Diameter(0.1mm)		
Night/day (^{o}C)		shoot	neck	ratio	shoot	neck	ratio
1.	19/19	49	32	.65	56	33	.59
2.	2-3 hrs 24/18.3	51	33	.65	59	33	.56
3.	3-6 hrs 24/17.3	49	32	.65	54	32	.59
4.	6-9 hrs 24/16.0	49	33	.65	54	32	.59
		*	*	*	*	*	*

The regression equations for the diameter of the shoot are: (for abbreviations see **2.8.**).

'Sweet P.' **DS**= 12.0 + 0.2985**ADR** - 16.36**T** + 8.80**RH** + 0.1234**WPS** (R^2* =92.8%).

'Varlon' **DS**=-307.2 + 0.2144**ADR** + 9.09**RH** + 0.3866**WPS** (R^2* =93.8.9%).

6.3.10. DIAMETER OF THE NECK

In the experiments GS2 until GS6 the diameter was measured in the middle of the neck. The 'models' are shown respectively in Figures 64 and 65 for 'Sweet Promise' and 'Varlon'. The diameter of the neck responds to the distribution of temperature between day and night in the same way as the diameter of the shoot does (Tables 9-12).
The ratio between the diameter of the neck and the stem is shown in Figure 66. This figure shows the mean temperature on the horizontal

axis and the ratio on the vertical axis. In the figure three lines are to be seen. The two short lines represent the ratio of the two cvs. in glasshouse soil (GS2), the long one, the results of 'Sweet Promise' in the phytotron on a much wider temperature range. The figure shows an increase in ratio if temperature decreases below about 17°C.
Between 17°C and 21°C the line is nearly parallel to the x-axis. The experiments with different distributions of the temperature over the 24 hours of the day at a given daily mean temperature did not show a reliable influence on the ratio (Table 9-12).

6.3.11. DIAMETER OF THE OVARY

The course of the diameter of the ovary during the winter season was comparable to the behaviour of the diameter of stem and neck. Roses harvested in February showed the smallest diameter. In the experiments with different temperature distribution between day and night, no reliable influence was found on the diameter of the ovary (Table 13).

Table 13. Roses cvs. Sweet Promise (S) and Varlon (V), grown in glasshouse soil. Average diameter of the ovary (0.1mm). For three winter seasons with each for temperature treatments.
Legend: see Table 4.

Diameter of the ovary (0.1mm)

	A		B		C	
	GS4		GS5		GS6	
Treatment	S	V	S	V	S	V
1.	87	85	84	86	89	89
2.	88	84	89	88	93	89
3.	88	87	83	84	87	86
4.	86	85	83	85	89	88
	*	*	*	*	*	*

6.3.12. NUMBER OF LEAVES

During the experiments the roses were cut on the first five leaflet-leaf above the joint. The number of leaves was monitored. In the first experiment (GS1), a distinction was made between leaves with three or more leaflets and leaves with less than three leaflets. The total number of leaves was not effected by temperature. The first and second highest leaf of shoots harvested in January and February however showed less leaflets if grown at a high temperature level than if grown at a low temperature level. The distribution of temperature over the 24 hours of the day did not reliably influence the total number of leaves. Also a higher night than day temperature did not influence it (Table 14).

Table 14. Roses cvs. Sweet Promise (S) and Varlon (V), grown in glasshouse soil. Average number of leaves of the cut roses for three winter seasons with each four temperature treatments. Legend: see Table 4.

Number of leaves

	A		B		C	
	GS4		GS5		GS6	
Treatment	S	V	S	V	S	V
1.	10.1	11.0	9.6	10.1	9.4	10.2
2.	10.1	11.1	9.5	10.0	9.6	10.3
3.	9.5	11.0	9.5	9.5	9.9	10.1
4.	9.5	11.1	9.4	10.4	9.4	10.1
	*	*	*	*	*	*

6.4. DISCUSSION

To account for the variation in the 'models' on shoot measurements, more explanatory variables are necessary than for the models on development time and fresh weight. Besides the variables: temperature, irradiance and relative humidity in a linear form, also the quadratic form of the temperature appears. A new variable is also the 'plant factor' (WPS), being the fresh weight of the parent shoot. But even with all those variables in the equation, no more than 86%-88% of the variation in shoot length can be accounted for. This means that more and unknown variables are involved, or that the influence of the variables already in the equation is more intricate than supposed. This last statement is certainly a fact. Shoot length is influenced by the distribution of temperature between day and night, but for the construction of the models only the mean temperature was used. A higher percentage of the the variation can also be accounted for if all variables are inserted in the quadratic form too. The equation then becomes less understandable however, and the Cp-value of Mallow (see Appendix 3) shows a big bias, which means an inadequate fit. The equations for the two cultivars do not always show the same variables nor are the variables always in the same sequence. Only the variables which significantly reduce the residual sum of squares are inserted. The sequence of the variables is according to their importance. The difference in growth behaviour between the two cultivars during winter as mentionned in the previous chapter appears in the difference in variables in the equations too.

Moe (1972a,b) mentioned that in his experiments daylength also was a factor that influenced shoot length. In the present experiments the natural radiation cycle was used so daylength was coupled with irradiance. Inserting daylength as an extra variable did not significantly improve the fit.

Both cvs. Sweet Promise and Varlon show an optimum temperature for shoot length at a mean of about 18^{o}C in the glasshouse. In the Phytotron experiments with 'Sweet Promise' the same optimum was found

(Figure 46).

No reliable interaction was found between temperature and stage of shoot development on shoot length. This does not mean however that such an interaction does not exist for temperatures or growth circumstances different from our experiments; but for the moment this is a matter of speculation.

The average daily shoot growth or average shoot extension rate (cm/day) during the development of a shoot shows a positive linear correlation with the air temperature (Figure 49-51). The difference between both cultivars is very small. Such a linear correlation has also been reported for other species, e.g. cucumber (Hey 1980) and for stem segments of Avena sativa (Jusaitis et al. 1982). Linear responses in relation to air temperature have been observed also for other plant parts, e.g. for barley leaves (Biscoe and Gallagher 1977).

The length growth rate also depends on the time of the year (Figure 50 and 51). In autumn this rate is higher than under the same irradiance and temperature conditions in early spring (Figure 67). This may be partly due to the higher relative humidity measured in autumn, but it can also be connected with the difference in growth vigour of the plant which is higher in autumn at decreasing light conditions than in the beginning of the year under increasing light conditions. The rate of growth in length and the rate of development both determine final shoot length. Because at higher temperatures the rate of development is promoted more strongly than the rate in length growth, shoots remain shorter.

The temperature distribution between day and night also influences shoot length. The optimum night temperature at a daily mean of 18-19(^{o}C) lies at about 15^{o}C for both 'Sweet Promise' and 'Varlon' (Figure 42 and 43). This agrees well with the average temperature in practice. A higher night than day temperature clearly reduces shoot length (Figure 44-46, Table 7), an effect that was also reported for peas by Monselise and Went (1958) and for roses by Hendriks (1984). The greater the number of nights with a higher night

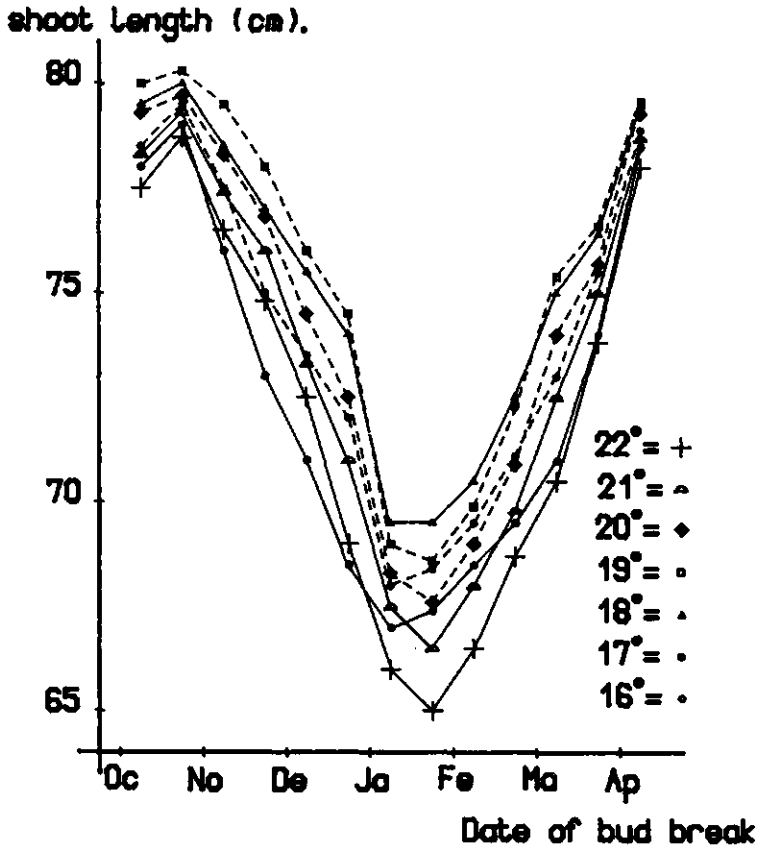
than day temperature, the shorter the shoot (Figure 47). If the diurnal period with a higher night than day temperature beginning at dawn is not longer than 6 hours however, no significant reduction in length appears (Table 7). The fact that night temperature has a strong influence on growth was already mentioned in the previous chapter and has been reported for other species. Boyer (1968) showed that leaf enlargment was stronger at night than in daytime because of a higher water potential during the night. Also results of Biscoe and Callagher (1976) point into that direction.

Neck length shows a similar reaction to temperature as shoot length. This was also reported for rose seedlings by De Vries and Smeets (1979).

The length and width of the flower bud shows a comparable reaction to temperature and irradiance as length and width of the petals, as reported by Moe and Kristofferson (1969). No significant influence of temperature on total leaf number was found. Only flowerless shoots had less leaves than flowering ones; a result that confirms the findings of Moe and Kristofferson (1969) and of De Vries and Smeets (1979).

An optimum temperature for neck length of 'Sweet Promise' was found at about 18°C (Figure 54), the same temperature as for the optimum for shoot length. For 'Varlon' no clear optimum was found in the temperature range 16°C -22°C, however. The ratio between neck and shoot length is constant on the temperature range 13°C to 25°C, according to the results from experiments performed in the phytotron. At lower temperatures however, this ratio strongly increases because of a sharp decrease in development of the vegetative part of the shoot (Figure 55). The ratio between the diameter of the middle of the neck and the shoot at the place of cut shows the same tendency and this can also be said for the ratio: flower bud weight/total shoot weight. Flower bud and neck both belong to the generative part of the shoot and show a different reaction to temperature then the vegetative part. A more detailled study in growth rooms was performed on leaves. In this study all leaves were graded according the number

of leaflets. The results showed that on the range 25°C to 17°C a decrease in temperature resulted in a decrease in the number of leaflets of the two leaves closest to the flower bud. The other leaves were not affected nor was the total number of leaves. As a consequence differences in shoot length were due to differences in the average internode length. These results were in harmony with those from the experiments with soil grown roses in glasshouses.



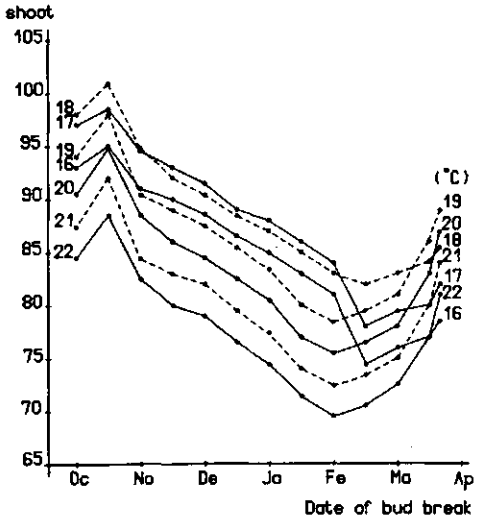


Fig.39 'Sweet Promise', grown in glasshouse soil. 'Model' for total shoot length at harvest stage in relation to the date of bud break and the mean temperature.

Fig.40 'Varlon', grown in glasshouse soil. 'Model' for total shoot length at harvest stage in relation to the date of bud break and the mean temperature.

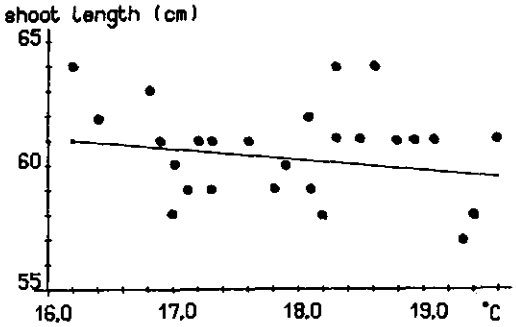


Fig.41 'Sweet Promise', container grown in the glasshouse. Relation between shoot length and the mean temperature, for 27 temperature treatments depending on shoot stage (see text).
Y=70.4-0.56X(r=-.29)

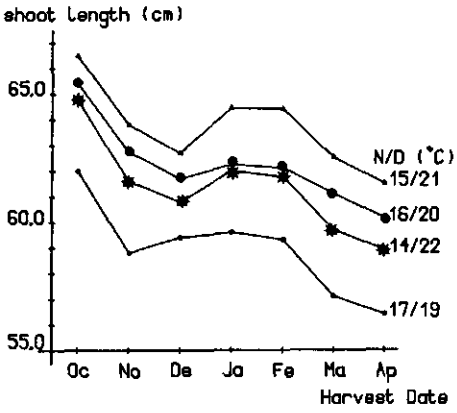


Fig.42 'Sweet Promise' grown in glasshouse soil. Shoot length of cut roses for four night/day temperature treatments. Daily mean is 18°C for all treatments.

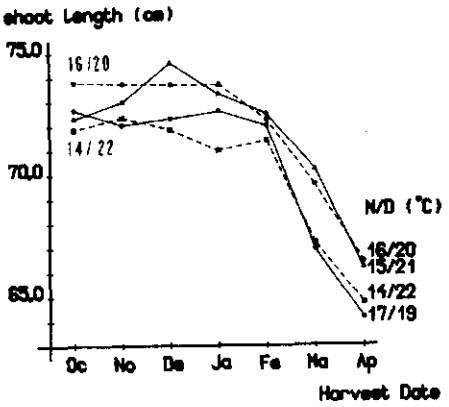
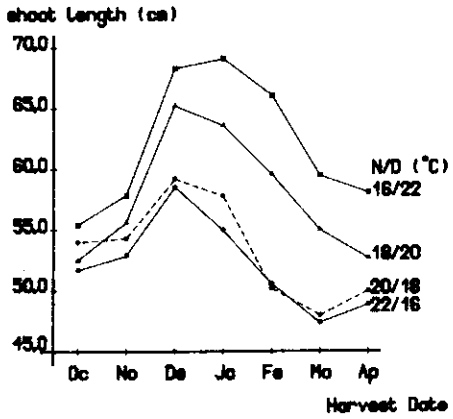


Fig.43 'Varlon' grown in glasshouse soil. Shoot length of cut roses for for night/day temperature treatments. Daily mean is 18°C for all treatments.



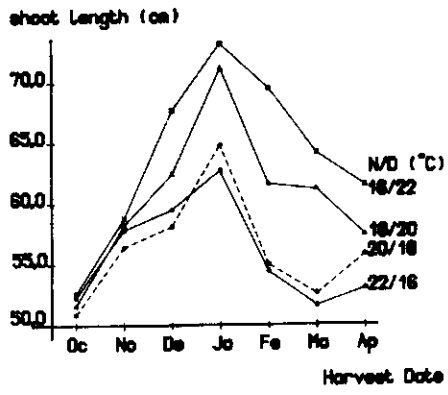
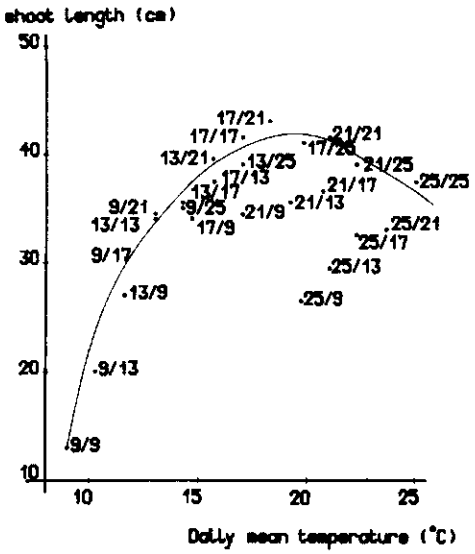


Fig.44 (l) 'Sweet Promise' and **Fig.45** (r) 'Varlon', grown in glasshouse soil. Shoot length of cut roses for four 12hrs night/12hrs day temperature treatments. Daily mean is 19°C for all treatments.



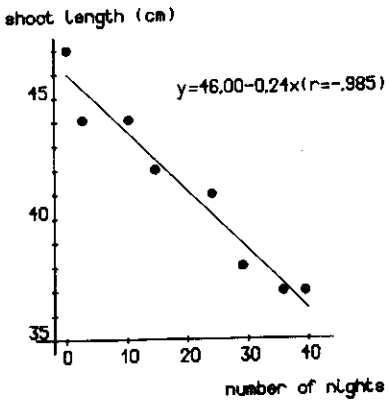
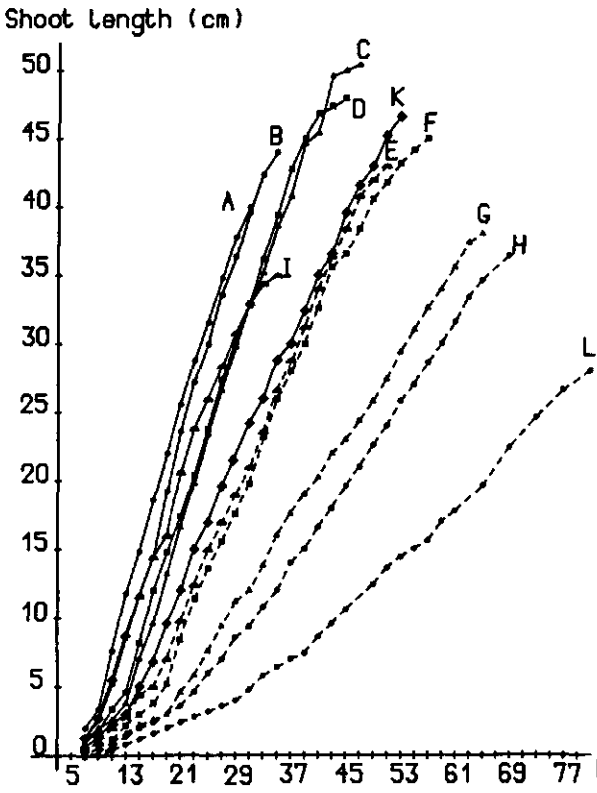


Fig.46 'Sweet Promise', container grown in growth rooms. Shoot length of cut roses in relation to the mean temperature, 25 combinations, 16hrs dark/8hrs light (°C).

Fig.47 'Sweet Promise', container grown in the glasshouse. Relation between shoot length and number of nights with a higher (12 hrs 24°C) than day temperature (12 hrs 16°C).



Night/Day	mean (°C)
A 25/25	25.0
B 21/25	22.3
C 17/25	19.7
D 17/21	18.3
E 13/25	17.0
F 13/21	15.7
G 13/17	14.3
H 9/21	13.0
I 25/21	23.7
K 17/17	17.0
L 9/17	11.7

Fig.48 'Sweet Promise', container grown in growth rooms. Length growth of daughter shoot after cut of the parent shoot at day 0, for different 16hrs night/8hrs day temperatures (°C).

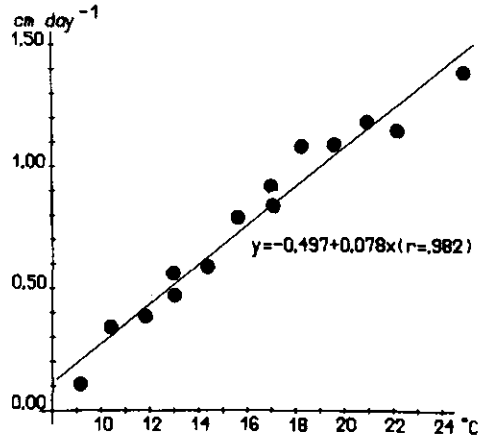
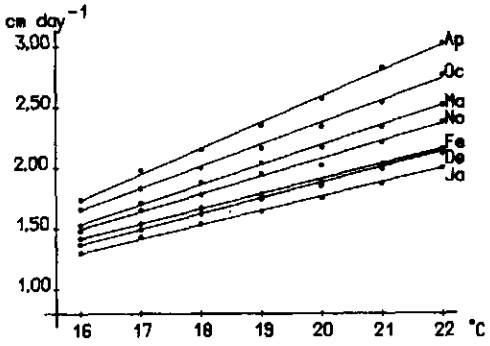


Fig.49 'Sweet Promise', container grown in growth rooms. Relation between the average shoot growth per day (cm) and the mean temperature.



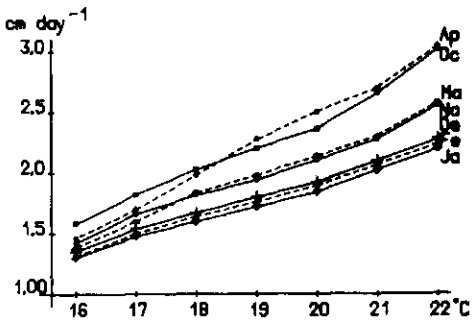
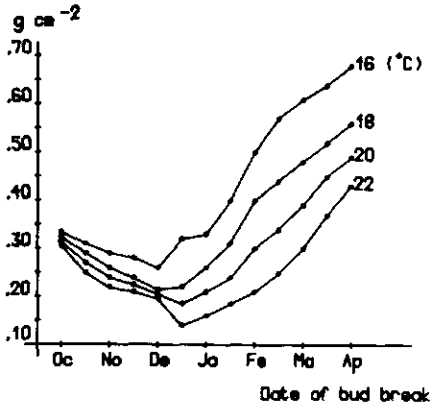


Fig.50 (l) 'Sweet Promise' and **Fig.51** (r) 'Varlon', grown in glasshouse soil. Relation between the average shoot growth per day (cm), the mean temperature and the date of bud break on the first day of the corresponding month.



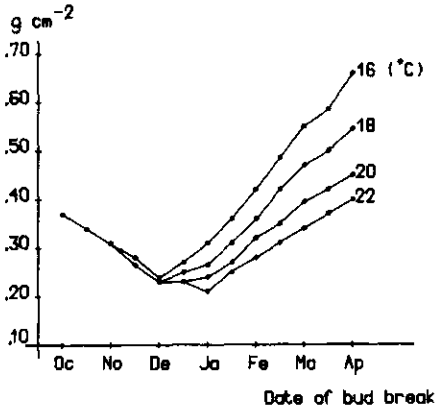


Fig.52 (l) 'Sweet promise' and **Fig.53** (r) 'Varlon', grown in glasshouse soil. Relation between fresh shoot weight per cm, the date of bud break and the mean temperature.

