SYSTEM DEVELOPMENT OF GLASSHOUSE ROSES

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universitair hoofddocent bij de vakgroep Tuinbouwplantenteelt

SYSTEM DEVELOPMENT OF GLASSHOUSE ROSES

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 11 oktober 1996
des namiddags te vier uur in de Aula
van de Landbouwuniversiteit te Wageningen.

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Kool, M.T.N.

System development in glasshouse roses /
M.T.N. Kool - [S.1.:s.n.]. Fig., Tab.
Thesis Wageningen. - With ref.- With summary in Dutch
ISBN 90-5485-592-4
Subject headings: rose production.

This thesis contains results of a research project of the Wageningen Agricultural University, Department of Horticulture, Haagsteeg 3, 6708 PM Wageningen.

This research was financially supported by:
* NOVEM
* PVS

Abstract

Kool, M.T.N., 1996. System development of glasshouse roses. Dissertation Wageningen Agricultural University, Wageningen, The Netherlands, 143pp; English and Dutch summaries.

Apart from the progress in control of environmental factors and optimization of the technical equipment with respect to an increase in productivity during the last decades, little attention has been paid to reveal the significance of plant structure and plant management on the growth and productivity of a rose crop. The aim of the present research was to enlarge the knowledge about the physiological background of rose crop production under controlled environmental conditions.

Plant architecture, as reflected in the number, diameter and cross sectional area (CSA) of basal shoots and laterals, can be highly controlled using plant related factors such as time of bending the primary shoot, removal of lateral or basal buds, height of pruning at harvest and disbudding of flowering shoots and by plant density. Treatments which invest in early stem development reduce flower production for the first 8 months but this financial loss amply pays itself in the next 2 cropping years. Plant architecture has a great influence on flower production. The number and diameter of second-order laterals as formed during the first 8 months, can explain more than 70% of the variation in number and weight of flowers harvested in the next 2 cropping years. Long-term flower production is hardly related to the number of basal shoots. New basal shoots compete with existing ones as indicated by the limited diameter increase, the higher mortality rate and the smaller flowering shoots for old basal shoots.

Disbudding of flowering shoots resulted in an increase in total non-structural carbohydrates in basal stem parts, mainly starch. Although used again for the subsequent flowering cycle, carbohydrate storage is much too low for playing an important role for new growth.

Rose crop growth primarily depends on the intercepted photosynthetically active radiation (PAR) which is closely related to plant architecture. Under natural light and CO_2-conditions, a linear relationship between crop dry weight increase and intercepted PAR by the canopy was observed. Average light conversion efficiency (LCE) was 2.5 g/MJ PAR. A uniform leaf area index, i.e. light interception, is maintained by a continuous harvesting system controlled by the height of cutting at harvest and the bending or removal of blind shoots. Flush harvesting reduces the light interception i.e. crop growth. The percentage of dry matter distributed to harvested flowers was influenced by environmental conditions and method of harvesting. Although flower quality was highly influenced, the harvest index was neither affected by the applied treatments nor by plant density.

Actual levels of dry-matter production as achieved by the existing climate and crop conditions can be evaluated by comparing with the potential one, as simulated with the crop growth model ALSIM(1.0).

Keywords: basal shoots, bottom breaks, carbohydrates, dry matter, flower production, harvest index, lateral shoots, leaf area, light conversion efficiency (LCE), light interception, method of harvesting, photosynthetic active radiation (PAR), plant architecture, potential production, *Rosa hybrida*, rose, stem quality.

'Alle tijd die je aan de roos - aan jóuw roos - besteedt,