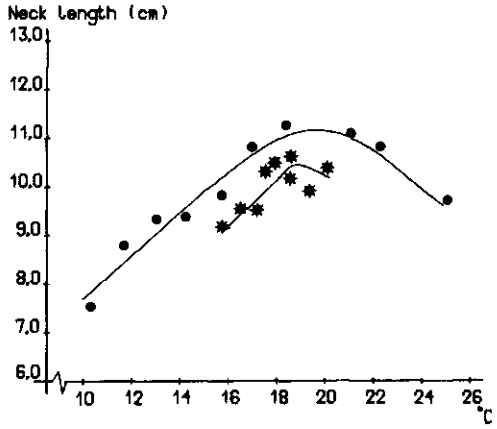


Fig.54 'Sweet Promise', container grown in growth rooms (dots) and grown in glasshouse soil (asterixes). Relation between the length of the neck and the mean temperature.

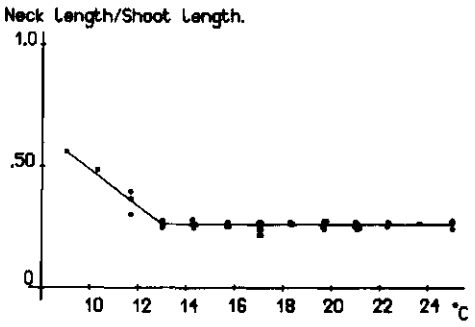
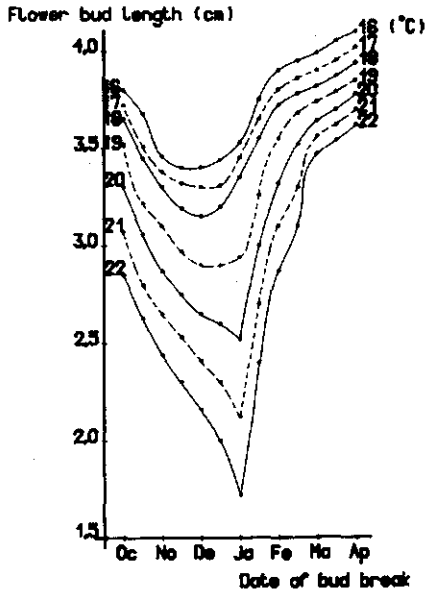


Fig.55 'Sweet Promise', container grown in growth rooms. Neck length as fraction of total shoot length, in relation to the mean temperature.



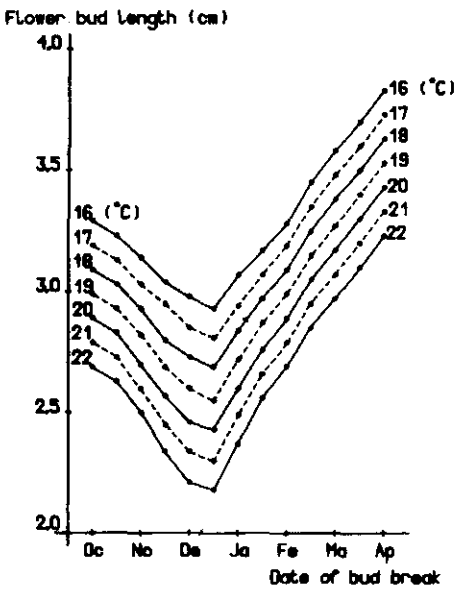
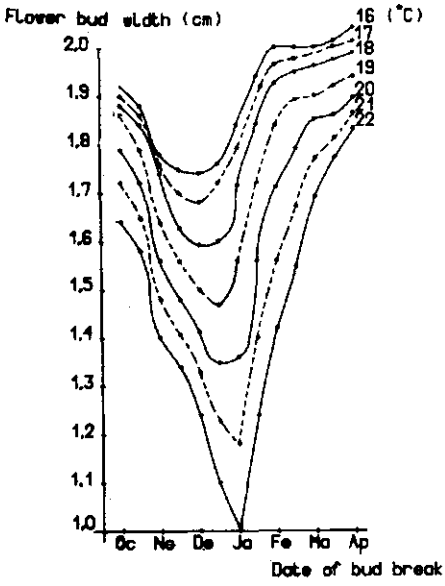


Fig.56 (l) 'Sweet Promise' and **Fig.57** (r) 'Varlon', soil grown in the glasshouse. 'Model' for flower bud length (cm) during harvest in relation to the date of bud break and the mean temperature.



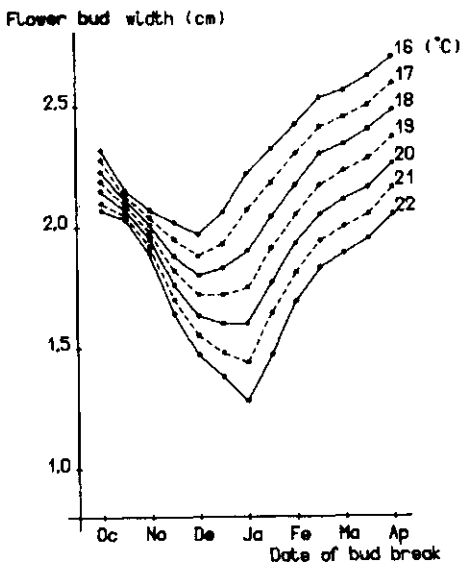
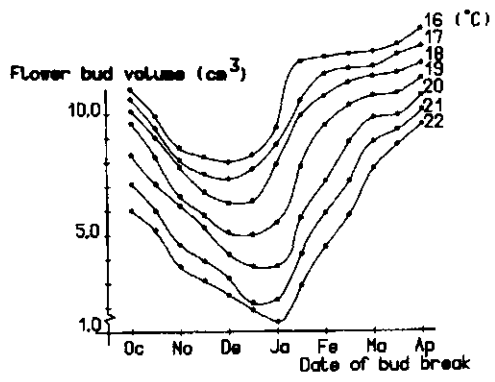


Fig.58 (l) 'Sweet Promise' and **Fig.59** (r) 'Varlon', soil grown in the glasshouse. 'Model' for flower bud width (cm) during harvest in relation to the date of bud break and the mean temperature.



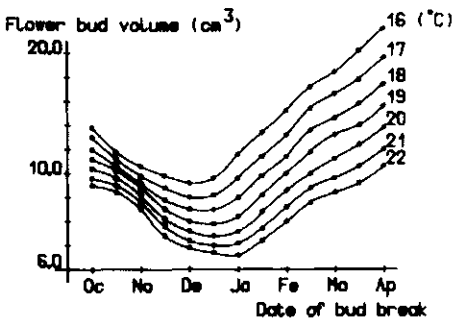


Fig.60 (l) 'Sweet Promise' and **Fig.61** (r) 'Varlon', soil grown in the glasshouse. 'Model' for flower bud volume (cm^3) during harvest in relation to the date of bud break and the mean temperature.

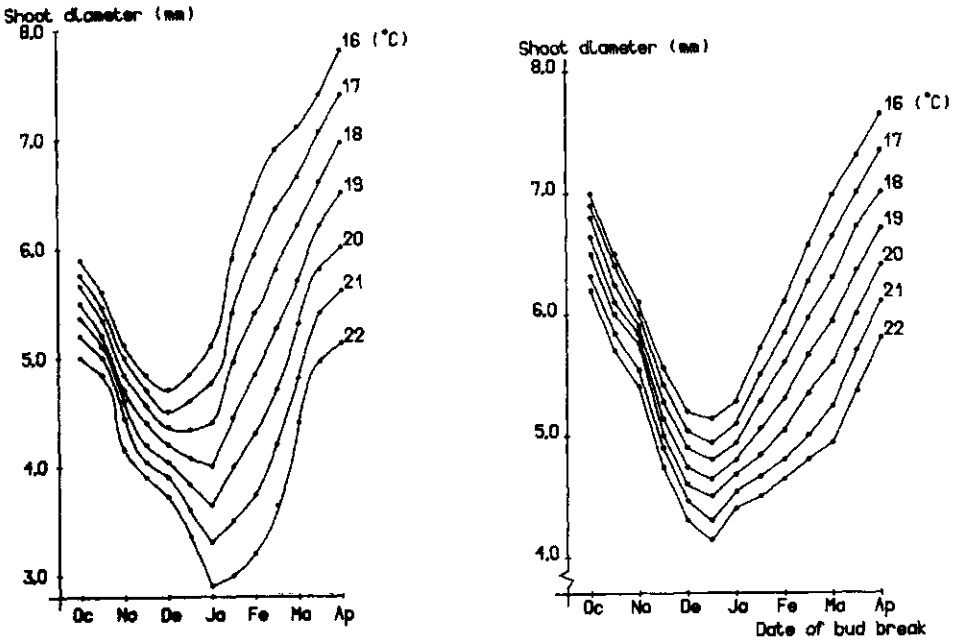


Fig.62 (l) 'Sweet Promise' and **Fig.63** (r) 'Varlon', soil grown in the glasshouse. 'Model' for shoot diameter (mm) during harvest in relation to the date of bud break and the mean temperature.

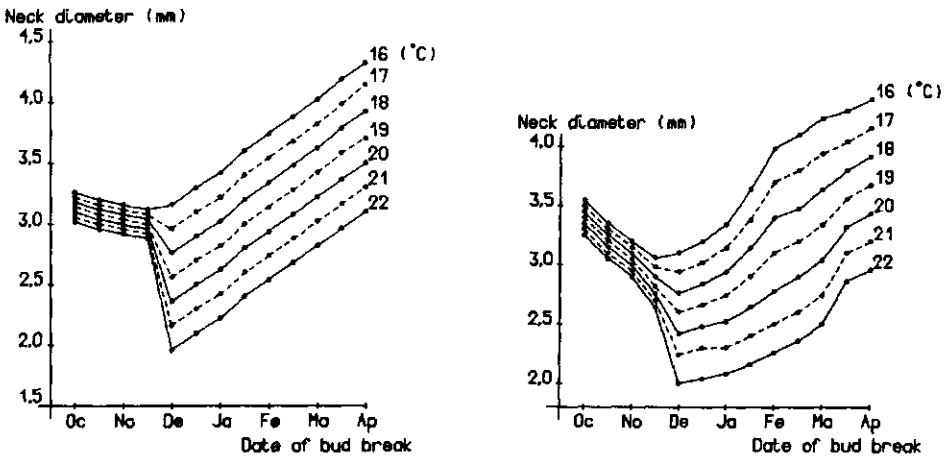


Fig.64 (l) 'Sweet Promise' and **Fig.65** (r), 'Varlon' soil grown in the glasshouse. 'Model' for neck diameter (mm) during harvest in relation to the date of bud break and the mean temperature.

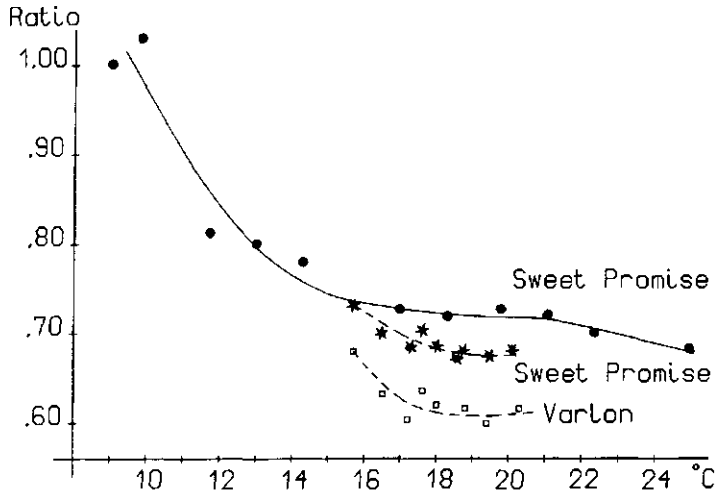


Fig.66 Relation between the ratio: diameter neck/diameter shoot and the mean temperature. For 'Sweet Promise', container grown in growth rooms (dots), soil grown in the glasshouse (asterixes) and for 'Varlon', soil grown in the glasshouse (Squares).

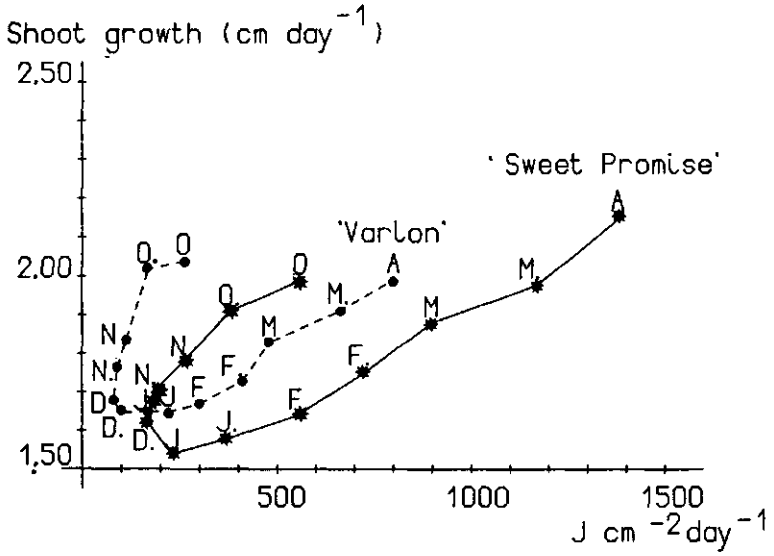


Fig.67 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between the average daily shoot growth (cm day^{-1}), the mean inside irradiance and the date of bud break. Naked capitals refer to bud break at the first day of the corresponding month, capitals with a dot refer to the middle of the month.

7. FLOWERLESS ROSE SHOOTS ('BLIND SHOOTS')

7.1. INTRODUCTION

As a result of self-induction differentiation flower organs start in all extending rose shoots (Halevy 1985). If flower development is not completed the flower atrophies, aborts and the shoot fails to flower. This phenomenon called 'blindness' ('blind shoot') has been a problem as long as roses have been cultivated. The morphology of 'blind shoots' in relation to its anatomy and the stage of floral development has been studied and described by several authors (Hubbell 1934a, Lindstrom 1956, Moe and Kristofferson 1969, Moe 1971b, Horridge and Cockshull 1974, Zieslin and Halevy 1975a, Nell and Rasmussen 1979b, Van Hove 1980, De Vries et al. 1981). Apart from the problem of 'blindness' Laurie and Bobula (1938) and Lindebaum and Ginzburg 1975 studied the anatomy of the apex during its change from vegetative to generative.

On the basis of anatomic research Hubbell (1934) concluded that the formation of 'blind' shoots is a result of the shedding of the flower bud at an early stage of its development. This phenomenom is commonly called flower bud abortion. Lindstrom (1956) confirmed Hubbell's view in his thesis. He found that the first signs of flower bud abortion occurred when the petal primordia started to develop. Cell disintegration could be seen beginning in the epidermal layers of the sepals. This disintegration progressed into the bud below the apical meristem. After the appearance of a necrotic band an abscission layer appeared and the flower bud died. The formation of 'blindness' could take place any time from petal through pistal formation. Van Hove (1980) confirmed these results for 'Sweet Promise'. De Vries et al. (1981), who worked with seedlings of Hybrid Tea roses, distinguished between early abortion which also results in the absence of the upper leaf and occurs without an abscission zone

in the flowerstalk, and late abortion including an abscission zone. The abortion of completed flower buds is also possible (Halevy 1985, De Haas 1985). Shedding of plant parts is, by the way, not an uncommon phenomenon in plant life and can be caused by different circumstances (Kozlowski 1973). The phenomenon that 'blind' shoots form less leaves and are shorter, thinner and lighter of color than flowering shoots is well known and can be seen in all rose canopies. It was reported by a.o.: Moe (1971a,b), Zieslin and Halevy (1975a,b), Nell and Rasmussen (1979a), Van Hove 1980, De Vries et al. (1981), and was also evident in the present experiments with 'Sweet Promise' and 'Varlon' roses.

To explain the formation of 'blind' shoots several theories have been advanced. Corbett (1902) stated that heredity was an important aspect. Hubbell (1934b) however, concluded that sensitivity to 'blindness' is not inherited but is a physiological phenomenon caused by low growth vigour of the stock. He stated that an improper balance of nutrients was at the basis of blindness. De Vries et al. (1978) showed that within a population of seedlings it is possible to select on sensitivity to blindness.

In experiments with nitrate and potassium levels, Lindstrom and Kiplinger (1955) found no effect on 'blindness' in 'Better Times' roses. Lindstrom (1956) mentioned results from several unpublished M.Sc. theses on nutrients in relation to 'blindness' in roses which do not support Hubbells statement. Results from some experiments pointed in the direction of a perhaps indirect effect of nutrients on 'blindness' via the growth vigour of the shrub, however.
Zieslin and Halevy (1975a,b) reported an increase in 'blindness' if soil temperature decreased until 15^{o}C, which they ascribe to changes in the metabolic activity of the roots. Besides the role roots have in the uptake of water and minerals, they are also an important production site for some fytohormones (Appendix 1).
Moe (1971) reported that hormones may play a role in the formation of 'blind' shoots. A low auxin level in the shoots promoted blindness. Hanisch ten Cate (1974) demonstrated that this hormone plays an

important role in the prevention of flower bud abscission in Begonia.

Low levels of some growth substances in roses are reported to correlate with a high percentage of 'blind' shoots (Zieslin and Halevy 1975a,b, 1976b). These authors studied the content of various growth substances in flowering and in non-flowering shoots at different stages of shoot development. They found a higher level of gibberellins, auxins and cytokinins in flowering shoots. Non-flowering shoots had a higher level of inhibitors, among which abscisic acid (Zieslin and Halevy 1976b). One may ask however what is cause and what is result.

Gibberellins are produced in the roots, in the young leaves and in the stamen too (Graebe and Ropers 1978, Hormonal regulation 1984). In the period between bud break and the start of the own gibberellin production the new shoot is sensitive to gibberellin shortage, which can lead to flower bud atrophy and blindness.
Zieslin and Halevy found a reduction in the gibberellin content if light intensity decreased.

The external addition of gibberellins and CCC can reduce 'blindness' (Zieslin and Halevy 1976c, Mor and Halevy 1984). This may be a direct effect on flower bud initiation and development or an indirect effect via influencing the assimilate supply to the apical meristematic regions (Sachs and Hackett 1977). The gibberellin level inside the plant can be reduced by applying cytokinins (McIhniewicz and Kamienska 1967, Sebanek 1966, Jackson and Field 1971).
Zieslin and Halevy (1976d) found no influence of applying cytokinins direct to the apex, however. If sprayed on individual branches, cytokinin resulted in an increase of the number of sprouting lateral buds of which, probably due to competition, a high percentage grew blind. CCC is reported to reduce the gibberellin level in plant tissue (e.g. Lang 1970), but is also reported to increase the gibberellin level (Jones and Phillps 1967, Van Bragt 1969, Halevy and Shilo 1970, Reid and Crozier 1972). Adding CCC together with cytokinins to lateral buds reduced the high percentage 'blindness' in shoots which were forced to sprout by the application of cytokinin

(Zieslin and Halevy 1975c, 1976c).

Tukey (1985) mentioned work of Chinese research workers, who found that in grapes a high concentration of cytokinins in the bleeding sap of rootstocks promotes inflorescence formation.

Halevy (1974) pointed out the possibility that the internal level of growth substances may play a role by influencing the mobilisation and the direction of assimilates. In a review on this subject, Weaver and Johnson (1984) give many articles that can back this view point. Goren (1983) who worked with citrus mentioned that hormones can act direct on the formation of abscission layers or indirectly by influencing the sink competition in plants. This may also be the case in flower bud abortion. Although 'blind' shoots appear all year round (own experience), the bulk of them are formed in winter (Zieslin and Halevy 1975a, Moe and Kristofferson 1969). Especially those shoots which develop around the shortest day are sensitive to blindness. In this part of the year the production of assimilates is very low because of the low light level and much of the reserves have already been used.

The sensitivity for 'blindness' also depends on the cultivar, on the growth vigour of the branch from which the shoot develops (present experiments) and on the location of the lateral bud on that branch (Zieslin and halevy 1976a, present experiments).

An increase in light intensity, either natural or artificial, reduces flower abortion and the formation of 'blind' shoots (Moe and Kristofferson 1969, Moe 1971b, Carpenter and Rodriguez 1971b, Carpenter and Anderson 1972, Cockshull 1975, Zieslin and Halevy 1975b, Kosh-Khui and George 1977, De Vries and Smeets 1979, Nell and Rasmussen 1979b, Van Hove 1980, De Vries et al. 1982). This effect of light is also known for other species e.g. lilies (Kamerbeek and Durieux 1971, Durieux 1974) and tomatoes (Atherton and Othman 1983). Mortensen and Moe (1983) found a decrease in 'blindness' as a result of raising the CO_2 concentration. A reasonable explanation is that an increased level of light and/or CO_2 enhances the production of assimilates and by this way reduces the change of starvation of the

flower bud.
An effect of daylength on the formation of 'blind' shoots was not found (Zieslin and Halevy 1975b).

Reports on the influence of temperature on 'blind' shoot formation are less similar than those on light intensity. In experiments with 'Baccara^{R}', cut back in February and March, Moe and Kristofferson (1969) found a decrease in 'blindness' if temperature increased. If the roses were cut back in January however, an increase in temperature led to an increase in blindness (Moe 1971b). De Vries and Smeets (1979), found no influence of temperature in the range $10^{o}C$ - $26^{o}C$ on 'blindness' in rose seedlings in growth rooms. They stated that: " given sufficient light energy, flower bud formation is not affected by temperature". This view can be backed by results from Zieslin and Halevy (1976d), which showed a decrease in the gibberellin content at low temperatures but an increase at high light intensities.
In the present study the influence of temperature on the formation of 'blind' shoots received special attention because of its importance to the grower, and the danger that in using unorthodox temperature regimes, 'blindness' might become an even bigger problem than it already is at the moment.

7.2. MATERIALS AND METHODS

Preliminary to the experiments with the rose cvs. Sweet Promise and Varlon in glasshouse soil, shoots were labeled and were monitored flush after flush. The percentage of 'blind' shoots was calculated. During the experiments groups of shoots outside the experimental plots were regulary labeled and the blind shoots counted. The influence of the temperature distribution between day and night on 'blindness' was studied with container grown roses of the cv. Sweet Promise in the glasshouse. Plant materials, methods, conditions, definitions, abbreviations and codes of the experiments have been described in chapter 2.

7.3. RESULTS

7.3.1. 'BLINDNESS' AND MEAN TEMPERATURE

In the first experiment (GS1), a constant day temperature was combined with four different night temperatures. The percentage of 'blind' shoots of roses grown in the period November until May was 8% for the cv. Sweet Promise and 4% for 'Varlon'. The differences in the formation of 'blind' shoots between the four treatments were not significant.

In the second experiment (GS2), each of three night temperatures was combined with three day temperatures. The percentage of 'blind' increased if the mean daily temperature increased too (Figure 68). This figure shows the mean daily temperature during shoot growth on the horizontal axis and the percentage of 'blind' shoots on the vertical axis. The lines A and B refer to the cvs. Sweet Promise and Varlon in the period November until May, and the line C refers to 'Sweet Promise' in the period March until May. In this last period the percentage of 'blind' shoots for 'Varlon' was less than one per cent and is not shown in the figure.

7.3.2. 'BLINDNESS' AND THE DISTRIBUTION OF TEMPERATURE BETWEEN DAY AND NIGHT

The influence of the temperature distribution between day and night on the formation of 'blind' shoots was studied in experiment GS3. In this experiment 5 different night/day temperature combinations were made at one given temperature. From this experiment emerged the fact, that if at a given temperature the night temperature increases, the percentage of 'blind' shoots decreases (Figure 69). In this figure the horizontal axis shows the average night temperature and on the vertical axis the percentage of 'blind' shoots for 'Sweet

Promise' in the period November until May.

As the cv. Varlon only showed some percents of 'blind' shoots with no significant differences between the treatments during the experiments GS3 until GS6, this cv. is further omitted in this chapter.

The influence of a higher night than day temperature on the formation of 'blind' shoots was studied in the experiments GS4, GS5 and GS6. During these experiments, each fortnight groups of 16 roses of the cv. Sweet Promise were selected at harvest stage, cut at the first five-leaflet leaf above the joint and labeled. These groups of roses were outside the experimental plots so they did not influence the main experiment. The percentages of 'blind' shoots that emerged in the three successive years from the uppermost lateral bud were calculated and are listed in Table 15. Because of the reason that outside the experimental plots only shrubs of the cv. Sweet Promise had been planted, no data of the cv. Varlon are available.

Table 15. Rose cv. Sweet Promise, grown in glasshouse soil. Percentages of 'blind' daughter shoots from labelled parent shoots (see text). Legend: see Table 4.

	'Blind shoots' (%)		
	A	B	C
Treatment	GS4	GS5	GS6
1.	11	15	8
2.	10	9	6
3.	5	6	4
4.	2	5	3

The results from experiment GS4 clearly show that if night

temperature is higher than day temperature (treatments 3 and 4), less 'blind' shoots are formed than in the opposite situation (treatments 1 and 2). The results from GS5 and GS6 show that if the period with a high temperature during the night increases, the percentage of 'blind' shoots shows a tendency to decrease.

7.3.3. 'BLINDNESS' AND INTERACTION WITH SHOOT STAGE AND TEMPERATURE

A closer examination of the formation of 'blind' shoots was made in experiments with container grown roses of the cv. Sweet Promise.
The containers made it possible to realise many combinations between temperature and development stage of the shoot, by simply transferring the containers between compartments with different temperature regimes.
The experiment were performed to detect the most sensitive stage for 'blindness' in the development of the shoot.
The first two experiments (GC1 and GC2) included 27 different temperature treatments. The results were split into three groups which had the same realised mean temperature during the whole development time from bud break until harvest, but different temperatures during the period from bud break until stem elongation. It became clear that during this period the bud is very sensitive to temperature in relation to 'blindness' (Table 16).

Table 16. Rose cv. Sweet Promise, container grown. Percentages of 'blind' shoots from two experiments, one started in November and the other in May, in relation to 3, 12hrs night/12 hrs day temperature (°C) treatments during the development from bud break until stem elongation (= 4 cm). The mean temperature during the whole shoot development was the same for all treatments: 18°C in GC1 and 22°C in GC2.

'Blind' shoots (%)

	November (GC1) night/day °C	%	May (GC2) night/day °C	%	average
1.	18/22	47a	22/24	27a	37.0a
2.	15/22	37b	18/20	12b	24.5b
3.	12/22	39b	14/16	10b	24.5b
Average		41a		16.3b	

The table shows, that a higher daily mean, in the period from bud break until stem elongation, stimulates blindness. It is also clear that the percentage of 'blind' shoots is higher for shoots that develop during winter (GC1) than for shoots that develop in summer (GC2). In the following experiment (GC3), 9 different temperature combinations were made at a given daily mean of 20°C. In this experiment higher night than day temperatures were involved. The results of this experiment are listed in Table 17.

Table 17. Percentage of 'blind' shoots in relation to 3 different 12 hrs night/12 hrs day temperature (°C) treatments, and 2 development stages of the shoot: (1) from bud break until elongation growth and (2) from elongation growth until harvest. Daily mean 20°C for all treatments.

		Night/Day (°C). From elongation growth until harvest			
Night/Day (°C)		24/16	20/20	16/24	average
From bud break	24/16	15	36	35	28.6
until	20/20	10	18	31	19.6
elongation growth	16/24	8	13	22	14.3
	average	11	22.3	29.3	

Table 17 shows a clear interaction between shoot stage and the night/day temperature combination. The distribution of temperature between day and night influences the formation of 'blind' shoots in two ways. In the period from bud break until stem elongation a higher night than day temperature stimulates the formation of 'blind' shoots, but in the following period it decreases it.

The influence of the higher night than day temperature was studied further in the experiments: GC3, GC4, GC5 and GC6. In these experiments, roses were transferred from a high night/low day to a low night/high day temperature regime and also the other way around at three stages of the development of the shoot: (1), when the lateral buds had just broken (=1cm); (2), at the start of stem elongation(= 4cm); (3), when the flower bud was visible to the naked eye (diameter 2-3mm). This resulted in a total of 8 different combinations (Table 18). In this table the results of these experiments are listed.

The table shows that the treatments 3-5 (underlined) show a

remarkable, significant low percentage of 'blind' shoots if compared with the other treatments.

It is clear that a constant high night/low day temperature regime (treatment 5) leads to less 'blind' shoots than the opposite combination, a low night/high day temperature (treatment 1). This last situation is common in commercial rose growing. The lowest percentage of 'blind' shoots appears in the treatments 3 and 4. These are the treatments in which a low night/high day temperature in the period from cut until bud break or stem elongation is followed by a high night/low day temperature regime. In the opposite temperature combinations, the treatments 7 and 6, there is a very high percentage of 'blind' shoots.

Table 18. Influence of two (00, XX) opposite night/day temperature combinations on the formation of 'blind' shoots in relation to 4 (I, ..., IV) stages of shoot development. Averages of 4 experiments (a), diameter of the parent shoot (b, c) and position of the lateral bud on the parent shoot (d, e, f).

Legend: **Temperature distribution between day and night:**

00 *12 hrs 16°C night/12 hrs 24°C day temperature.*
XX *12 hrs 24°C night/12 hrs 16°C day temperature.*

Development stage of the shoot:

I *From cut until bud break (= 1 cm).*
II *Next until elongation growth (= 4 cm).*
III *Next until flower bud 2-3 mm.*
IV *Next until cut.*

a Average from 4 experiments (GC3-GC6).

b,c **Diameter of the parent shoots:**

b *more than 4mm at place of cut.*
c *less " 4mm " " " " .*

d,e,f **Bud position:**

d *uppermost bud, closest to place of cut.*
e *second bud, counted downward from the place of cut.*
f *third " , " " " " " " " .*

	Shoot stage				'blind' shoots (%)					
	I	II	III	IV	a	b	c	d	e	f
1.	00	00	00	00	35	18	100	47	93	100
2.	00	00	00	XX	31	26	81	40	87	100
3.	00	00	XX	XX	14	3	35	13	71	100
4.	00	XX	XX	XX	16	8	22	13	75	100
5.	XX	XX	XX	XX	22	7	41	16	80	100
6.	XX	XX	XX	00	44	21	100	45	87	100
7.	XX	XX	00	00	46	25	100	46	100	100
8.	XX	00	00	00	46	31	100	48	91	100
				Average	32	17	70	34	86	100

7.3.4. 'BLINDNESS' AND THICKNESS OF PARENT SHOOT AND BUD POSITION

The influence of the thickness of the parent shoot on the percentage 'blind' daughter shoots and the influence of the bud position on the parent shoot on 'blindness' was studied for container grown roses cv. 'Sweet Promise. The lower buds were only taken into account if the higher bud produced a flowering shoot. If the higher bud produced a flowerless shoot, the buds situated lower on the parent shoot always produced 'blind' shoots too. The results are listed in Table 18.
Table 18 shows that:

- Shoots emerging from lateral buds on thick parent shoots (b) are less sensitive to 'blindness' than shoots emerging from thin parent shoots (c).
- Counted downwards from the place of cut, the second bud (e) is much more sensitive to 'blindness' than the first and upper one (d). The third bud (f) always formed 'blind' shoots in the experiments.
- In column (a) are the averages given of four experiments performed during two years. The figures refers to the terminal bud of shoots

cut back at the first five leaflet-leaf.

The difference in propensity to the formation of 'blind' shoots between thick and thin parent shoots was further studied in an experiment with roses of the cvs. 'Sweet Promise' and 'Merko'. Parent shoots were divided into two groups, one group with a diameter of more than 4mm and one group with a diameter less than 4 mm. Both groups were cut at the first five-leaflet leaf above the joint and the daughter shoots were followed during their development. The temperature during bud break and shoot growth was kept at 20°C in airconditioned glasshouse compartments. The percentage of 'blind' shoots was calculated. The results are listed in Table 19.

Table 19. Rose cvs. Sweet Promise and Merko, container grown in glasshouses. Percentage of 'blind' daughter shoots from thick and thin parent shoots.

	'Blind' shoots (%)	
	Diameter of the parent shoot	
Cultivar	thin (< 4mm)	thick (> 4mm)
Merko	48a	19b
Sweet Promise	43a	28b

Table 19 shows that the thickness of the parent shoot has a strong influence on the formation of 'blindness' in the daughter shoots. On thick parent shoots less 'blind' daughter shoots are formed than on thin ones.

7.4. DISCUSSION

The results from the experiments with soil grown roses of the cvs. Sweet Promise and Varlon refer to selected and labeled shoots (see chapter 2). Compared to the container grown roses, the percentage of 'blind' shoots is low. These low figures can be explained by the larger diameter of the shoots of the soil grown roses. Thick, vigorous, shoots are less vulnerable to 'blindness' than thin, weak, ones (Table 18 and 19). As the labeled shoots formed a positive selection of all shoots in an experimental plot, this meant that the average diameter of all shoots was lower than that of the labeled ones and as a logical result the percentage of 'blind' shoots of all shoots in a plot was higher too.

The positive linear relation between the percentage of 'blind' shoots and temperature during the period November until May (Figure 68, line A and B) can be explained by the fact that higher temperatures result in thinner shoots (chapter 5), which are more vulnerable to blindness. If we consider the shoots grown in March and April apart from the others, a negative linear relation with temperature appears (Figure 68, line C). This indicates an interaction between the period in which a shoot grows and temperature in relation to blindness. Such a reaction was also reported by Moe (1971b). An increase in temperature influences 'blind' shoot formation in two different ways. (1) It has a direct, reducing effect, on blindness. (2) It has an indirect, stimulating effect, on 'blindness' because it leads to thinner shoots which are more propensive to 'blindness' than thick ones. In a period with a low light intensity the first effect is overuled by the second, resulting in more 'blindness'. In a period with more light the second effect of temperature increase is not strong enough and less 'blind' shoots are formed. Calculations for the whole period November until May show an increase in 'blindness' at an increase in temperature (Figure 68A,B). An explanation of this difference in 'blind' formation in relation to the growth period, may be that a smaller quantity of assimilates is

available in winter than in spring. According to several authors (Hale 1960, May 1965, Wardland 1968, Halevy 1972) it is stated that a developing flower bud is until the stage of anthesis a relatively weak sink, and because the development rate is high, which means a high use of assimilates, the flower bud dies of starvation.

At a given 24 hours temperature an increase in night temperature, which of course means a proportional decrease in day temperature, resulted in less 'blind' shoots (Figure 69). This effect has also been reported by Zieslin and Halevy (1975b).

If the night temperature is higher than the day temperature this effect (fewer 'blind' shoots) holds true even if extreme temperature combinations are imposed. In an experiment in the phytotron a 16 hours dark period at 25°C was combined with a 8 hours light period at 9°C. In that situation nearly all shoots came into flower, although the shoots were very short and thin and completely white (chlorofyllless). The leaves soon became necrotic and dropped spontanously. As in this situation the new shoots could not or scarcely produce assimilates and hormones, these substances must have been mobilised and transported from the parent shoots which had developped under normal temperature conditions and had green leaves. It looks that in this situation the flower bud is a stronger sink than the leaves; at least it attracts enough assimilates to develop while the leaves drop. This result also strengthens the idea that lack of nutrients and/or hormones during a sensitive stage of floral development leads to 'blind' shoots. This explanation also makes it understandable that in case of a multiple break, the shoots lower on the parent shoot are more sensitive to 'blindness' than the upper one. The higher bud generally breaks earlier and its emerging shoot then becomes a strong sink that competes for nutrients and hormones with the lower shoots. If in spring enough assimilates are available to bring both shoots to flower, a difference in shoot length and fresh shoot weight are measured at harvest. The higher shoot is heavier and longer. In winter when there is a lack of assimilates only the highest and most competative shoot flowers. The other ones

grow 'blind' because they are 'deprived' by nutrients and may be hormones by the higher stronger shoot. A similar reaction can be seen in summer if more than two lateral buds break on the same branch.
The reducing effect of a higher night than day temperature on 'blind' formation already becomes evident when the high night temperature, given at sunset lasts 2-3 hours (Table 15B,C).

The most vulnerable period for a developing shoot to go 'blind' is from bud break until the flower bud is visible with the naked eye. In this period the reaction to temperature however is not constant. In the first part from cut until stem elongation a high night temperature improves blindness, while in the second part until harvest it reduces 'blindness' (Table 18). At the start of the elongation growth the flower bud has developed sepals and petals but not yet the stamen, pistils and carpels. This is stage 4 in the diagram of Moe and Kristofferson (1969) and stage 7 in that of Horridge and Cockshull (1974). This stage is very vulnerable to flower bud abortion (Hubbell 1934a, Van Hove 1980). If the stamen are developped they produce GA, which enhances the sink-activity of the developing flower bud and make it less vulnerable to abortion. Although it was not possible to determine the exact stage of each bud, without destroying the flower, it was intended to transfer all the plants in the container experiments in this vulnerable stage. This may have resulted in less pronounced results!
In the experiments in which also the second and the third lateral bud were considered, those buds were of course in development behind the first and higher bud. Because the plants were transferred when the uppermost bud was in the desired stage this may have influenced the results. The effect of a high night temperature combined with a low day temperature on 'blindness' may be that the relative sink strength of the flower bud is higher at night than in daytime when the developing leaves form a stronger sink. Because the low day temperature does not affect photosynthesis very much but reduces the use of the assimilates at daytime, at night more assimilates are available for the flower bud. It seem that the temperature

distribution between day and night is a tool to direct the assimilate stream. This tool can be used by the grower and probably not only for roses. In this respect results of Hori and Shishido (1978) who worked with tomato plants are interesting. They found that night temperature affects the distribution pattern of C-assimilates. The higher the night temperature the lower the percentage distribution to the lower parts including the roots, and the higher the percentage to the upper parts including the inflorescence.

The above mentioned hypothesis can be considered a so called 'nutrient diversion hypothesis'. The core of this hypothesis is that the genetic information, in this case for flower initiation and development, can only be expressed if enough nutrients are available at the site were they are needed. If nutrient levels are too low because of action of competing sinks or inadequate supply by photosynthetic tissue, the information is not expressed and the flower bud atrophies (see also Appendix 1).

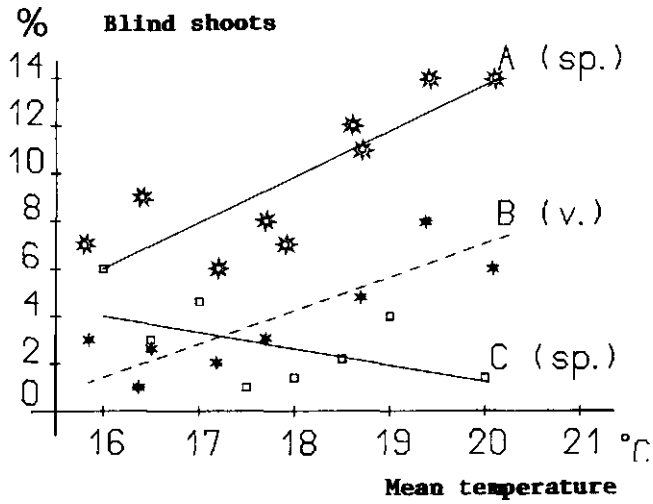


Fig.68 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Percentage of 'blind' shoots in relation to the mean temperature and the harvest period. Line A: 'Sweet Promise', November until May: Y=-23.19+1.83X (r=.83). Line B: 'Varlon', November until May: Y=-19.52+1.30X (r=.80). Line C: 'Sweet Promise', March until May: Y=15.31-0.70X (r=-.56).

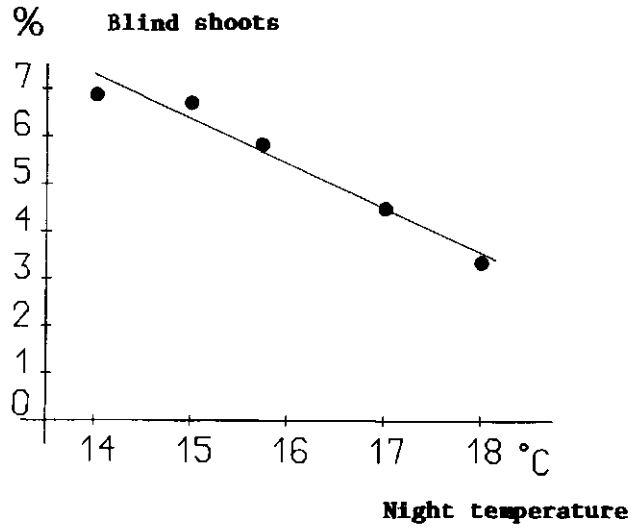


Fig.69 'Sweet Promise', grown in glasshouse soil. Percentage of 'blind' shoots in relation to the night temperature at a daily mean of 18°C. Y=21.49-1.02X (r=-.98)

8. FLOWER AND FRESH WEIGHT PRODUCTION

8.1. INTRODUCTION

Previous chapters dealt with consecutively, the influence of temperature on bud break, development time, fresh shoot weight, measurements of the shoot and formation of 'blind' shoots. In this chapter the effect of temperature on the number of roses harvested and total fresh weight production per shrub is the subject. The patterns of bud break and subsequent harvest are presented as they appeared in the experiments with the rose cultivars Sweet Promise and Varlon, grown in glasshouse soil. The effect of soil heating and of a 12% reduction in light on glasshouse grown 'Sweet Promise' is discussed too.

8.2. MATERIALS AND METHODS

This chapter deals with rose production in the experimental plots of the experiments GS1 to GS6 (See chapter 2). The production is calculated as number of roses harvested per shrub. The plant density is 6.4 shrubs per square meter gross glasshouse soil surface.
The production within the plots was not influenced by any other factor than the glasshouse climate and the normal harvest operations. Extra samples of rose shoots used for studies on bud break or the formation of 'blind' shoots were not taken out of these plots. At the start of the experiments 72 shoots were selected for each treatment and each cultivar. These labeled shoots within the plots were cut in the same way as the other shoots in a plot and no destructive measurements were performed on the plants. These selected shoots were cut back to the first five leaflet-leaf. The course of bud break, growth and harvest of the daughter shoots was monitored for each labeled shoot.

The influence of soil heating on 'Sweet Promise' was studied in

plots with electric soil heating at 3 air temperatures (see 2.5.). The influence of a 12 percent reduction in light was studied in a glasshouse compartment with special glazing (see 2.6.).

Plant materials, methods, conditions, definitions, abbreviations and codes of the experiments have been described in chapter 2.

8.3. RESULTS

8.3.1. COURSE OF BUD BREAK AND PRODUCTION

In experiment GS2 nine temperature combinations were applied. The course of bud break of the daughter shoots from the labeled shoots is shown in Figure 70 for 'Sweet Promise' and in Figure 71 for 'Varlon'. Each figure is subdivided in histograms, which refer to the treatments. The imposed night/day temperatures are written above the histograms. The experiment started in the second week of October. Until this week all temperature regimes had been the same for all treatments. On the horizontal axis the figures show the number of the week in which a lateral bud had broken and on the vertical axis the number of broken buds. The histogram shows that a lower temperature results in delayed bud break. At the start of the experiment (arrow) the roses in a plot were 'on flush'. The course of bud break influences the course of harvest as is shown in the Figures 72 and 73 for the cultivars Sweet Promise and Varlon respectively.
In these two figures the weekly harvest from the whole plot is given, including labeled as well as non labeled shoots. The figures show that a Lower temperature results in a delayed and lower production. The 'on flush' structure of the production gradually disappears.

8.3.2. PRODUCTION PER SHRUB

The total production per shrub during the experiment GS1 and GS2 is plotted against the harvest date in Figures 74 for both cultivars. A

positive linear relationship with the mean temperature appears. Total fresh weight production per shrub in relation to temperature is shown in Figure 75. The figure shows a higher production for 'Sweet Promise' than for 'Varlon'. Both cultivars show an increase in fresh weight production if the temperature increases. In experiment GS3 different night/day temperature combinations were imposed at a given daily mean temperature of 18°C. At the start of the experiment all treatments were 'on flush'. The tops of the production flushes (weeks in which the flushes culminate) during the experiment are shown in table 20.

Table 20. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. Week numbers in which the production 'flushes' culminated, for 5 night/day temperature combinations with the same daily mean of 18°C.
The experiment started in week 40.

Top of the production flushes

N/D	'Sweet Promise' Flush number:						'Varlon' Flush number:			
(°C)	1	2	3	4	5	6	1	2	3	4
14/22	33	40	48	5	12	18	34	42	52	12
15/21	33	40	49	5.5	12	18	34	42	52	12
16/20	33	40	49	5.5	12	18	34	42	52	12
17/19	33	40	49	5.5	12	18	34	42	52	12
18/18	33	40	48.5	5	12.5	18.5	34	42	52	12

The table makes it clear that the production pattern of the different treatments is synchronous during the whole experiment. The average production per shrub during the period November until May, is shown in Table 21 for both cultivars.

Table 21. Rose cvs. Sweet Promise and Varlon, grown in glasshouse soil. The production of roses per shrub in the period November until May, for five night/day temperature treatments at a given mean temperature of 18°C. Plant density 6.4 shrubs per gross m2.

Treatment Night/Day (°C)	Flower production per shrub 'Sweet Promise'	'Varlon'
1. 18/18	11.4	4.6
2. 17/19	12.0	5.3
3. 16/20 (mean of 2)	12.5	5.9
4. 15/21 (mean of 3)	12.4	5.3
5. 14/22 (mean of 2)	12.3	5.3
	*	*

Table 21 supports the idea that the production responds to night temperature with an optimum curve. The differences between the treatments are not significant, however.

In the forth (GS4), fifth (GS5) and sixth (GS6) experiment in the glasshouse soil higher night than day temperatures were involved at a given daily mean temperature of 19°C for all treatments. The production per shrub in these experiments is listed in Table 22.

Table 22. Rose cultivars Sweet Promise and Varlon, grown in glasshouse soil. Production of roses during three experiments, GS4, GS5 and GS6.
Legend: see Table 4.

Flower production per shrub

	A		B		C	
	GS4		GS5		GS6	
Treatment	Sweet P.	Varlon	Sweet P.	Varlon	Sweet P.	Varlon
1.	9.2	3.9	9.0	5.2	8.4	4.4
2.	10.2	4.9	9.3	4.8	8.5	3.7
3.	11.4	5.1	9.7	5.4	9.2	5.0
4.	13.1	5.7	12.4	5.6	11.0	5.4

The results from the experiments show for both cultivars an increase in production, if at a given daily mean, night temperature increases and day temperature decreases. The course of the production of 'Sweet Promise' and 'Varlon' in experiment GS4 is shown in Figure 76 for two reversed night/day temperature treatments: 16/22 ^{o}C and 22/16 ^{o}C. Table 22 and Figure 76 make it clear that at a given daily mean temperature an increase in night temperature results in a higher production.

8.3.3. PRODUCTION AND SOIL HEATING

The results from the experiment on soil heating with 'Sweet Promise' are listed in Table 23. The heating was only in action in the

treatments with an imposed night temperature of 12°C and 15°C. In the other treatment with an imposed night temperature of 18°C, soil temperature at a depth of 10 cm hardly ever dropped below 20°C, which was the setpoint for soil heating. The table shows no significant differences between plots with, and plots without soil heating.

Table 23. Rose cv. Sweet Promise, grown in glasshouse soil. Influence of soil heating '+' (setpoint 20°C) or non heated soil '-', in combination with three air temperatures: 12, 15 and 18 (°C) at night at one 20-22°C day temperature, on flower production per plant, on average fresh shoot weight and on average shoot length of cut roses. Period November until May.

	Flowers per plant		Shoot weight		Shoot length	
Night(°C)	+	-	+	-	+	-
12	9.6	9.2	22.0	22.7	66.0	66.8
15	10.0	10.0	22.6	21.2	67.5	67.7
18	14.0	14.4	20.1	19.8	64.7	64.8
mean	11.2	11.2	21.6	21.2	66.1	66.4
	a	a	b	b	c	c

8.3.4. INFLUENCE OF PARENT SHOOT ON FRESH WEIGHT OF DAUGHTER SHOOTS

The labeled shoots selected before the start of the experiments, formed a positive mass selection of all shoots in a plot. During the October flush the weight of the labeled shoots was on average 23 percent higher than that of the other shoots in an experimental plot. In the 6 years with experiments with soil grown roses in glasshouses

(GS1 to GS6) was determined whether this difference in favour of the labeled shoots was maintained during winter and spring. The results are given in Figure 77. In this figure, averages of six years of the ratio between the 'heavy' (labeled) and the 'light' (unlabeled) shoots are shown on the vertical axis, the harvest date is shown on the horizontal axis. The figure shows, that the large difference in weight in favour of the labeled shoots sharply decreases but does not fully disappear during winter, and increases again in spring.

8.3.5. INFLUENCE OF A 12% LIGHT REDUCTION ON PRODUCTION AND QUALITY

During the experimental years 1979-'80 and 1980-'81 the influence of a 12 percent reduction in light was studied on the production and quality of the cv. Sweet Promise. For materials and methods see chapter 2.6. The results of the experiments are presented in Table 24 and in Figure 78.

Table 24. Rose cv. Sweet Promise, soil grown in the glasshouse. The influence of a 12% reduction in light (coated glass) compared with the normal light level (clear glass) on the flower production per shrub, the average fresh shoot weight (g), the average shoot length (cm) and the average fresh weight per cm, of the cut roses, for two successive winter periods: October until May.

	Period 1		Period 2	
	15°C Night/18°C Day		15°C Night/ 21°C Day	
	clear	coated	clear	coated
Flowers per shrub	8.2	7.6	13.6	12.6
Fresh shoot weight (g)	25.4	23.4	18.2	15.9
Shoot length (cm)	61	62	60	58
Shoot weight (g) per cm	.42	.38	.30	.27

Table 24 shows a tendency for a decrease in production and in quality, expressed as fresh weight per rose and per cm shoot length, if the light level is reduced by 12%. Figure 78 gives a clear view of the decrease in fresh weight during the season.

8.4. DISCUSSION

The course of bud break and harvest under different temperature conditions supports the effects discussed in the previous chapters. Lower mean temperatures result in a delayed bud break (Figures 70, 71) and production (Figures 72, 73). At a given mean temperature the production pattern is not influenced by the temperature distribution between day and night (Figure 76, Table 20). If night temperature is lower than day temperature the production shows a linear positive correlation to the mean temperature (Figure 74). The reaction to temperature is caused by:

(1). Quicker bud break (chapter 3).
(2). Shorter development time (chapter 4).
(3). Less 'blind' shoots in spring (chapter 7).

At a given mean, a higher night than day temperature of 12 hours on a diurnal base clearly results in a higher production (Table 22A). A diurnal period of at least 4 hours with a temperature of 24^{o}C starting at sunset already shows a positive effect on production. The longer the period of 24^{o}C per night, the higher the production (Table 22B,C). This effect must be ascribed to a reduction in the formation of 'blind' shoots, although incidently a stimulation of bud break by a higher night than day temperature was observed. The effect on 'Varlon' is less pronounced then on 'Sweet Promise'. This last cultivar is more sensitive to blindness than the first one (see chapter 7).

Total fresh weight production is higher for 'Sweet Promise' than for 'Varlon' and increases with temperature (Figure 75). A maximum for temperature was not reached, so this must be higher than 20.5°C. The lower production for 'Varlon' was due to the lower number of structural branches compared to 'Sweet Promise' and not to a lower fresh weight production per shoot per day (see chapter 5) or to a higher percentage of 'blind' shoots (see chapter 7). Improving the architecture of the shrub by stimulation of the formation of 'bottom breaks' may be a possibility to increase the production of 'Varlon' and other cultivars with few structural branches. Producing plants by tissue culture may be a method for this as plants propagated in this way form more structural branches (Van den Berg 1986).

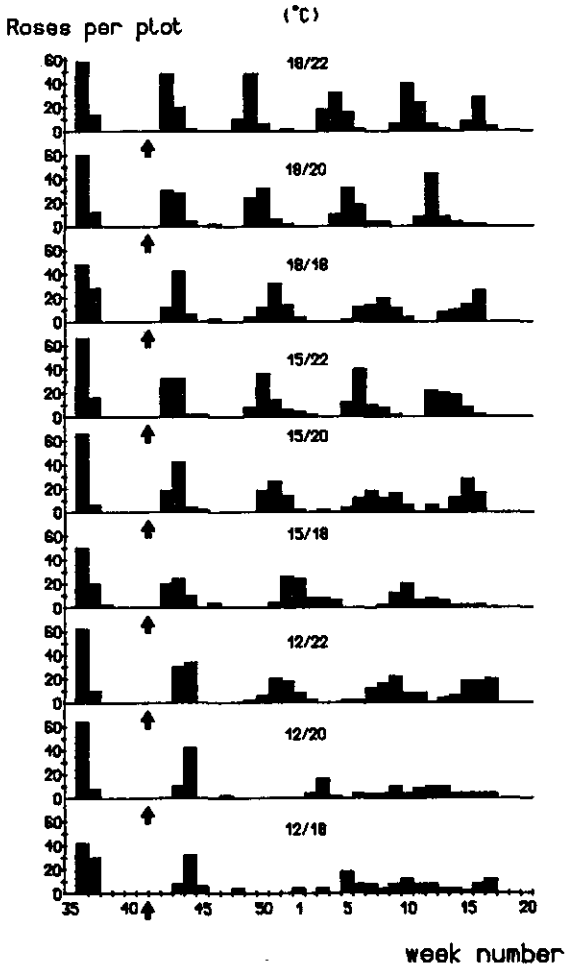
No influence of soil heating on production was found. This result is contrary to expectation. For many species a clear reaction of shoot growth to root temperature has been reported (Reviewed by Cooper 1973). An explanation is that due to the low lying poly-ethylene heating pipes, soil temperature at the depth of the temperature sensors (10 cm below soil surface) in the plots with soil heating was only a few degrees above the non-heated plots. These differences appeared to be too small to have a distinct influence on production. Momentary temperatures in the non heated plots were never lower than 15°C. In commercial glasshouses, mostly two thirds or more of the heating pipes are installed at or just above soil level. In this situation soil heating is not expected to have a positive influence on production. If roses are grown in less voluminous substrates like rockwool slabs laid on the glasshouse soil or on movable benches, root temperature follows air temperature closer than in soil grown plants. In this last situation a positive effect on the production by substrate heating can be expected.

At a constant daily mean temperature, an increase in night temperature combined with a decrease in day temperature brought about in such a way that the realised night temperature stayed lower than the realised day temperature, had no reliable influence on production (Table 21). This is contrary expectation. In such a situation a

reduction in 'blind' shoot formation should result in an increase in production (See chapter 7). This was not found in the experiments, however. The reason might be, that to realise the low day temperatures, the ventilators were opened wider and more often than in the treatments with a higher setpoint. This resulted in a lower CO_2 level in the glasshouse, which has a negative influence on production (Hand and Cockshull 1975, Mortensen and Moe 1983). In a practical situation this can be avoided by maintaining a larger distance between the setpoints for heating and ventilation than in the present experiment, in which it was only $1^{o}C$.

The lead in fresh weight gained by daughter shoots of heavy parent shoots over daughter shoots of lighter parent shoots, strongly decreases during winter, but does not disappears completely. In spring the lead increases again (Figure 77). The positive influence of a heavy, vigorous parent shoot only comes into its full expression if light is not at a minimum.
A better access to the supply of nutrients via the root system, or to reserve nutrients in the lower branches which probably lies at the base of the vigorous growth of heavy shoots, is only fully effective if assimilates are not limited.

The results from the experiments with a 12% reduction in light show a reduction in production and fresh weight. Although the experiments were done without simultanous replications, which make it impossible to speak in terms of statistical significance, the trend is clear and seen in the light of the previous chapters, is as could be expected. Light loss results in losses in production and quality. For this reason the maximum possible light level inside the glasshouse must have full priority in glasshouse construction. Light is the basis of production but also the production factor most expensive to supply artificially.



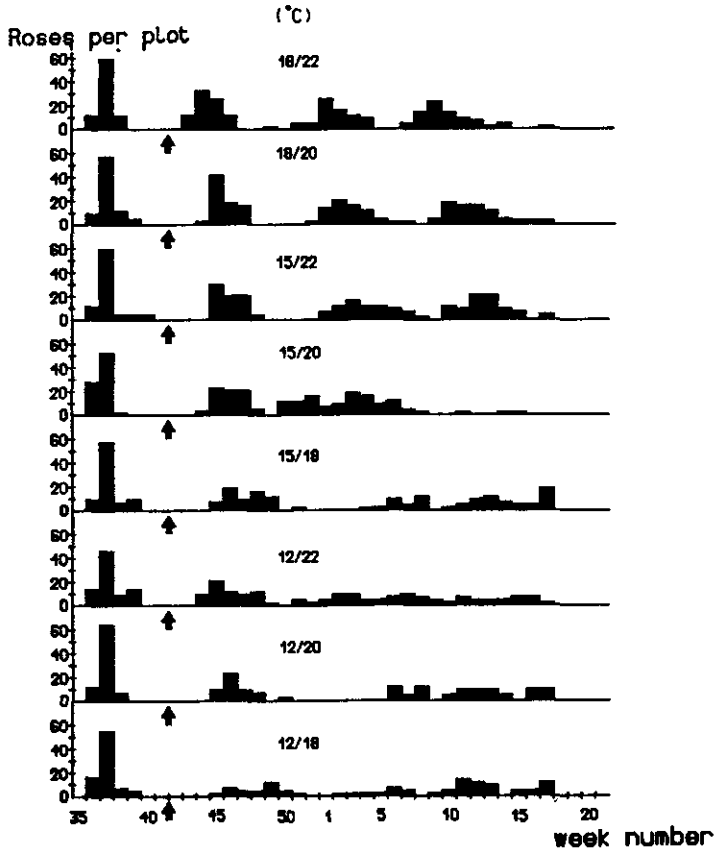
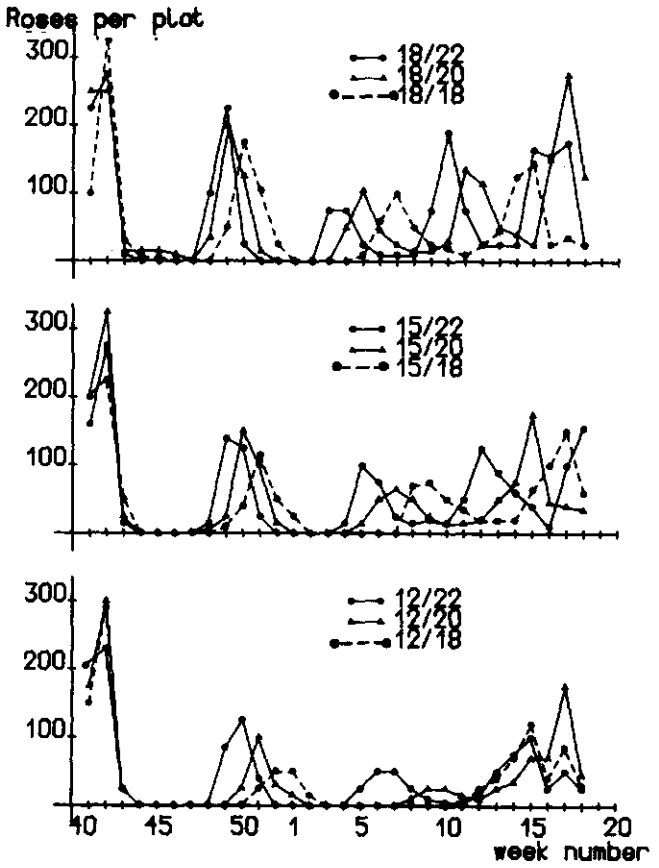


Fig.70 (l) 'Sweet Promise' and **Fig.71** (r) 'Varlon', grown in glasshouse soil. Course of bud break of 72 labelled shoots, for 9 night/day temperature treatments.



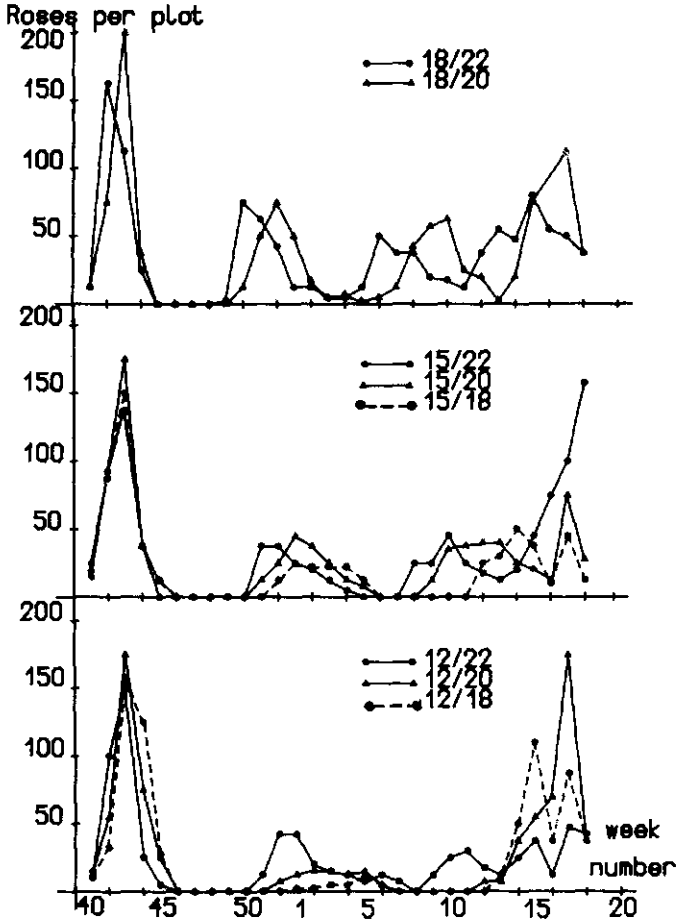


Fig.72 (l) 'Sweet Promise' and **Fig.73** (r) 'Varlon', grown in glasshouse soil.
Course of harvest, for 9 night/day temperature treatments.

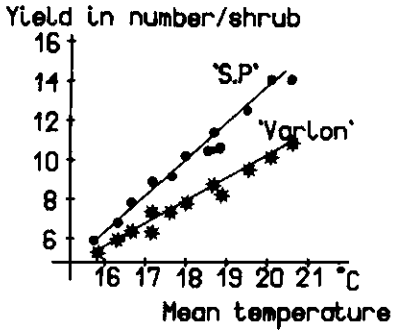


Fig.74 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between flower production per shrub and mean temperature in the period November until May.
'SP':Y=-24.15+1.89X (r=.97)
'V':Y=-12.88+1.11X (r=.96)

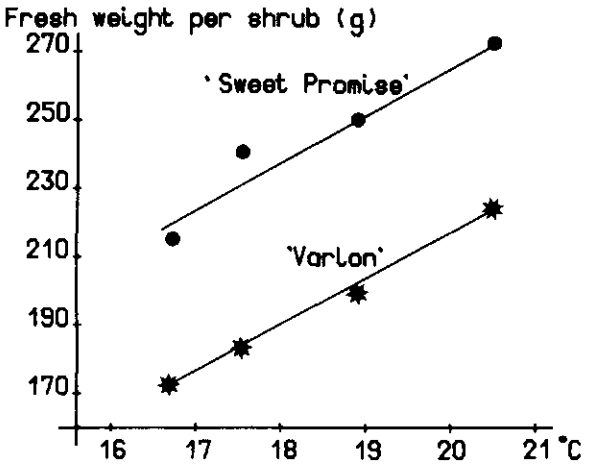


Fig.75 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Relation between fresh weight production per shrub and mean temperature. Period November until May.
'SP': Y=-14.42+14.03X
(r=.97)
'V': Y=-51.07+13.37X
(r=.99)

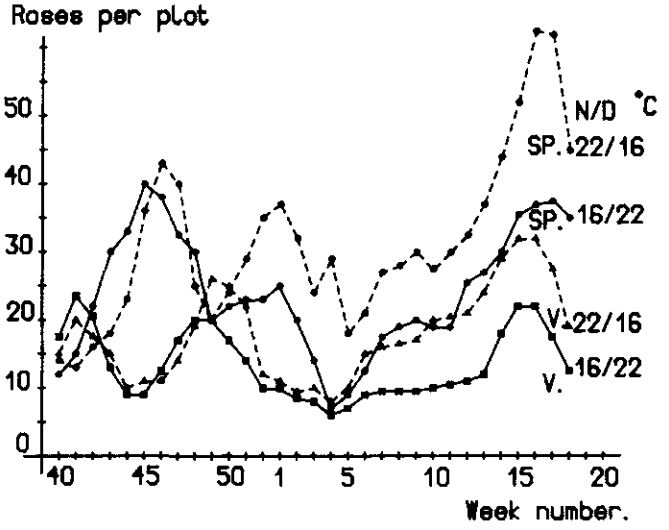


Fig.76 'Sweet Promise' and' Varlon', grown in glasshouse soil. Course of the harvest for two imposed opposite night/day temperature treatments at one. daily mean temperature of 19°C.

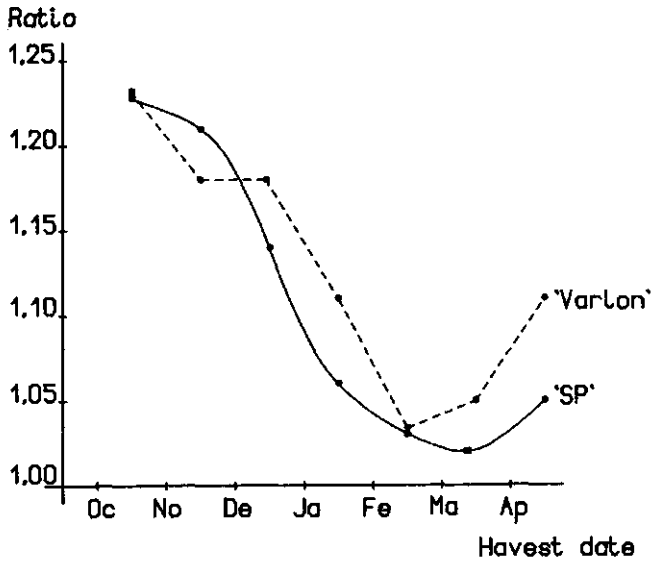


Fig.77 'Sweet Promise' and 'Varlon', grown in glasshouse soil. Course of the fresh weight ratio between daughter shoots of 'heavy' and of 'light' parent shoots during winter. Averages from 6 years.

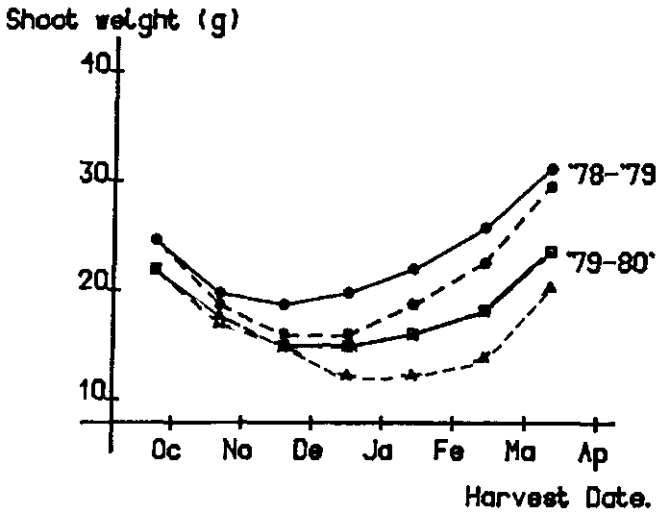


Fig.78 'Sweet Promise', grown in glasshouse soil. Average fresh weight per cut rose for roses grown under natural (solid line) and under a 12% reduced light level (broken line), for two winter seasons.

9. FINAL DISCUSSION

In this concluding chapter a condensed review of the work reported in this thesis is offered. The results and conclusions are discussed and some suggestions for commercial rose growing are made.
This thesis deals with the influence of temperature under natural light conditions on growth and production of grafted soil-grown glasshouse roses of the cultivars Sweet Promise and Varlon. Insight into shoot growth was widened by experiments with container grown bushes of the cultivar Sweet Promise in glasshouses and in growth rooms.

For common glasshouse conditions with a night temperature equal to or lower than the day temperature, 'models' were constructed for the time a terminated lateral bud needs to break (Fig. 1-4), the development time of the shoot from bud break until harvest (Fig. 10, 14), shoot weight (Fig. 18, 19), flower bud weight (Fig. 26, 27), shoot length (Fig. 39, 40), length (Fig. 56, 57) and width (Fig. 58, 59) and volume (Fig. 60, 61) of the flower bud, diameter of the shoot (Fig. 62, 63) and diameter of the neck (Fig. 64, 65). The 'models' demonstrate how these entities behave for shoots of lateral buds broken during the period October until April in relation to the mean air temperature in the range $16^{o}C$-$22^{o}C$. The 'models' can be used for production and quality planning. Even more interesting than the absolute levels of the entities which may vary from nursery to nursery, are the relative differences between the levels in the 'models', or the percentueel effect of changing the temperature by one or more degrees centigrade (e.g. Fig. 15,20). These relative effects can considered being more stable than the absolute effects and can be used for all nurseries. The 'models' are constructed with the date of bud break on the horizontal axis. Some calculating using the development time (Fig. 10, 14) can transform the 'models' to show the harvest date on this axis, which is not shown separately. The

'models' open the possibility of predicting what can be expected if temperature is manipulated in a certain way. The 'models' can be used in combination with the price expectation of roses and e.g. the energy price so as to develop an 'optimization program' for control of the glasshouse temperature in a more sophisticated way than at present. Such an optimization strategy has been developed by Challa et al. for cucumber (1980). The 'models' can be used as a source for a computer program or for making calculations by hand, and give the user insight into the possiblities that manupulation of the air temperature offers for control of production and quality. The method as described in these thesis for making a 'model' can probably also be used for other crops.

The reaction of the shoot properties to the distribution of temperature between day and night determines the limits for temperature control without losing quality. If at dusk a period with a temperature higher than during daytime is given for no longer than 6 hours, the 'models' are hardly affected. A temperature difference between night and day of 5 ^{o}C or more in the advantage to the night as used in the experiments with soil grown roses is extreme, however. Smaller differences will undoubtedly be usable without any problem. Differences in reaction strength between cultivars is possible, of course. In this context it is also important to know the price elasticity of a cultivar in relation to fresh shoot weight and shoot length. This knowledge can be used to attain maximum profit of a thermal screen. Less energy is needed to maintain a high temperature at night when the screen is closed than in daytime when it is open. At a given daily mean temperature an increase in night temperature combined with a proportional decrease in day temperature gives an extra energy saving, which can add up to more than 10 percent on an annual basis. This way of energy conservation requires no extra investments if a thermal screen has already been installed, and enhances the profit of the screen.
Although a decrease in shoot length as caused by a higher night than

day temperature is unwanted for roses such an effect can be considered positive for those cutflowers and potplants which need length control by means of growth retardents.

Within the limits of the experiments only a small or no interaction was found between temperature and stage of the shoot with development time, fresh shoot weight and shoot length. The plant seems to integrate temperature more or less. This result implies that it must be possible to control air temperature during shoot growth on a basis of a mean daily (average day and night) temperature or temperature sum, instead of trying to secure a previously fixed day and night temperature. The practical consequence of this is that there is no need for heating systems designed for the realisation of any inside temperature at any moment, whatever the outside conditions are. This also has consequences for the use of heating systems with a slow response to changes in setpoint, like heated concrete floors. Overshoot and undershoot of the set temperature does more harm to the controlling technician than to the plant. Days with a lower temperature than the wanted mean can be compensated by days with a higher temperature without disturbing crop planning and quality. This does not mean of course, that extreme temperatures cannot disturb growth. Setting the limits and quantification of the effects of the 'border region' on growth must have attention in order to develop reliable optimization programs for climate control. Such programs for heating glasshouses, based on temperature sums instead of fixed day and night temperatures need more attention in research, and not only for floriculture. They will be importent for the way in which among others low temperature heating systems can be made usable for heating glasshouses. Together with what has been said about temperature distribution between day and night, a change in heating strategy will be the necessary consequence. It will be evident that in commercial glasshouses the results of such a heating strategy will only come to its full deployment if temperature distribution inside the glasshouse is homogenous.

The decrease in the formation of blind shoots is a welcome side

effect of a high night temperature regime. It directly results in an increase of production in the winter period when rose prices are highest. As thin shoots are especially vulnerable to blindness, the increase in production is mainly a result of these thin shoots. These shoots will probably not produce roses of the highest grade but this is not such a disadvantage, however. A lower graded rose is better than no rose at all.

A practical and positive consequence of a high night temperature underneath a closed thermal screen is that, because of the lower pipe temperatures, the relative air humidity does not drop as much as without a screen. This has a positive effect on bud break.

The method of linear least square analysis was used to analyse the 'models'. The equations cannot be used to predict what will happen to the dependent variable if only one of the carrier variables is changed. Because of correlation a change in one of them also changes the other ones.
The development time of a shoot can be explained almost completely by the two climate variables, air temperature and irradiance. These variables account for 98 percent of the variation in the 'models'.
To account for 97 percent in the 'models' on fresh shoot weight the variable relative humidity is also needed in the regression equation. Flower bud weight can for 91 percent be accounted for by adding 'day length' as a fourth variable. Although irradiance and daylength were not independent we can assume that, according to work of a.o. Cathey et al. (1981), growth response like development time and total weight are more related to total irradiance as to daylength. The distribution of fresh weight over flower bud and stem was influenced by daylength, however.

Concerning shoot length, five variables are needed: temperature, temperature squared, irradiance, relative humidity and the fresh weight of the parent shoot. These five variables together account for 86 percent of the variation in the 'models'. This percentage is lower than the others. This means that the variables work in a more

intricate way than supposed or that other unknown factors are involved. In the equations, the variable 'Weight of the Parent Shoot' (WPS) indicates that internal plant factors influence shoot length. The variable WPS is also significant in the regression equation on flower bud length and on the diameter of the shoot. The variable WPS itself is mainly determined by the climate conditions during its own development. It appears that shoot growth can be explained with only a handfull of variables. Of these variables, temperature is relatively easy and 'cheap' to control. Because of the high electricity costs, increasing the irradiance inside the glasshouse by supplementary lighting is in most situations too expensive. Improvement of the irradiation level must for this reason be a primary factor in the construction of the glasshouse and in the covering material. The negative effect on production and quality of a decrease in light has been clearly demonstrated in Table 24 and in Figure 78.

The appearence of hysteresis in the average daily fresh weight production per shoot (Figure 36) and in the average daily shoot lengthening (Figure 67) may partly be due to differences in air humidity, but also supports the idea of a role of internal factors. Shoots that develop in autumn grow on plants with a well developed active root system. The plants gradually pass from conditions promotive to growth to conditions which are much less favourable. These plants can probably easily meet the need for nutrients from reserves built up in summer. These reserves will gradually be exhausted, so that few or no reserves are available in the second part of winter. Shoots which then develop grow on weakened plants although in improving growing conditions. This means that the shoots demand gradually more supplies from the root system. To meet this increasing demand for minerals, water and hormones, the root system must expand its capacity. For this expansion assimilates synthesised by the shoots are needed. Compared to autumn the situation is now reversed.

In experiments performed in the glasshouses under natural light conditions the mean irradiance and the mean daylength during shoot growth are not independent from the air temperature. A change in the air temperature automatically resulted in a change in the other variables. Temperature determines the development time of a shoot. If temperature decreases, the development time increases and the shoots stay longer on the plant. As a result, the shoots receive more light, grow taller until a maximum is reached and also become heavier. The Figures 79 and 80 show development time, fresh shoot weight and shoot length for the lateral buds broken on the first day of the months October until April. Each line in the figure represents the first day of the relevant month. The seven data points per line from left to right represent seven mean temperatures 22°C to 16°C. The line for the first of March makes this clear. The figures above the data points mention the development time of the shoot.

During shortening days, an increase in development time results in a raise in the irradiation sum for the shoot, and a decrease in the average daily irradiance, which results in an increase in light efficiency (Fig. 34,35) for fresh weight production. The relation between development time and fresh shoot weight is a nearly straight one (Figure 81). On the horizontal axis this figure shows the development time in days and on the vertical axis fresh shoot weight in grams. The figures near the data points mention the mean temperature. The lines belonging to the first of the months April and December make this clear.

If growth takes place during lengthening days, average and total irradiation both increase, but the light efficiency decreases. The effect of the development time on shoot weight is lower under decreasing light intensities in autumn, than under increasing light intensities in spring, when the irradiation sum increases much more. The line from December and partly the line from February which represent 'Sweet Promise', lies lower than the lines for 'Varlon'. The first cultivar is weakened more by a higher temperature than the second one. A weakened shoot needs more light to produce one gram of

fresh weight than a stronger shoot. For efficient light use, a weak crop must be prevented. The practical consequence is that 'Sweet Promise' cannot be heated as high as 'Varlon' in wintertime, without becoming less efficient with light.

The phenomenon that flower (Figure 74) and fresh weight (Figure 75) production per shrub is lower for 'Varlon' than for 'Sweet Promise' is caused in the first place by the quicker bud break of 'Sweet Promise' (Chapter 1). As a consequence a shrub of 'Varlon' has on average less stems and a lower Leaf Area Index (LAI) with productive leaves than a shrub of 'Sweet Promise'. For this reason a canopy of 'Sweet Promise' catches more of the available light than a canopy of 'Varlon' with the same plant density. Improving the LAI by increasing the number of stems per shrub is important to raise winter production of 'Varlon' and of course also of cultivars that behave in the same way. All light that does not fall on productive green leaves must be considered as being lost which means that the maximum possible production at the actual light level is not reached. In research, methods and techniques to obtain a year round high LAI with productive leaves must have a high priority. Improving the architecture of the shrub by in-vitro propagation of plants might be a possibility (Van den Berg 1986).

In the experiments all shoots, with the exception of the 'blind' ones, were upper cut, i.e. cut above the node. In commercial rose growing, some rose flushes are cut below the node (under cut) in the period October/November until February/March (Rozenbrochure 1984). From the point of view of light efficiency, to under cut is a bad method, especially in winter time. It reduces the LAI and all the young most productive leaves are removed. According to research from Aikin (1974a,b) these young rose leaves are fotosyntheticaly most active. (see also Ticha et al. 1984). The older and lower leaves were formed under different light conditions than to which they are exposed after under cut. This may influence their photosynthetic efficiency with a lower productivity as a consequence. Withers et al.

(1983) have demonstrated this for tomato leaves. The light level under which leaves develop influence, according to a.o. Lichtenthaler (1984), the photosynthetic apparatus and in this way the photosynthetic capacity of a leaf.
The reason that growers under cut is to let buds on lower and thicker stems break, which results in heavier daughter shoots. Such shoots are less susceptible to flower bud atrophy (Table 18b,c, 19). At the start of the experiments the roses in the glasshouse compartments were 'on flush', which means that most of the shoots were in the same development stage. For harvest planning this has advantages. It makes it easier to manipulate air temperature in dependence of the development stage of the shoot.
A negative aspect of growing 'on flush' is that nearly all shoots are harvested within a very short time. This means the removal of the most photosynthetic productive leaves and hormone producing shoot meristems. Until new shoots develop, the light is less efficient used. It also causes a strong disturbance in the shoot/root ratio. Experiences in wintertime showed that especially for roses grown in rockwool this has a negative effect on growth and production (Van den Berg 1986). If it is possible to prevent this negative effect, year round growing 'on flush' can improve planning, labour productivity and mechanisation. Stimulation of root development by the application of growth substances might be a possiblity for roses grown in less voluminous artificially substrates.
If no special measures are taken, the 'on flush' situation gradually disappears. This happens most rapidly at lower temperatures (Fig. 72 and 73) and is mainly caused by the big variation in bud break at low temperatures (Fig. 70 and 71).

During the experiments attention was also paid to the quality of the roses. Quality is a resultant of good and bad points of the rose such as grade, shoot measurements, shoot and flower bud weight, firmness, colour, the expected vase life and the presence of damage from any source. The 'models' give insight into the effect of temperature on a

number of these factors. The 'models' give no information about the colour of the flower bud and the leaves. In the experiments a higher temperature generally resulted in a lighter colour of leaves and flower bud. At a given daily mean temperature an increase in night temperature led to lighter colours. The bigger the difference between night and day temperature and the longer the period with a higher night than day temperature the lighter the colours. Experiments in growth rooms with a night temperature of 25 ^{o}C during 16 hours, combined with a day temperature of 9 ^{o}C during 8 hours led to yellowish-white, thin, short shoots with necrotic leaves and light reddish flowers. In this experiment only some shoots grew blind, however. This result triggered the experiments with container grown roses on the formation of blind shoots as described in Chapter 7. The strength of change in colour differed between the cultivars. The colour of 'Sweet Promise' decreased more than that of 'Varlon'.

During the experiments vase life of the flowers was tested from time to time. Higher temperature did not influence vase life directly, but reduced firmness and led to slacker roses. High temperatures can reduce in this way the sales value of the roses and the vase life.
The translation of the results from container grown experiments to soil grown roses often appeared to be good feasible. However, big differences between day and night temperatures can lead to mistakes because of big differences in root and shoot temperature. These can have a negative influence on rose growth. In less voluminous substrates root temperature follows air temperature closely, but in soil the average temperature of the whole root system scarcely changes between day and night. For this reason for roses grown in less voluminous substrates, 'root' warming must have attention.

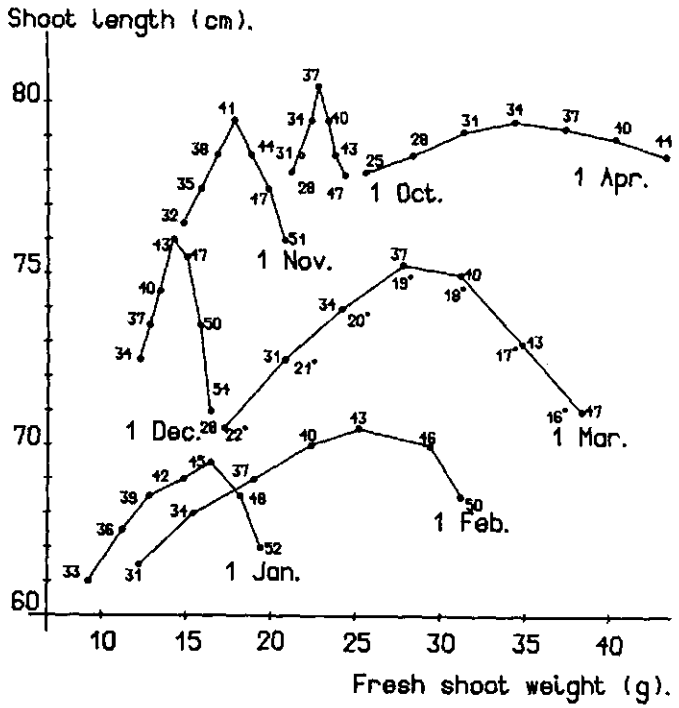


Fig.79 'Sweet Promise', grown in glasshouse soil. Shoot length (vertical), fresh shoot weight (horizontal) and development time (above the lines), in relation to the date of bud break (1 October, ..., 1 May) and temperature. The 7 points per line refer from left to right to seven 7 mean temperatures: 22°C-16°C. (example: see 1 March).

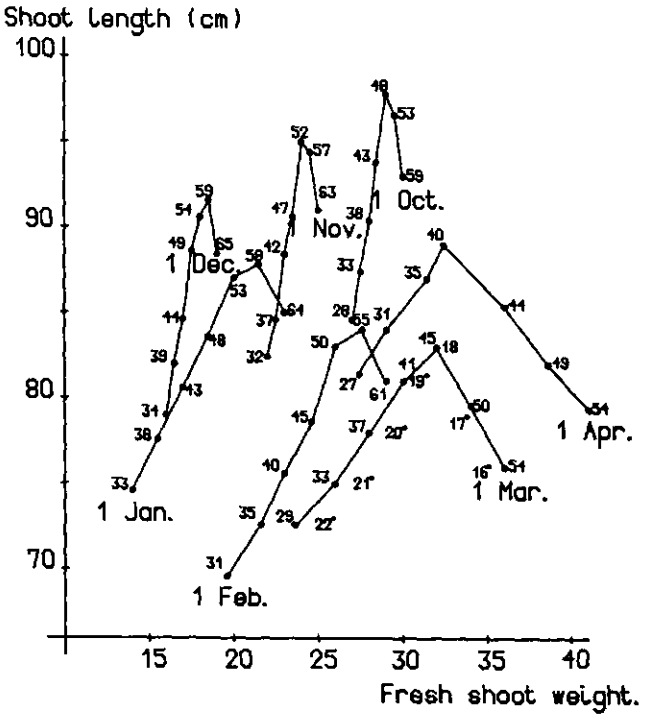


Fig.80 'Varlon', grown in glasshouse soil. Shoot length (vertical), fresh shoot weight (horizontal) and development time (above the lines), in relation to the date of bud break (1 October, ..., 1 May) and the mean temperature. The 7 points per line refer from left to right to 7 mean temperatures: 22°C-16°C (example: see 1 March).

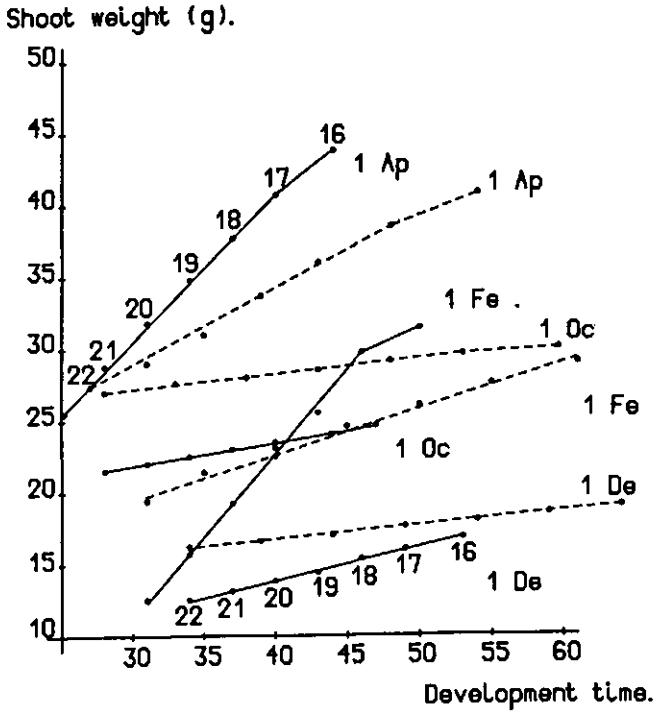


Fig.81 'Sweet Promise' (solid line) and 'Varlon' (broken line), grown in glasshouse soil. Relation between fresh shoot weight at harvest and the development time, for 4 dates of bud break. The 7 points per line refer from left to right to 7 mean temperatures: 22°C-16°C (example: see 1 April and 1 December).

10. SUMMARY

The influence of temperature in the range 15-22 °C on growth, production, quality and flower bud atrophy ('blindness') of the rose cultivars Sweet Promise and Varlon was studied. The roses were grown in Dutch glasshouse soil under natural light conditions and studied from October until May during 7 successive years. The influence of the distribution of the air temperature between day and night was studied. Besides the usual night-lower-than- day-temperature regime, also the reverse situation was studied. 'Models' were constructed for: bud break, development time from bud break until harvest, shoot and flower bud weight, shoot length, the length, width, volume and freshweight of the flower bud during harvest and the diameter of shoot and neck, in relation to date of bud break and mean daily temperature during shoot growth.

Complementary studies including roses of the cv. Sweet Promise grown in transferable containers were performed in glasshouses and in growth rooms (Phytotron). In these experiments the interaction of temperature and shoot stage with the development time of a shoot, with shoot weight and with shoot length was studied. Shoot weight showed a clear interaction with temperature if night temperature was higher than day temperature. Various shoot stages showed a different sensitivity to temperature with respect to the formation of flowerless ('blind') shoots. A low night temperature during the period cut until shoot elongation (=4cm) decreased blindness, but increased blindness when given in the next period until the flower bud is clearly visible. Higher night temperatures than those commonly used increased production by decreasing the percentage of blind shoots.

At a given daily mean temperature an increase in night temperature showed no significant influence on bud break and development time of a shoot but fresh shoot weight and shoot length are significantly reduced, if night temperature increases above day temperature. The mean temperature and the mean irradiance during

shoot growth could account for 98 % of the variation in the relevant 'models' when analysed by linear regression analysis. Adding the variable 'relative humidity' to the regression equation explained 97 % of the variation in shoot weight. To explain 87 % of shoot length the variable 'Weight of the Parent shoot' and the square of the temperature had also to be introduced.

Heavy parent shoots produced heavier daughter shoots than light parent shoots. The difference in fresh weight for daughters of heavy parent shoots compared to those of light shoots decreased in autumn and increased again in spring. If light intensity decreased in autumn, less light was used to produce one gram fresh shoot weight, while under increasing light intensities more light was used.

Fresh weight production per shoot per day increased with temperature for the cultivar Varlon and as a consequence, the amount of light needed per gram fresh weight decreased. In the period December until the middle of March 'Sweet Promise' showed another, reversed, situation: fresh weight production decreased with temperature. This was caused by the fact that 'Sweet Promise' was weakened more by a raise in temperature than 'Varlon'. Production in number of flowers and in grams fresh weight per shrub showed a positive linear correlation with temperature for both cultivars.
The course of bud break and harvest was studied for 9 night/day temperature combination. A lower temperature resulted in delayed bud break and production.

The research made it clear that it is possible and profitable to control temperature on the basis of the daily mean temperature or the temperature sum during bud break and shoot growth, instead of in the orthodox way with a fixed night-lower-than-day temperature regime. Practical applications of the results are given for commercial rose growing. Heating glasshouses on a basis of a daily mean temperature or temperature sum instead of a given day and night temperature is a possibility of saving energy, as also is the maintaining of a diurnal period of up till 6 hours with a higher night than day temperature beginning at sunset when the thermal screens are closed.

Soil heating until 20°C did not influence production and quality, whilst a 12% reduction in light had a negative effect on both.

11. SAMENVATTING

De invloed van de kasluchttemperatuur op het traject 15-22°C werd bestudeerd op de groei, de productie, de kwaliteit en de loosvorming van de rozencultivars 'Sweet Promise' (Sonia®) en 'Varlon' (Ilona®) in de periode oktober tot mei in 6 achtereen volgende jaren. De rozen werden geteeld in de kasgrond onder natuurlijke licht omstandigheden. Naast de invloed van de gemiddelde etmaaltemperatuur tijdens de groei werd ook de invloed van de temperatuurverdeling tussen dag en nacht bestudeerd. Behalve de gebruikelijke situatie met een lagere nacht- dan dag temperatuur werd ook de tegenovergestelde situatie met een hogere nacht dan dagtemperatuur bestudeerd. 'Modellen' werden geconstrueerd voor de ontwikkelingsduur van een scheut, het versgewicht van de scheut en van de bloemknop, de scheutlengte, de diameter van de scheut en de nek, de lengte, de breedte en het volume van de bloemknop tijdens de oogst. Al deze facetten in relatie tot de uitloopdatum en de gemiddelde etmaaltemperatuur tijdens de groei.

Aanvullend onderzoek met in containers gekweekte rozen van de cultivar 'Sweet Promise' werd verricht in zowel de kas als in groeikamers (Fytotron). In die experimenten werd de interactie bestudeerd tussen de temperatuur en het ontwikkelingsstadium van de scheut met de ontwikkelingsduur, het vers scheutgewicht en de scheutlengte. Als de nachttemperatuur lager of gelijk aan de dagtemperatuur was werd er geen duidelijke interactie waargenomen. Als de nachttemperatuur hoger steeg dan de dagtemperatuur vertoonde het vers scheutgewicht wel een duidelijke interactie. Een hogere nacht dan dagtemperatuur in het begin van de groeicyclus van een scheut resulteerde in rozen met een geringer gewicht dan gegeven in een latere groeifase.

De verschillende ontwikkelinsstadia van de scheut vertoonden een duidelijk verschil in temperatuurgevoeligheid met betrekking tot de vorming vorming van bloemloze ('blinde') scheuten. Een lage nachttemperatuur gegeven in de periode van snijden tot aan de strekkinsgroei (ca. 4cm) verminderde de loosvorming, maar indien gegeven in de periode vanaf de strekkingsgroei tot aan het stadium waarin de bloemknop duidelijk zichtbaar is met het ongewapend oog, vermeerderde het juist de loosvorming.

Bij een constante etmaaltemperatuur had een verhoging van de nachttemperatuur bij een evenredige verlaging van de dagtemperatuur geen betrouwbare invloed op de uitloopsnelheid of op het uitlooppercentage en de ontwikkelingsduur van de scheut maar verminderde het versgewicht en de scheutlengte; met name bij een hogere nacht dan dagtemperatuur. De gemiddelde etmaaltemperatuur en het gemiddelde verlichtingsniveau verklaarden tesamen 98% van de variatie in de 'modellen' voor scheutgroei (lineaire regressie analyse). Toevoeging van de variabele 'relatieve luchtvochtigheid' aan de regressie vergelijking kon 97% van de variatie in vers scheutgewicht verklaren. Om 87% van de variatie in de scheutlengte te verklaren moesten ook de variabelen 'Gewicht van de ouderscheut' en het 'Kwadraat van de luchttemperatuur' worden toegevoegd. Dikke (zware) ouderscheuten produceerden gedurende de gehele winter dikkere dochterscheuten dan dunne (lichte) ouderscheuten. Het verschil in versgewicht ten gunste van dochterscheuten afkomstig van dikke ouderscheuten t.o.v. dochterscheuten van dunne ouderscheuten nam in het najaar af en gedurende het voorjaar weer toe. Bij een afnemend lichtniveau (najaar) was het gemiddeld lichtniveau waaronder 1 gram vers scheutgewicht werd geproduceerd minder dan onder een toenemend lichtniveau (voorjaar).

De gemiddelde versgewicht productie per scheut per dag nam toe met de temperatuur voor 'Varlon', met als logisch gevolg een afname van het benodigde lichtniveau voor de productie van 1 gram versgewicht. Tot december en vanaf maart was het beeld voor 'Sweet Promise' gelijk aan dat voor 'Varlon'. In de periode vanaf december

tot en met maart vertoonde 'Sweet Promise' echter het tegengestelde beeld. Dit werd veroorzaakt door het feit dat 'Sweet Promise' meer verzwakte bij een hogere temperatuur dan 'Varlon'.

De productie van het aantal bloemen per struik en de versgewicht produktie per struik vertoonden voor beide cultivars een positieve lineaire relatie met de gemiddelde etmaal temperatuur gedurende de teelt. De productie in stuks en in versgewicht van een struik 'Sweet Promise' lag duidelijk boven die van een struik 'Varlon'. Een verlaging van de kasluchttemperatuur leidde tot een vertraagd uitlopen gevolgd door een vertraagde groei.

Het onderzoek maakt het duidelijk dat het mogelijk en uit het oogpunt van efficient energiegebruik profijtelijk is de temperatuur te regelen op basis van de gemiddelde etmaal temperatuur of de temperatuursom gedurend de ontwikkeling van een scheut in plaats van op een van te voren ingestelde vaste nacht/dag temperatuur, hetgeen de traditionele manier is. Hetzelfde geldt met betrekking tot het handhaven van dagelijkse periode met een hogere nacht dan dag temperatuur van 6-9 uur beginnende bij zonsondergang. Grondverwarming tot 20^{o}C had geen invloed op de productie in vergelijking tot geen grondverwarming. Een lichtvermindering van 12%, gerealiseerd door gebruik te maken van z.g. gecoat glas had op zowel de kwaliteit als de kwantiteit een negatief effect.
Voor de praktische rozenteler worden een aantal mogelijke toepassingen van de onderzoeksresultaten gegeven.

12. APPENDIXES

12.1. APPENDIX 1

HORMONAL BACKGROUND OF BUD BREAK

The apex of a growing shoot inhibits the lower lateral buds from growing out. The way in which the inhibitory influence from the apex is transmitted and the factors that are involved have already been the subject of study for more than half a century. In a review article Phillips (1975) gives 201 references on this subject; a number that has steadily increased since that date.

Endogenous growth substances (fytohormones) play an important role in apical dominance, but also the nutrient condition of the plant, its water balance and the environment of root and shoot are involved.

The five principal fytohormone groups connected with apical dominance are:

(1). Auxins, synthesised in the young top leaves.

(2). Cytokinins, synthesised in root tips.

(3). Gibberellins, synthesised in root tips, stamen and in young leaves.

(4). Abscisins (ABA), synthesised in root tips and in older leaves.

(5). Ethylene, synthesised especially in senescent or immature dividing or expanding tissues, although tissues of all ages possess the capacity. 'Wound' ethylene is formed after cut.

(Hormonal Regulation of Development 1984)

The first four groups contain many different members. For gibberellins for example more than 60 forms are known. This large number makes it difficult to get a detailed insight into what is happening inside the plant and to be able to draw the right conclusions from experiments.

One of the problems one faces if interpretating the found endogenous

hormone levels in plant tissue extracts is that the hormones can be compartimentalised and are in that situation inactive. The in vivo active concentration then may be much lower than the extracted one (Bruinsma 1980).

It has been known for a long time that apical dominance is mediated by auxins (e.g. Thiman 1939). By girdling the stem it can be shown that the inhibition of the lateral buds in plants may be attributed to the downward movement through the adjacent cells of the phloem-elements of an agent originated in the apex (Thimann 1977). Rudded and Pharis (1966) showed that gibberellins participate with auxins in apical dominance.

Skoog and Tsui (1948) reported that cytokinins play an important role in the control of bud formation in plant tissue cultures. Miller and co-workers found that cytokinins are involved in bud initiation (Miller et al. 1955). It soon became clear that cytokinins are involved in the release of inhibited buds too (Skoog and Miller 1957). Wickson and Thimann (1958) showed the existence of an antagonism between auxins and cytokinins in apical dominance. Buds of pea stem sections inhibited by auxins could be released by adding cytokinins and then sprouted. These investigators also found that gibberellins promote bud elongation after the inhibition of buds has already been released. Results from Sachs and Thimann (1964) confirmed this view. They found that bud break is initiated by cytokinins while gibberellins only act subsequent to the release. These authors reported that auxins counteract at least one component of apical dominance, namely the elongation of the internodes (Sachs and Thimann 1967). Buds however, already released from apical dominance by cytokinins which did not elongate as strong as control buds, could be elongated normally by the application of auxins locally to their apices. This indicates that in the processes involved in inhibition and release from it, the same hormones do play a different role.

Van Staden and co-workers studied the level of endogenous cytokinins in roses and their relation to lateral bud growth. They

found in buds of intact rose shoots a gradient of endogenous cytokinins. In the upper buds little or no cytokinins could be detected while the lower and more inhibited buds contained high levels of them (Van Staden et al. 1981). They suggested that a low level of endogenous cytokinins within the buds indicates that they are ready to break. This was reported earlier for other plants and may be an indication that the cytokinins are utilised prior to bud breaking (Tucker and Mansfield 1972,1973; Van Staden and Brown 1978, Van Staden and Dimalla 1978).

An endogenous growth regulator with a strong inhibitory effect on bud growth is Abscisic acid (ABA), (Dorffling 1964, Tucker and Mansfield 1972, 1973, Bellandi and Dorffling 1974, Praeger 1983). Zieslin and co-workers extracted abscisics from rose shoots and found a higher level in the lower part than in the upper part (Zieslin et al. 1978). Abscisins were also found in the bark tissue near the base of the plant. After removal of the top, the concentration decreased sharply (Zieslin and Khayat 1983). Van Onckele (1980) found the same for beans. The Abscisic acid concentration in the leaves adjacent to inhibited buds appeared to be very high. As abscisins are especially synthesised in older leaves, from which they are transported to the axillary buds, removal of the subtending leaf stimulates bud break (Durkin 1965). Removing this leaf or breaking the vascular strand which connects the leaf with the stem is a method used by growers to stimulate bud break. This method is not always effective, however. Especially late in autumn the results can be disappointing (Van den Berg 1986). Also spontanous leaf shedding did not improve bud break (Present experiments). An explanation can be found in work of Tinklin and Schwabe (1970), who worked with Ribes nigrum. These authors demonstrated that leaf-produced inhibitors accumulate also in the bud scales (see also Addicott 1983). If the concentration in the scales has risen high enough, removal of the subtending leaf did no longer influence bud break. They also demonstrated that in Ribes nigrum the inhibitory effect on bud break is not restricted to the bud subtended

by the leaf. The effect is translocatable. A period with a low or a high temperature decreased the concentration of inhibitors inside the bud and resulted in bud break. Benzioni and Dunstone (1985) showed for Jojoba that low temperatures decreased the ABA level in the flower buds and led to flowering.

ABA can occur in the tissue as 'free' ABA, or bound to glucose as 'bound' ABA. The last form is not transportable. The ratio free/bound changes during the year.

'Free' ABA has two forms, the in vivo active cis-form and the inactive trans-form. The synthesis of the active cis-ABA is stimulated by auxins. In this way auxins may be involved in the inhibition of bud break.

Cytokinins are reported to promote the conversion of ABA into bound forms (Even Cheu and Itai 1975) and in this way may change the ratio between growth promotors like gibberellins and cytokinins and growth inhibitors like abscisic acid. Depending on the actual hormonal situation inside the plant a change in this ratio may tip the ratio towards inhibition or release.

It must not be excluded that more, still unknown, growth substances may be involved in bud inhibition and bud break (Addicott 1983, Naylor 1985). Nishitani and Hasegawa (1985) found in pea seedlings that IAA exerts its effect by increasing an inhibitor different from ABA.

There are indications that the hormones actually function by activating special enzymes which release more specific chemical messengers (Oligosaccharins) from the cell walls. Each of these messengers on its turn should regulate a particular function (Albersheim 1976, Albersheim and Darvil 1985). These oligosaccharins are active in concentrations of less than 100 to 1000 times the amount of fytohormones and may represent a tier in a hierarchical hormone system

Against this background one may say that the afore mentioned fytohormones are not control factors which control a reaction by change of their concentrations. They are growth substances essential

for the various development steps (See Trewavas 1980). The oligosaccharins then can be considered the real control factors.

Hormones can interact in different ways. Leopold and Nooden (1985) mentioned in a review four types of interaction. Regulation processes may be controlled by: (1) a balance ratio between hormones, (2) by opposing effects, (3) by alterating the effective concentrations of one hormone by another and (4) by sequential action of differential hormones.
This mutual influence of hormones makes it difficult to elucidate fully the actual regulation of bud inhibition, bud release and development of the sprout by growth regulators.

Beside the fytohormones, specific hormone-binding proteins (receptors), who recognize the hormones may be very important. Any change in availability of the corresponding receptor will influence hormone turn over rate apart from the concentration of the hormone under consider. Bruinsma (1980) mentions that the endogenous level itself is not always a reliable indicator for its physiological importance. Its turnover rate may be far more relevant.

The breaking bud is made up from different cell types, which make it feasible that various hormone control systems are active in the bud at one time. Plant extracts as used in hormone experiments contain hormones from different cell types and possibly from different compartments within a cell, which makes it difficult to draw the right conclusions about what actually happens inside the plant and inside the breaking lateral bud.

Last but not least, hormones or their precursors must if their site of production is different from their site of action be transferred, which can be located in another part of the plant. There are five possible paths by which this transport can take place: via the (1) xylem, (2) phloem, (3) cellwalls, (4) symplast and the (5) intercellulair air spaces. It will be clear that any factor, chemically as well as physically that influences hormone transport, influences the hormonal balance at site of action and in this way the hormonal controlled processes.

More chemicals with effects on bud break were discovered. External application of TIBA, PBA, BA, and ethanol but also of ethylene which is also an internal produced growth substance, could stimulate bud break in several plant species (Asen 1954, Morgan and Gausman 1966, Skoog and Armstrong 1970, Carpenter and Rodriguez 1971, Masuda and Ashira 1980, Hosaki 1983).
The working of these chemicals may be via influencing the production and/or the transfer of the fytohormones. TIBA for example, inhibits the basipetal polar transport of auxins (Schneider and Wightman 1978), while ethylene decreases auxin synthesis and transport (Lurssen 1981). Auxin influences also the endogenous production of ethylene and via ethylene probably the concentration of ABA.

External application of hormones seemed to be a possibility for the stimulation of bud break. A big disadvantage of the external supply of hormones however, was that most of the sprouts from buds forced to break stopped growth, died or formed flowerless buds ('blindness'). This negative side-effect of chemically stimulated bud break was also reported for roses (Zieslin and Halevy 1975c, 1976c, Faber and White 1977).
If beside terminal buds also subterminal buds were forced to break at high temperatures the same negative effect could be seen for the subterminal buds, especially in winter time (Present experiences). A strong competition between the sprouts for nutrients may be the reason for this phenomenon.
Drawing conclusions from exogenously applicated hormones must be done very carefully. Bruinsma (1980) mentioned that because of compartimentalisation it is possible that exogenous applied hormones do not or only for a part arrive at the action site where they should play their role. The transport of exogenous hormones differs strongly from endogenous hormones. This means that exogenous hormones may arrive at another site than the endogenous hormones and function in a different way.

The first step that triggers bud release is not yet exactly

known. After a bud has been released from inhibition and breaks, it does not necessarily mean that the new sprout continues growth and will reach the flowering stage. Things may still go wrong. Parallel to the growth out of a bud, the bud xylem providing the new sprout with water, nutrients and hormones from elsewhere in the plant, has to be connected with the xylem of the subtending shoot. Xylem connections were studied by Sokorim and Thimann (1964). The movements of nutrients towards the breaking lateral bud, which has become a sink for metabolites, are also influenced by hormones (Booth and Moorby 1962, Bowen and Wareing 1971,). Hundreds of articles have been written on transport of hormones and nutrients in plants (see Hormonal Regulation 1984). A main conclusion is that hormones have the potential to direct assimilate movement to sinks, namely, spots with a high metabolic activity (e.g. Patrick and Wareing 1980). Hormones can act on sink activity and/or sink size and play a role in the uptake from nutrients by the sink (phloem unloading). Auxins produced by the shoot top faciliate transfer of assimilates through the phloem and also stimulate vascular differentation (Shiniger 1979). The effect of sink-produced hormones could be amplified by attracting root-produced cytokinins and gibberellins swept along in the assimilate stream (Patrick and Wareing 1980).

If nutrient or hormone supply is insufficient the flower bud starves, aborts and the shoot grows blind or even dies. This could be demonstrated with rose cuttings in rockwool if the axillary bud of the cutting sprouted before roots had developped (Van den Berg 1986). This phenomenon was reported earlier by Moe (1973). The nutrient state of the plant influences the level of root derived cytokinins and consequently shoot development. The effect may be partly due to root growth, which in its turn may be due to the supply of assimilates by the shoot. In this way nutrients may indirectly influence bud break (Goodrich et al. 1978). The stimulating effect of substrate heating on bud break as reported by Moss (1984) may also be due to enhanced root activity and cytokinin production.

Production and translocation of hormones or their precursers and

the combined action of the hormones is influenced by climate conditions. Low temperatures are reported to stimulate in some cases gibberellin synthesis or a GA-producing system that becomes active if temperature increases (Graebe and Ropers 1978). In this way a cold period followed by a higher temperature might promote bud break, an effect well known in rose growing. In Phaseolus leaves such a change in temperature is reported to stimulate the formation of ethylene (Osborne 1978). The same reaction is reported for cytokinins (Lethan 1978). Stress situations, for example water stress, also stimulate the synthesis of ethylene and ABA and in this way may influence bud break. Also the formation of wound ethylene after cut may influence bud break. Ethylene probably plays its role in bud release via influencing the concentration of ABA.

Of special interest is the Red/Far red ratio of light reaching the leaves. Red light stimulates the synthesis of gibberellins and auxins and reduces the endogenous ABA content, but far red stimulates the synthesis of abscisins and in that way enhances bud inhibition (Kaspenbauer 1971, Tucker and Mansfield 1972, Tucker 1976, Heins and Wilkins 1979, Tillberg (1985). This effect was also reported for roses by Mor and Halevy (1984).

To complicate the issue of bud break even more, one has to keep in mind the possibility that different control mechanisms are operating during the early stages of bud release and the subsequent outgrowth of the bud. In the consecutive processes the individual hormones can play different roles depending on the state of bud release.

From the many factors that influence lateral bud break a 'red line' can be distinguished. If one consider shoots with (before cut) and without (after cut) an active top meristem, the following line can be seen.

(1) Shoot with an active top meristem.
- The apex is a strong sink for metabolites, hormones and minerals.
- This sink is a strong competitor for the lateral buds.
- The top meristem produces auxins which convert the inactive

trans-ABA in the active cis-ABA (and keeps a non-ABA inhibitor on a high level), which in its turn inhibits bud break.
- All factors together prevent sprouting of the lateral buds.

(2) Shoots without an active top meristem (after cut or pinch).
- The apex is no longer a sink.
- The apex is no longer a competitor for the lateral buds.
- Auxins are no longer produced and the active cis-ABA is transformed in the inactive trans-ABA (and a non-ABA inhibitor decreases). Wound ethylene is produced.
- The inhibition decreases. The cytokinin/auxin ratio increases and the lateral bud releases unless the gibberellin concentration is too low.

As soon as the new top meristem of the released bud becomes active situation (1) is reinstalled.
If the supply of nutrients and hormones from the roots and assimilates from the leaves of the parent shoot or from stored reserves is sufficient, new apex develops leaves and flower buds. The most critical period is when the young leaves and the stamen do not yet produce fyto hormones by themselves and are still relatively weak sinks. In that period flower bud atrophy which results in flowerless or blind shoots is a major danger.

12. APPENDIX 2

SMOOTHING

According to Tukey (Exploratory Data Analyse 1977).

The following example shows the way in which the rough data were smoothed to get Figure 8. The data in the example have no connection with the experiments.

1 Rough values	2 Medians of 3	3 Skip means	4 "Hanning"
4	4	4	4 (copied)
6	4	5	5
3	6	6	6
8	8	7.5	8
9	9	9	9
10	10	10.5	10
12	12.5	12	12
15	15	13.5	14
16	15	14.5	15
14	14	12.5	13
10	10	11.5	11
6	9	9	9
9	8	8.5	8
8	8	8	8 (copied)

Explanation of the columns:
1= rough values, these are the medians of the week groups.
2= running medians of 3
3= skip means of 2, example 5=(4+6)/2, 6=(4+8)/2
4= line means of colums 2 and 3 example: 5=(4+5)/2 rounded, 6=(6+6)/2

The name 'Hanning' is after Julius von Hann, who used this smoothing method for weather information.

The data from column 4 are used for the graph.

12.3. Appendix 3

REGRESSION ANALYSIS

To analyse the data from the experiments the technique of linear regression was used (Daniel and Wood 1971, Mosteller and Tukey 1977, Draper and Smith 1981).
Analyses were performed with the computer program " A GENERAL STATISTICAL PROGRAM" (GENSTAT), release 4.04B, from the Statistical Department Rothamsted Experimental Station.
This program is implemented in the VAX-750 computer system at the Experimental Station in Aalsmeer.

The least-square method says: "Find the values of the constants (the regression coefficients) in the chosen equation that minimize the sum of the squared deviations of the observed values from those predicted by the equation" (Daniel and Wood, 1971).
Linear Least Square Estimation partitions the total variation in the dependent variable, expressed as the Total Sum of Squares about the mean (TSS), into two parts:

1. The Sum of Squares due to the fitted equation, or the sum of squares due to regression (SS).
2. The Residual Sum of Squares or the sum of squares about regression (RSS).

Divided by its corresponding degrees of freedom, the total sum of squares gives the Total Mean Square (TMS) and the regression sum of squares gives the Regression Mean Square (RMS).
If the fitted equation contains no bias, this RMS is the estimated Variance (s^2y) of the dependent Y-variable.

The percentage variation in the data about the average accounted for by the regression is: 100*(TMS-RMS)/TMS, and is expressed as R^2* in this booklet.

This percentage makes part of the standard output of the GENSTAT program and should not be confused with the statistic R-squared or Multiple Correlation Coefficient Squared (R^2), which is calculated as R^2*, but with the TSS and the RSS instead of the TMS and the RMS. The advantage of using percentage variation is that it takes into account the number of parameters fitted in the model.

Due to the fact that the regression coefficients change depending on which explanatory variables are present and because too many variables make the regression less transparant and understandable, it was necessary to differentiate among the following possible variables: irradiation sum or average irradiation during different parts of shoot development, temperature sum or average temperature during shoot development, vapour pressure deficit, relative humidity, daylength, and weight of the parent shoot, which gives a relation to the previous growth cycle. These variables could also appear in the regression in their plain or in a re-expressed e.g. squared form.

To avoid unnecessary large stocks of explanatory variables (over fitting), the number of variables was chosen by using the criteria:
- The value of R^2*
- Mallow's Cp statistic.
- The value of s^2, the residual mean square.

In the regression equations the variable that, alone, accounts for the biggest part of the variation, is introduced first into the equation and is followed by the variable that has the next biggest effect after the variable that is already in, and so on.
As much variation as possible was tried to account for with variables representing the climate factors: irradiation inside the glasshouse, air temperature and relative humidity of the air. These are factors with can 'easily' be related to plant growth and have meaning to the growers.
Because the inside and outside irradiation were highly correlated

(r=.99), both gave nearly the same R^2* in the regression equations. Under the natural light conditions of the experiments, irradiation itself was highly correlated with length of day, which on its turn was correlated with the date of bud break. This means that irradiation, length of day and date of bud break can substitute for each other for a large part in the regression equations, and all give a high R^2*.

Because the variables are highly correlated, it is dangerous to change just one of them and predict what the response of the dependent variable will be. In the glasshouse situation from which the data originated no variable changes without affecting the others. A danger of regression is always the chance of channeling through a proxy, or like Mosteller and Tukey write in their book: "If A and B are closely correlated, if A is not related to what we are studying, if B is quite strongly related, if A is in the regression but B is NOT in, then we are likely to find A carrying a appreciable part of our regression. When this happens, we are tempted to believe that A is "relevant", but a more appropriate interpretation would be that " A appears relevant because it is a proxy for B, which I am sure ought to be relevant because....." (Mosteller and Tukey 1977: page 317).

13. REFERENCES

Abd el Rahman, A.A., Kuiper, P.J.C. and Bierhuizen, J.F., 1959. Preliminary observations on the effect of soil temperature on transpiration and growth of young tomato plants under controlled conditions. Mededelingen Landbouwhogeschool Wageningen, 59(15).

Addicott, Frederick T., 1983. Abscisic acid. Praeger Scientific USA, 607 pp.

Aikin, W.J., 1974a. Photosynthesis in roses I. Effect of light intensity. Roses Incorporated Bulletin, December 1974:50-52.

Aikin, W.J., 1974b. Photosynthesis in roses II. Effect of leaf age. Roses Incorporated Bulletin, December 1974:54-57.

Albersheim, P., McNeil, M. and Labavitch, J.M., 1977. The wall of growing cells. Plant growth regulation. Proceedings of the 9th International Conference on plant growth substances. Lausanne, 1976. pag:1-13.

Albersheim, Peter and Darvill, Allan G., 1985. Oligosaccharins. Scientific American, September 1985:44-50.

Armitage, A.M. and Tsujita, M.J., 1979. The effect of nitrogen concentration and supplemental light on the growth and quality of 'Caliente' Roses. HortScience, 14(5):614-615.

Asen, Sam and Hamner, Charles L., 1954. Effect of growth-regulating compounds on development of basal shoots of greenhouse roses. Bot.Gaz., 115:86-89.

Aston, M.J., 1973. Changes in internal water status and the gas exchange of leaves in response to ambient evaporative demand. Proc. Uppsala Symposium pag. 243-247. Unesco Paris 1973.

Atherton, J.G. and Othman, S., 1983. Effects of irradiance and waterstress on flower abortion in the glasshouse tomato. Acta. Horti. 134, 133-138.

Benzioni, A. and Dunstone, R.L., 1985. Jojoba flower buds: A possible role for absicsic acid in controlling dormancy. Abstracts of the 12th international conference on plant growth substances, Heidelberg.

Bellandi, Deise M. and Dorffling, Karl, 1974. Effect of abscisic acid and other plant hormones on growth of apical and lateral buds of seedlings. Physiol. Plant., 32:369-372.

Barrick, William E. and Sanderson, Kenneth C., 1973. Influence of photoperiod, temperature and node position on vegetative shoot growth of greenhouse Azaleas, Rhododendron cv. J.Amer.Soc.Hort.Sci.,98(4):331-334.

Berg, G.A. van den, 1976. Influence of lowering the night temperature on the production and quality of 'Baccara' roses. Acta Hort., 64:149-154.

Berg, G.A. van den, 1978, 1979, 1980, 1981, 1982, 1983, 1984. Bloemisterij Onderzoek in Nederland. Annual reports.

Berg, G.A. van den, 1981. The influence of temperature on winter production of 'Sonia' and 'Ilona' roses in Dutch glasshouses. Acta Hort., 115:75-83.

Berg, G.A. van den, 1984. Lowering heating costs per rose through increased production by use of movable benches. Acta Hort., 148 III:97-104.

Berg, G.A. van den, 1984. Influence of a higher night than day temperature on the winter production of 'Sonia' roses under Dutch glasshouse conditions. Acta Hort., 148:581-590.

Berg, G.A. van den, 1986. Unpublished results.

Bierhuizen, J.F. and Slatyer, R.O., 1965. Effect of atmospheric concentration of water vapour and CO_2 in determining transpiration-photosythesis relationship of cotton leaves. Agric. Meteorol., 2:259-270.

Biran, I. and Halevy, A.H., 1974. Effect of varying light intensities and temperature treatments applied to whole plants, or locally to leaves of flower buds, on growth and pigmentation of 'Baccara' roses. Physiol.Plant., 31:175-179.

Biscoe, P.V. and Callagher, J.N., 1977. Weather, dry matter production and yield. Environmental effects on crop physiology. Proceedings fifth Long Ashton Symposium. Academic Press, London, New York, San Francisco 388 pp.

Booth, A., Davies, C.R. and Moorby, J., 1962. Effects of Indolyl-3-Acetic Acid on the movement of nutrients within plants. Nature, 194:204-205.

Bowen, M.R. and Wareing, P.F., 1971. Further investigations into

hormone-directed transport in stems. PLanta (Berl.), 99:120-132.
Boyer, John S., 1968. Relationship of water potential to growth of leaves. Plant Physiol., 43:1056-1062.
Boyer, J.S., 1970. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol., 46:233-235.
Breuring, R., 1986. Personal communication.
Brix, H., 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and Loblolly seedlings. Physiol.Plant., 15:10-20.
Brouwer, R., 1964. Responses of bean plants to root temperatures. I. Root temperatures and growth in the vegetative stage. Jaarb. IBS. 1964:11-22.
Brouwer, R., Kleinendorst, A. and Locher, J.Th., 1973. Growth responses of maize plants to temperature. Unesco, 1973. Plant response to climate factors. Proc. Uppsala Symp., (Ecology and conservation, 5.)
Brown, W.W. and Ormrod, D.P., 1980. Soil temperature effects on greenhouse roses in relation to air temperature and nutrition. J.Amer.Soc.Hort.Sci., 105(1):57-59.
Bruinsma, J., 1981. Present state and prospects of research into natural and synthetic plant growth-regulating substances. Aspects and prospects of plant growth regulators. Wessex Press. Wantage.
Bunce, James A., 1984. Effects of humidity on photosynthesis. J.Exp.Bot., 158:1245-1251.
Byrne, Thomas G., Doss, Robert P. and Tse, A.T.Y., 1978. Flower and shoot development in the greenhouse roses, 'Cara Mia' and 'Town Crier', under several temperature-photoperiodic regimes. J.Amer.Soc.Hort.Sci., 103(4):500-502.
Byrne, Thomas G. and Doss, Robert P., 1981. Development time of 'Cara Mia' rose shoots as influenced by pruning position and parent shoot diameter. J.Amer.Soc.Hort.Sci., 106(1):98-100.
Cameron, S.H., 1941. The influence of soil temperature on the rate of transpiration of young orange trees. Proc.Amer.Soc.Hort.Sci., 38:75-79.
Carpenter, W.J. and Rodriguez, R.C., 1971a. The effect of plant growth regulating chemicals on rose shoot development from basal and axillary buds. J.Amer.Soc.Hort.Sci., 96(3):389-391.
Carpenter, W.J. and Rodriguez, R.C., 1971b. Supplemental lighting effects on newly planted and cut-back greenhouse roses. Hort.Sci., 6(3):207-208.
Carpenter, W.J. and Anderson, G.A., 1972. High intensity supplementary lighting increases yields of greenhouse roses. J.Amer.Soc. Hort.Sci., 97(3):331-334.
Carpenter, W.J., Rodriguez, R.C. and Carlson, W.H., 1972. Effect of daylength on the growth and flowering of roses (Rosa hybrida). J.Amer.Soc.Hort.Sci., 97(1):135-138.
Cathey, H.M., Campbell,L.E. and Thimijan, R.W., 1981. Radiation and plant response: A new view. Strategies of plant reproduction (6). Beltsville Symposia in Agricutural Research. Allanheld, Osmun Publishers. Granada,London,Toronto,Sydney.
Challa, H., 1976. An analysis of the diurnal course of growth, carbon dioxide exchange and carbohydrate reserve content of cucumber. Centre for Agricultural Publishing and Documentation wageningen 88 pp. (Thesis).
Challa, H., Bakker, J.C., Bot, G.P.A., Udink ten Cate, A.J., and Van den Vooren, J., 1980. Economical optimization of energy consumption in an early cucumber crop. Acta Hort., 118:191-199.
Chandler, Edward L. and Watson, Donald P., 1954. Contribution of various light intensities to the growth and yield of greenhouse roses. Proc.Amer.Soc.Hort.Sci. 60:441-447.
Cockshull, K.E., 1975. Roses II: The effects of supplementary light on winter bloom production. J.Hort.Sci., 50:193-206.
Cockshull, K.E., Hand, D.W. and Langton, F.A., 1982. The effects of day and night temperature on flower initiation and development in chrysanthemum. Acta Horti., 125:101-110.

Cooper, A.J., 1973. Root temperature and plant growth. Research 1973 review No4. Commonwealth agricultural bureaux East Malling, Maidstone, Kent.
Corbet, L.C., 1902. Improvement of roses by bud selection. Mem.Hort.Soc.New York I:93-101.
Cotter, D.J. and Walker, J.A., 1967. Occurrence and biological effect of humidity in greenhouses. Proc. XVII Int.Hort.Congress, 3:353-368.
Dale, J.E., 1964. Some effects of alternating temperature on growth of french bean plants. Ann.Bot. N.S., 109:127-135.
Daniel, Cutbert and Wood, Fred S., 1977. Fitting equations to data. John Wiley & Sons, Inc., 342 pp.
Dobben, W.H. van, 1962. Influence of temperature and light conditions on dry-matter distribution, development rate and yield in arable crops. Neth.J.Agric.Sci., 10:377-389.
Doorenbos, J., 1953. Review of the literature on dormancy in buds of woody plants. Mededelingen van de Landbouwhogeschool te Wageningen, no 53.
Dörfling, Karl., 1964. Uber das Wuchsstoff-hemmstoffsystem von Acer Pseudoplatanus L. II. Die Bedeutung von "Inhibitor-b" für die korrelative Knospenhemmung und für die regulation der Kambiumtatigkeit. Planta, 60:413-433.
Dorland, Robert E. and Went, F.W., 1947. Plant growth under controlled conditions. VIII. Growth and fruiting of the chili pepper
Dosser, Amy L. and Larson, Roy A., 1981. Influence of various growth chamber environments on growth, flowering, and senescence of Tulipa gesneria L. cv. Paul Righter. J.Amer.Soc.Hort.Sci., 106(2):247-250.
Draper, Norman R. and Smith, Harry., 1981. Applied regression annalysis. Second edition. John Wiley & Sons. Inc. New York-Chichester-Brisbane-Toronto. 709pp.
Durieux, A.J.B., 1974. Additional lighting of lilies (cv. 'Enchantment') in the winter to prevent flower-bud abscission. Acta Hort., 47:237-240.
Durkin, Dominic J., 1965. Bud dormancy in the Better Times rose. J.Amer.Soc.Hort.Sci., 86:798-805.
Elfving, Don C., Kaufmann, Merrill R. and Hall, Anthony E., 1972. Interpreting leaf water potential measurements with a model of the soil-plant-atmosphere continuum. Physiol.Plant., 27:161-168.
Esh, H. van, 1976. Plant- en oogsttijden bij sla. Groenten & Fruit, 32:143.
Faber, William R. and White, John W., 1977 The effect of pruning and growth regulator treatments on rose plant renewal. J.Amer.Soc.Hort.Sci., 102(2):223-225.
Farmer, Roger and Holley, W.D., 1954. The effect of partial shading on the quality and production of Better Times rose. Proc.Amer.Soc.Hort.Sci., 64:448-458.
Ford, Margaret A. and Thorne, Gillian N., 1974. Effects of atmospheric humidity on plant growth. Ann.Bot., 38:441-452.
Frenz, F.W. and Lechl, P.,1981.The influence of different water suctions on yield and water requirements of tomatoes, cucumbers, radishes and lettuce in greenhouses. Acta Hort., 119:323-331.
Friend, D.J.C. and Helson, V.A., 1976. Thermoperiodic effects on growth and photosynthesis of wheat and other crop plants. Bot.Gaz., 137(1):75-84.
Gaastra, P., 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. Meded. Landbouwhogesch. Wageningen, 59(13):1-69.
Gates, C.T., 1955. The response of the young tomato plant to a brief period of water shortage I. The whole plant and its principal parts. Austr.J.Biol.Sci., 8:196-214.
Gelder, A. de., 1984. Telen van nieuwe rozencultivars bij verschillende temperaturen. Bloemisterij Onderzoek Over 1984, 343-346.
Goren, R., 1983. Physiological aspects of abscission in citrus. Acta Horti., 137:15-29.
Goodwin, P.B., Gollnow, B.I. and Letham, D.S., 1978. Phytohormones and growth correlations. Phytohormones and related compounds Volume II.

Elsevier/North-Holland 648 pp.
Graebe, J.E. and Ropers, H.J. 1978. Gibberellins. Phytohormones and related compounds: A comprehensive treatise Volume I. Chapter 5. Elsevier/North-Holland 641 pp.
Haas, T. de, 1985 Personal communication.
Hagen, Paul and Moe, Roar, 1981. Effect of temperature and light on lateral branching in Poinsettia (Euphorbia pulcherrima Willd.). Acta Hort., 128:47-54.
Hale, C.R. and Weaver, R.J., 1960. Hilgardia, 33:89-131.
Halevy, A.H. and Zieslin, N., 1969. The development and causes of petal blackening and malformation of Baccara rose flowers. Acta Hort., 14:149-156.
Halevy, A.H. and Shilo, Ruth., 1970. Promotion of growth and flowering and increase in content of endogenous gibberellins in Gladiolus plants treated with the growth retardant CCC. Phys.Plant., 23:820-827.
Halevy, Abraham H., 1972. HortScience, 7:113-114.
Halevy, Abraham H., 1974. Light energy flux and distribution of assimilates as factors controlling the flowering of floral crops. Proc. XIXth Intern.Hort.Congress. Warszawa pag.:125-134.
Halevy, Abraham H. and Mor, Yoram., 1980. Promotion of sink activity of developing rose shoots by light. Plant Physiol., 66:990-995.
Halevy, Abraham H. and Mor, Yoram., 1984. Dual effect of light on flowering and sprouting of rose shoots. Physiol.Plant., 61:119-124. Copenhagen.
Halevy, Abraham H., 1985. Handbook of flowering IV., CRC Press, Inc. 575pp.
Hanan, Joe J., 1979. Observation of a low temperature effect on roses. J.Amer.Soc.Hort.sci., 104(1):37-40.
Hand, D.W. and Cockshull, K.E., 1975. The effects of CO_2 concentration on the canopy photosynthesis and winter bloom production of the glasshouse rose 'Sonia' (Syn. 'Sweet Promise'). Acta Hort., 51:243-252.
Hanisch ten Cate, Ch.H., 1974. Abscission of flowerbud pedicels in Begonia. Department of Plant Physiology Agricultural University Wageningen.
Haroon, Mohammed, Long, R.C. and Weybrew, J.A., 1972. Effect of day/night temperature on factors associated with growth of Nicotianum tabacum L. in controlled environments. Agro.Journ., 64:509-515.
Heins, R.D. and Wilkins, H.F., 1979. The influence of node number, light source, and time of irradiation during darkness on lateral branching and cutting production in 'Bright Golden Ann' Chrysanthemum. J.Amer.Soc.Hort.Sci., 104(2):265-270.
Hendriks, L., 1984. Licht und Temperaturwirkung bei Rosen. Zierpflanzen Versuche 1984:58-70. Lehr- und Verschuchanstalt für Gartenbau Hannover-Ahlen.
Hey, G., 1980 Glasshouse cucumber, stem elongation and earliness of fruit production as influenced by temperature and planting date. Acta Hort., 118:105-121.
Hiron, R.W.P. and Wright, T.C., 1973. The role of endogenous abscisic acid in the response of plants to stress. J.Exp.Bot., 24:769-781.
Hoad, G.V., 1973. Effect of moisture stress on abscisic acid levels in Ricinus communis L. with particular reference to phloem exudate. Planta(Berl.), 113:367-372.
Hoeven, A.P. van der, and Groenewegen, J.H., 1970. Zaai- plant- en oogsttijden bij sla. Tuinderij, 10:567-570.
Hoffman, G.J., Rawlins, S.L., Garber, M.J. and Cullen, E.M., 1971 Agr.Journ., 63:822-824.
Holsteijn, G.P.A. and Vogel, A.H., 1984. Kleine verschillen grote gevolgen. Tuinderij, 18:34-37.
Holsteijn, G.P.A., 1985. Invloed van schermen op het klimaat. Groenten & Fruit, 15:38-41.
Hori, Y. and Shishido, Y.,1978. The effects of feeding time and night temperature on the translocation and distribution of 14C-assimilates in tomato plants. Acta Horti. 87, 225-232.

Hormonal regulation of development I & II. Encyclopedia of plant physiology. Springer Verlag Berlin-Heidelberg, New York.
Horridge, J.S. and Cockshull, K.E., 1974. Flower initiation and development in the glasshouse rose. Scientia Hort.,2:273-284.
Hosaki, Takashi., 1983. Breaking dormancy with ethanol and storage. HortScience, 18(6)876-878.
Hove, L.W.A. van, 1980. Bloemknopatrofie bij stekken van de rozencultivar 'Sonia^{R}'. Students Research Report, Lab. for Horticulture of the Agric. University, Wageningen.
Hsiao, T.C., 1973. Plant responses to water stress. Ann.Rev.Plant Physiol., 24:519-570.
Hubbell, D.S., 1934a. A morphological study of blind and flowering rose shoots, with special reference to flower differentiation. J.Agric.Res., 48:91-95.
Hubbell, D.S., 1934b. Causes of blind wood in roses. Plant Physiol., 9:261-282.
Hughes, A.P., 1965. The importance of light, compared with other factors affecting plant growth. Light as an ecological factor. Symposium of the British ecological society. Blackwell Scientific Publications. Oxford.
Hurd, R.G. and Groves, C.J., 1984. The influence of different temperature patterns having the same integral on the earliness and yield of tomatoes. Acta Hort., 148(II):547-554.
Hussey, G., 1965. Growth and development in the young tomato III. The effect of night and day temperatures on vegetative growth. J.Exp.Bot., 16:373-385.
Incoll, L.D., 1976. Field studies of photosynthesis monitoring with CO_2. Environmental effects on crop physiology. Proceedings fifth Long Ashton symposium 1975. Academic Press. Londen, New York.388 pp.
Itai, Chanan and Yoash, Vaadia, 1971. Cytokinin activity in water-stressed shoots. Plant.Physiol., 47:87-90.
Jackson, D.I. and Field, R.J., 1971. Apical dominance in Phaseolus vulgaris. Ann.Bot., 36:525-532.
Jones, R.L. and Phillips, I.D.J., 1967. Effect of CCC on the gibberellin content of excised sunflower organs. Planta(Berl.), 72:53-59.
Jones, Russell L. and Phillips. I.D.J., 1966. Organs of gibberellin synthesis in light-grown sunflower plants. Plant Physiol., 41:1381-1386.
Jusaitis, Manfred, Paleg, Leslie G. and Aspinall, Donald, 1982. The influence of gibberellic acid and temperature on the growth rate of Avena sativa stem segments. Plant Physiol., 70:532-539.
Kamerbeek, G.A. and Durieux, A.J.B., 1971. Influence of light on flowerbud abscission in plants of lily cultivar 'Enchantment'. Acta Horti., 23:71-75.
Kamp, J.R., 1948. The incidence of blindness in the Better Times rose. Proc.Am.Soc.Hort.Sci., 52:490-500.
Kaspenbauer, M.J., 1971. Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. Plant Physiol., 47:775-778.
Khayat, E. and Zieslin, N., 1982. Environmental factors involved in the regulation of sprouting of basal buds in rose plants. J.Exp.Bot., 33:1286-1292.
Khosh-khui, M and George, R.A.T., 1977. Responses of glasshouse roses to light conditions. Scientia Hort., 6:223-235.
Klapwijk, D.,1979. Seasonal effects on the cropping-cycle of lettuce in glasshouses during the winter. Scientia Hort., 11:371-377.
Klapwijk, D and Lint, P.J.A.L. de, 1975. Growth rates of tomato seedlings and seasonal radiation. Neth.J.Agr.Sci., 23:259-268.
Klapwijk, D and Lint, P.J.A.L. de, 1975. Growth and development of young tomato plants. Acta Hort., 51:147-161.
Klapwijk, D., 1980. Personal correspondence.
Kleinendorst, A. and Brouwer, R., 1970. The effect of temperature of the root medium and of the growing point of the shoot on growth, water content and sugar content of maize leaves. Neth.J.Agri.Sci., 18:140-148.
Kleinendorst, A. and Brouwer, R., 1972. The effect of local cooling on growth

and water content of plants. Neth.J.Agri.Sci., 20:203-217.
Kohl, Harry C. and Mor, Yoram, 1981. Producing pot chrysanthemums at low night temperature. J.Amer.Soc.Hort.Sci., 106:89-91.
Kohl, H.C., Fosler, G.M. and Weinard, F.F., 1948. The effect of several soil temperatures on flower production in roses. Proc.Amer.Soc.Hort.Sci. 54:491-496.
Kohl, Harry C.Jr. and Thigpen, Stephen P., 1979. Rate of dry weight gain of chrysanthemum as a function of leaf area index and night temperature. J.Amer.Soc.Hort.Sci., 104:300-303.
Kohl, Harry C. and Post, Kenneth, 1952. Time for production of roses as influenced by season and method cutting. J.Amer.Soc.Hort.Sci., 59:527-530.
Koop, L., 1984. Temperatuurongelijkheid kost productie. Groenten & Fruit, 8:20-24.
Kozlowski, 1973. Shedding of plant parts. Academic Press, Inc. New York, London 560 pp.
Kramer, P.J., 1940. Root resistance as a cause of decreased water absorption by plants at low temperatures. Plant Physiol., 15:63-79.
Kramer, Paul J., 1983. Water relations in plants. Academic Press, New York Londen, 489 pp.
Kramer, Paul J., 1969. Plant and soil water relationships: A modern synthesis. Mc.Craw-Hill Book Company. New York - London 482 pp.
Kristoffersen, Trygve, 1963. Interactions of photoperiod and temperature in growth and development of young tomato plants (Lycopersicon esculentum Mill.). Physiol.Plant. Suppl.1, 98 pp.
Krizek, D.T., Bailey, W.A. and Kleuter, H.H., 1971. Effects of relative humidity and type of container on the growth of f_1 hybrid annuals in controlled environments. Amer.J.Bot., 58:544-551.
Krussmann, Gerd, 1986. Rosen rosen rosen. Paul Parey, Berlin 305 pp.
Kuiper, P.J.C., 1964. Water uptake of higher plants as affected by root temperature. Meded. Landbouwhogeschool Wageningen, 64-4:1-11.
Laibach and Kribben, 1953. Beitr.Biol.Pflanzen. 30:127-158.
Lang, A., 1970. Gibberellins, structure and metabolism. Ann.Rev.Plant.Physiol., 21:359-384.
Lange, O.L., Losch, R., Schulze, E.D. and Kappen, L., 1971. Responses of stomata to changes in humidity. Planta, 100:76-86.
Laurie, Alex and Bobula, Paul F., 1938. A study of flowering rose shoots with reference to flower-bud differentiation. Proc.Amer.Soc.Hort.Sci., 44:767-768.
Leemans, J.A. and Laar, H.J. van der, 1977. Rozenonderstammen Kenmerken en gebruikswaarde. Stichting Plant Propaganda Holland Boskoop 53 pp.
Leopold, A.C. and Nooden, L.N., 1984. Hormonal regulatory systems in plants. Encyclopedia of plant physiology part: 10. Springer Verlag Berlin.
Lepage, I., Jong, J. de, and Smeets, L., 1984. Effect of day and night temperature during short photoperiods on growth and flowering of Chrysanthemum morifolium Ramat. Scientia Hortic, 22:373-381.
Letham, D.S., 1978. Cytokinins. Phytohormones and related compounds: A comprehensive treatise Volume I. Chapter 5. Elsevier/North-Holland.
Letham, D.S., Higgins, T.J.V., Goodwin, P.B. and Jacobsen, J.V., 1978. Phytohormones in Retrospect. Phytohormones and related compounds: A comprehensive treatise Volume I. Chapter 5. Elsevier/North-Holland.
Lichtenthaler, Martmut K., 1984. Advances in photosynthesis research, Vol.IV., 3.241-3.244. Martinus Nijhoff/Dr W.Junk Publishers,The Hague /Boston/Lancaster.
Lindebaum and Ginzburg, 1975. A morphological studyof bullhead malformation in the Baccara rose. Annals of Botany, 39(160)219-223.
Lindstrom, Richard S., 1956. Developmental anatomy of the stem apex of the Better Times rose. Thesis Ohio State University, pp.52.
Lindstrom, Richard S.and Kiplinger, D.C., 1955. Blind wood of Better Times roses as affected by selection of stock and nitrogen and potassium

nutrition. Proc.Amer.Soc.Hort Sci., 66:374-377.
Lurssen, 1982. Manipulation of crop growth by ethylene and some implications of the mode of generation. Chemical manipulation of crop growth and development. Butterworths Scientific London-Boston-Toronto. P:67-79.
Lyons, J.M., 1973. Chilling injury in plants. Ann.Rev.Plant.Physiol., 24:445-466.
May, P., 1965., Aust.J.Biol.Sci., 18:463-473.
Masuda, M. and Asahira, T., 1980. Effect of ethylene on breaking dormancy of freesia corms. Scientia Hort., 13:85-92.
Mattson, Richard H. and Widmer, Richard E., 1971. Effects of solar radiation, carbon dioxide and soil fertilization on Rosa hybrida. J.Amer.Soc.Hort.Sci., 96(4):484-486.
McCready, C.C., 1966. Translocation of growth regulators. Ann.Rev.Plant Physiol.:283-292.
McIntyre, Gordon I., 1964. Mechanism of apical dominance in plants. Nature, 203:4949-4950.
McIntyre, G.I., 1971. Water stress and apical dominance in Pisum sativum. Nature New Biology, 230:87-88.
McNiel, Donald R., 1977. Interactive data analysis. John Wiley & Sons, Inc., 186 pp.
Michniewicz, Marian and Kamienska, Aniela., 1967. Effect of kinetin on the content of endogenous gibberellins in germinating seeds of some plant species. Naturwissenschaften: 372.
Milthorpe, F.L. and Moorby, J., 1969. Vascular transport and its significance in plant growth. Rev.Plant Physiol., 20:117-138.
Moe, R. and Kristoffersen, T., 1969. The effect of temperature and light on growth and flowering of Rosa 'Baccara' in greenhouses. Acta Hort., 14:157-166.
Moe, Roar., 1971a. The relationship between flower abortion and endogenous auxin content of rose shoots. Physiol.Plant., 24:374-379.
Moe, Roar., 1971b. Factors affecting flower abortion and malformation in roses. Physiol. Plant., 24:291-300.
Moe, Roar., 1972a. Effect of daylength, light intensity, and temperature on growth and flowering in roses. J.Amer.Soc.Hort.Sci., 97(6):796-800.
Moe, Roar., 1972b. Entwicklungsgeschwindigkeit und Blutenproduction bei Hausrosen. Gartenwelt, 23:498-501.
Moe, R., 1973. Propagation, growth and flowering of potted roses. Acta Hort., 33:35-50.
Moe, Roar., 1977. Effect of light, temperature and CO_2 on the growth of Campanula isophylla stock plants and on the subsequent growth and development of their cuttings. Scientia Hort., 6:129-141.
Monselise, Shaul P. and Went, Frits W., 1958. Effects of temperature on growth and dry matter accumulation of peas. Plant Physiol., 33:372-375.
Moore, Thomas C., 1979. Biochemistry and physiology of plant hormones. Springer Verlag New York-Bern 274 pp.
Mor, Yoram and Halevy, Abraham H., 1984. Dual effect on flowering and sprouting of rose shoots. Physiol.Plant., 61:119-124.
Moreshet, S., Plaut, Z. and Zieslin, N., 1976. Spatial variation in glasshouse rose flower production in relation to solar radiation. Scientia Horti., 5:269-276.
Morgan, Page W. and Gausman, Harold W., 1966. Effects of ethylene on auxin transport. Plant Physiol., 41:45-52.
Morison, James J.L. and Gifford, Roger M., 1983. Stomatal sensitivity to carbon dioxide and humidity. Plant Physiol., 71:789-796.
Mortensen, L.M. and Moe, R., 1983. Growth responses of some greenhouse plants to environment VII. The effect of CO_2 on photosynthesis and growth of roses. Meld. Norg. Landbr Hogsk., 62(3):1-11.
Mortenson, L.M. 1984. Personal communication.
Moss, G.I., 1983. Rootzone warming as a means to save energy in production of greenhouse crops in Australia. Acta Hort., 133:31-38.

Moss, Gerald I. and Dalgleish, Robert., 1984. Increasing returns from roses with root-zone warming. J.Amer.Soc.Hort.Sci., 109(6):893-898.
Moss, G.I., 1984. The effect of rootzone warming on the yield and quality of roses grown in a hydroponic system. J.Hort.Sci., 59(4):549-558.
Mosteller, Frederick and Tukey, John W., 1977. Data analysis and regression. A second course in statistics. Addison and Wesley Pub.Comp., 588 pp.
Mpelkas, Christos C., 1981. Greenhouse supplemental lighting for roses with high pressure sodium lamps. Acta Horti.,128:85-97.
Naylor, A.W., 1985. Functions of hormones at organ level of organisation. Encyclopedia of plant physiol. 10, Springer verlag, Berlin.
Nederhoff, E.M., 1984. Light interception of a cucumber crop at different stages of growth. Acta Hort., 148(II):525-534.
Nell, T.A. and Rasmussen, H.P., 1979a. Floral development and blindness in roses: a SEM study. J.Amer.Soc.Hort.Sci., 104(1):18-20.
Nell, T.A. and Rasmussen, H.P., 1979b. Blindness in roses: effects of high intensity light and blind shoot prediction techniques. J.Amer.Soc.Hort.Sci., 104(1):21-25.
Nishitani, K. and Hasegawa, K., 1985. Mode of action of IAA in apical dominance in peas. Abstracts of the 12th international conference on plant growth substances, Heidelberg.
Nonnecke, I.L., Adedipe, N.O. and Ormrod, D.P., 1971. Temperature and humidity effects of Pea cultivars. Can.J.Plant Sci., 51:479-484.
Ohkawa, K., 1979. Promotion of renewal canes in greenhouse roses by 6-Benzylamino purine without cutback. HortScience, 14(5):612-613.
O'Leary, James W. and Knecht, George N., 1971. The effect of relative humidity on growth, yield and water consumption of bean plants. J.Amer.Soc.Hort.Sci. 96(3):263-265.
O'Leary, James W. and Knecht, George N., 1972. Salt uptake in plants grown at constant high relative humidity. Arizona Academy of Science, 7(3):125-128.
O'Leary, James W., 1975. The effect of humidity on crop production. Physiological aspects of dryland farming (Edited by U.S. Gupta) Oxford & IBH Publishing Co., New Delhi.
Onckelen, H.A. van, Horemans, S and Gref, J.A. de., 1980. Abscisic acid metabolism during early stages of development plants (Phaseolus vulgaris L.). Aspects and prospects of plant growth regulators. Wessex Press. Wantage.
Osborne, D.S., 1978. Ethylene. Phytohormones and related compounds: A comprehensive treatise Volume I. Chapter 5. Elsevier/North-Holland.
Owen, P.C. and Watson, D.J., 1956. Effect on crop growth of rain after prolonged drought. Nature, 177:847.
Palmer, J.H., 1964. Comparative study of the effects of applied indoleacetic acid and horizontal orientation of the primary shoot, upon internode extension and petiole orientation in Helianthus annuus and the modifying influence of gibberellic acid. Planta, Bd.61:283-296.
Paranjothy, K and Wareing, P.F., 1971. The effects of abscisic acid, kinetin and 5-fluorouracil on ribonucleic acid and protein synthesis in senescing radish leaf disks. Planta (Berl.), 99:112-119.
Patrick and Wareing, 1980. Hormonal control of assimilates movement and distribution. Present state and prospects of research into natural and synthetic plant growth-regulating substances. Wessex Press. Wantage.
Phillips, I.D.J, 1964. Root-shoot hormone relations. II. Changes in endogenous auxin concentration produced by flooding of the root system in Helianthus annuus. Ann.Bot.,N.S., 28(109):17-35.
Phillips, I.D.J, 1975. Apical dominance. Ann.Rev.Plant Physiol., 26:341-367.
Pieters, G.A., 1985 Personal communication.
Plant, Z., Arnon, L., Zislin, N. and Shmneli, E., 1974. The effect of soil moisture on rose production under protected conditions. Acta. Hort.,35:59.
Post, Kenneth, and Howland, Joseph E., 1946. The influence of nitrate level and

light intensity on the growth and production of greenhouse roses. Proc.Amer.Soc.Hort.Sci., 47:446-450.
PVS. 1985, Annual report. Productschap Voor Siergewassen.
Rajan, A.K. and Blackman, G.E., 1975. Interacting effects of light and day and night temperatures on the growth of four species in the vegetative phase. Ann.Bot.,39:733-743.
Reid, D.M. and Crozier, A. 1972. Stimulation of the levels of gibberellin-like substances by the growth retardants CCC and AMO 1618. Plant growth substances (edited by D.J. Carr), pp.420-427. Springer Verlag, Belin.
Rijssel, E. van, 1979. Opbrengstbepalende factoren bij de teelt van kasrozen in het winterhalfjaar. Landbouw Economisch Instituut (LEI) pub.4.84, 96 pp.
Rijssel, E. van, 1982. Oorzaken van verschillen in opbrengsten van kasrozen. Landbouw Economisch Instituut (LEI) pub. 4.97, 103 pp.
Robinson, M., 1983. Influence of Abscisic acid and ethylene on assimilate distribution in Gladiolus grandiflorus. Ann.Bot.,51:779-785.
Rozenbrochure, 1984. Consulentschap voor de tuinbouw, Aalsmeer.
Ruddat, Manfred and Pharis, Richard P., 1966. Participation of gibberellin in the control of apical dominance in soybean and redwood. Planta(Berl.), 71:222-228.
Sachs, R.M. and Hackett, W.P., 1977. Chemical control of flowering. Acta Horti., 68:29-38.
Sachs, Tsvi. and Thimann, Kenneth V., 1964. Release of lateral buds from apical dominance. Nature, 201:939-940.
Sachs, Tsvi and Thimann, Kenneth V., 1967. The role of auxins and cytokinins in the release of buds from dominance. Amer.J.Bot., 54(1)136-144.
Sanden, P.A.C.M., 1985. Effect of air humidity on growth and water exchange of cucumber seedlings. Preliminary study. Acta Horti., 174:259-267.
Schneider, E.A. and Wightman, F. 1978. Auxins. Phytohormones and related compounds: A comprehensive treatise Volume I. Chapter 5. Elsevier/North-Holland.
Schrock, Dennis, and Hanan, Joe J., 1981. The effect of low temperature on yield and renewal cane production in relation to carbohydrate levels in roses. Scientia Horti., 14:69-76.
Schulze, E.D., Lange, O.L., Buschbom, U., Kappen, L. and Evenari, M., 1972. Stomatal responses to changes in humidity in plants growing in the desert. Planta, 108:259-270.
Scott, Tom K., Case, David B. and Jacobs, William P., 1967. Auxin-gibberellin interaction in apical dominance. Plant Physiol., 42:1329-1333.
Sebanek, Jiri, 1966. Einflusz des Kinetins auf den Gehalt endogener Gibberelline in den Wurzeln dekapitierter Erbsenkeimlinge. Naturwissenschaften:336.
Selman, I.W. and Sandanam, S., 1972. Growth responses of tomato plants in non-aerated water culture to foliar sprays of gibberellic acid and benzyladenine. Ann.Bot., 36:837-848.
Sheriff, 1975. The effect of humidity on water uptake by, and vicious flow resistance of exiced leaves of a number of species: Physiological and anatomical observations. J.Exp.Bot., 28:1399-1407.
Shiniger, T.L. and Schwabe, W.W., 1979. Lateral bud dormancy in the black currant Ribes nigrum (L). Ann.Rev.Plant.Physiol., 30:313-337.
Simpson, G.M. and Saunders, P.F.,1972. Abscisic acid associated with wilting in dwarf and tall Pisum sativum. Planta(Berl.), 102:272-276.
Skoog, F. and Miller, C.O., 1957. Chemical regulation of growth and organ formation in tobacco stem segments and callus cultured in vitro. Amer.J.Bot., 35:782-787.
Skoog, F. and Armstrong, D.J., 1970. Cytokinins. Annu.Rev.Plant.Physiol., 21:359-384.
Slatyer, R.O., 1967. Plant water relationships. Academic Press. London, New York 366 pp.
Staden, J. van, and Brown, N.A.C., 1978. Changes in the endogenous cytokinins of bark and buds of Salix babylonica as a result of stem girdling.

Physiol.Plant., 43:148-153.
Staden, J. van, and Dimalla, G.G., 1978. Endogenous cytokinins and the breaking of dormancy and apical dominance in potato tubers. J.Exp.Bot. 112:1077-1084.
Staden, J. van, Zieslin, N., Spiegelstein, H. and Halevy, A.H., 1981a. The effect of light on the cytokinin content of developing rose shoots. Ann.Bot., 47:155-157.
Staden, J. van, Spiegelstein, H., Zieslin, N and Halevy, A.H., 1981b. Endogenous cytokinins and lateral bud growth in roses. Bot.Gaz., 142(2):177-182.
Stanhill, G., Fuchs, M., Bakker, J. and Moreshet, S., 1973. The radiation balance of a glasshouse rose crop. Agri.Meteo., 11:385-404.
Stanhill, G., Moreshet, M.,Jurgrau, M. and Fuchs, M., 1975. The effect of reflecting surfaces on the solar radiation regime and carbon dioxide fixation of a glasshouse rose crop. J.Amer.Soc.Hort.Sci., 100(2)112-115.
Swalls, A.A. and O'Leary, J.W., 1975. The effect of relative humidity on growth, water consumption, and calcium uptake in tomato plants. Arizona Aca.Sci., 10(2):87-89.
Taylor, A.O. and Rowley, J.A., 1971. Plants under climate stress. I. Low temperature, high light effects on photosynthesis. Plant Physiol., 47:713-718.
Tesi, R., 1974. Effects of evaporative cooling system in greenhouses used for roses and carnations. Acta Hort., 43:113-123.
Thimann, K.V., 1937. On the nature of inhibitions caused by auxin. Amer.J.Bot., 24:407-412.
Thimann, Kenneth.V., 1977. Hormone action in the whole live of plants . The university of Massachusetts press. 448 pp.
Thinklin, I.G., 1970. Ann.Bot., 34:691-706.
Threwavas, 1980. What is the function of growth substances in the intact growing plant. Aspects and prospects of plant growth regulators: 197-208. Wessex Press Wantage.
Tibbits, T.W. and Bottenberg, G., 1976. Growth of lettuce under controlled humidity levels. J.Amer.Soc.Hort.Sci., 101(1):70-73.
Ticha, Ingrid, Catsky, J., Peisker, M. and Kase, M., 1984 The ontogenetic pattern of leaf photosynthesis as affected by irradiance, carbon dioxide concentration and temperature. Advances in photosynthesis research, Vol.IV., 3.255-3.258. Martinus Nijhoff/Dr. W. Junk Publishers,The Hague /Boston/Lancaster.
Tillberg, E., 1985. Abscisic acid in relation to primary and secondary dormancy. Abstracts of the 12th international conference on plant growth substances, Heidelberg.
Tsujita, M.J. and Dutton, R.G., 1983. Rootzone temperature effects on greenhouse roses in relation to supplementary lighting at reduced air temperature. HortScience, 18(6):874-876.
Tucker, D.J., 1976. Effects of far-red light on the hormonal control of side shoot growth in the tomato. Ann.Bot., 40:1033-1042.
Tucker, D.J. and Mansfield, T.A., 1972. Effects of light quality on apical dominance in Xanthium strumarium and the associated changes in endogenous levels of abscisic acid and cytokinins. Planta(Berl.), 102:140-151.
Tukey, John W., 1977. Exploratory Data Analysis. Addison and Wesley Pub. Comp., 506 pp.
Van Bragt, J., 1969. The effect of CCC on growth and gibberellin content of tomato plants. Neth.J.Agric.Sci., 17:183-188.
VBN. Statistiek Boek 1985. Association of Dutch flower auctions.
Vegis, A., 1964. Dormancy in higher plants. Ann.Rev.Plant Physiol., 15:185-224.
Vonk Noordegraaf, C., 1976. Supplementary lighting at the rose cv. 'Sonia'. Acta Hort., 64:155-163.
Vonk Noordegraaf, C. and Krogt, Th.M. van den , 1976. Belichting bij de roos 'Sonia'R. Bloemisterij Onderzoek in Nederland over 1977: 149-150.
Vonk Noordegraaf, C., 1978. Belichting bij de rozen 'Mercedes' and 'Motrea'.

Bloemisterij onderzoek in Nederland over 1977:253-254.
Vries, D.P., 1977. Shoot production in cut roses with reference to breeding for winter flowering. Euphytica, 26:85-88.
Vries, D.P. and Smeets, L., 1978. Hybrid tea-roses under controlled light conditions. 1. The effect of the level of irradiance on the growth and development of seedlings. Neth.J.Agric.Sci., 26:119-127.
Vries, D.P., Dubois, Lidwien A.M. and Smeets, L., 1978. Hybrid tea-roses under controlled light conditions. 3. Flower and blind shoot production in the glasshouse of seedlings selected for flowering or flower bud abortion at low irradiances in a growth room. Neth.J.agric.Sci., 26:399-404.
Vries, D.P. and Smeets, L., 1979. Effects of temperature on growth and development of hybrid tea-rose seedlings. Scientia Horti.,11:261-268.
Vries, D.P., Smeets, L and Dubois, Lidwien A.M., 1980. Genetic variation for the time of first flower and shoot length in hybrid tea-rose seedling populations under a range of temperatures. Scientia Horti., 13:61-66.
Vries, D.P., Kuyper,E.P.M. And Dubois, Lidwien A.M.,1981. Anatomy of flower differentiation and abortion, in relation to the growth and development of hybrid tea-rose seedlings. Scientia Horti., 14:377-385.
Vries, D.P., Smeets, L and Dubois, Lidwien A.M.,1982. Interaction of temperature and light on growth and development of hybrid tea-rose seedlings, with reference to breeding for low-energy requirements. Scientia Horti., 17:377-382.
Wakhloo, J.L., 1970. Role of mineral nutrients and growth regulators in the apical dominance in Solanum sisymbrifolium. Planta(Berl.), 91:190-194.
Wareing and Nasr 1961. Ann.Bot.N.S. 25:321-340.
Warrington, I.J., Peet, M., Patterson, D.T., Bunce, J., Halsemore, R.M. and Hellmers, H., 1977. Growth and physiological responses of soybean under various thermoperiods. Aust.J.Plant.Physiol., 4:371-380.
Wardlaw, J.F., 1968. Bot.Rev., 39:79-105.
Weaver, R.J. and Johnson, J.O., 1984. Relations of hormones to nutrient mobilisation and the internal environment of the plant. Hormonal regulation of development III. Encyclopedia of plant physiology. Springer Verlag. Berlin-Heidelberg, New York.
Webb, D.P., Staden, J. van and Wareing, P.F., 1973. Seed dormancy in Acer. J.Exp.Bot. 24:741-750.
Weel, P.A., 1984. Bench heating for potplants or cutflower production. Acta Hort.,148:57-64.
Went, F.W., 1944. Plant growth under controlled conditions III. Amer.J.Bot., 31:597-618.
Went, F.W., 1953. The effect of temperature on plant growth. Ann.Rev.Plant.Physiol., 4:347-362.
White, J.W. and Richter, D., 1973. Supplementary fluorescent lighting and low moisture stress improve growth of greenhouse roses. J.Amer.Soc.Hort.Sci., 98(6):605-607.
White, J.W. and Sherry, W.J., 1981. High intensity lighting and reflective thermal blanket combination for economy of energy. Acta Hort., 128:119-129.
Wickson, Margaret and Thimann, Kenneth V., 1958. The antagonism of auxin and kinetin in apical dominance. Physiol.Plant., 11:62;74.
Wiebe, H.J., 1981. Influence of soil water potential during different growth periods on yield of cauliflower. Acta Hort., 119:299-300.
Wisely, Donald K. and Lindstrom, Richard S., 1972. Supplemental light and growth of rose during periods of low light intensity. HortScience, 7(3):292-293.
Withers, A.C., Besford, R.T., Chow, W.S. and Ludwig, L.J., 1984. Light adaption in tomato leaves. Advances in photosynthesis research, Vol.IV., 3.297-3.300. Martinus Nijhoff/Dr W.Junk Publishers, The Hague/Boston /Lancaster.
Wright, S.T.C. and Hiron, R.W.P., 1969. (+)-Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. Nature,

224:729-720.
Zeroni, Moshe and Gale, Joseph, 1982. The effect of root temperature on the development, growth and yield of 'Sonia' roses. Scientia Horti., 18:177-184.
Zieslin, N., Halevy, A.H. and Biran, I., 1973. Sources of variability in greenhouse rose flower production. J.Amer.Soc.Hort.Sci., 98(4):321-324.
Zieslin, N. and Halevy, A.H., 1975a. Flowerbud atrophy in 'Baccara' roses. I. Description of the phenomenon and its seasonal frequency. Scientia Horti.,3:209-216.
Zieslin, N. and Halevy. A.H., 1975b. Flowerbud atrophy in 'Baccara' roses. II. The effect of environmental factors. Scientia Horti., 3:383-391.
Zieslin, N and Halevy. A.H., 1975c. Interaction between Cytokinins and CCC in bud breaking, flower bud atrophy and gibberellin content of roses. Z.Pflanzenphysiol. Bd., 77:160-166.
Zieslin, N. and Halevy, A.H., 1976a. Flower bud atrophy in 'Baccara' roses.III. Effect of leaves and stems. Scientia Horti., 4:73-78.
Zieslin, N. and Halevy, A.H., 1976b. Flower bud atrophy in 'Baccara' roses.IV. The activity of various growth substances in leaves of flowering and non-flowering shoots. Physiol.Plant., 37:317-325.
Zieslin, N. and Halevy, A.H., 1976c. Flower bud atrophy in 'Baccara' roses.V. The effect of different growth substances on flowering. Physiol.Plant., 37:326-335.
Zieslin, N. and Halevy, A.H., 1976d. Flower bud atrophy in 'Baccara' roses.VI. The effect of environmental factors on gibberellin activity and ehtylene production in flowering and non-flowering shoots. Physiol.Plant., 37:331-335.
Zieslin, Naftaly and Halevy, Abraham H., 1978. Components of axillary bud inhibition in rose plants. III. Effect of stem orientation and changes of bud position on the stem by budding. Bot.Gaz., 139(1):60-63.
Zieslin, Naftaly, Spiegelstein, Hana, and Halevy, Abraham H., 1978. Components of axillary bud inhibition in rose plants. IV. Inhibitory activity of plant extracts. Bot.Gaz., 139(1):64-68.
Zieslin, Naftaly, Madori, Gila, and Halevy, Abraham H., 1979. Involvement of hormonal balance in the control of the 'bullhead' malformation in Baccara rose flowers. J.Exp.Bot., 30(114):15-25.
Zieslin, N., Kirscholz, J and Mor, Y., 1980. Effect of night temperature and growth-practices on the winter yield of roses. Scientia Horti., 8:363-370.
Zieslin, N. and Khayat, E., 1983. Involvement of cytokinin, ABA and endogenous inhibitors in sprouting of basal buds in rose plants. Plant Growth Regulation 1:279-288.

14. CURRICULUM VITAE

Gustaaf Anton van den Berg werd op 10 maart 1945 te Loosduinen geboren. Na de MULO te hebben doorlopen was hij werkzaam op het ouderlijk tuinbouwbedrijf en behaalde hij via studie aan het 'Avond Lyceum Noctua' te 's-Gravenhage het Staatsexamen HBS-B in 1964.
Na vervulling van de militaire dienstplicht studeerde hij van af september 1966 tot september 1972 aan de Landbouwhogeschool te Wageningen. Het doctoraal examen werd met lof afgelegd in de richting Tuinbouwplantenteelt, met als bijvakken Fytopathologie (verzwaard) en Plantenveredeling.
Hierna volgde een tijdelijke werkkring bij het Proefstation voor Tuinbouw Onder Glas te Naaldwijk, waar hij in opdracht van de Coordinatiecommissie Onderzoek Bodempathogenen van de Nationale Raad voor Landbouwkundig Onderzoek TNO onderzoek deed aan de invloed van selectieve warmtebehandeling op enige biologische processen in kasgrond. Vanaf novenber 1973 is hij werkzaam bij het Proefstation voor de Bloemisterij in Nederland te Aalmeer, sinds oktober 1986 als hoofd van de afdeling Teelt.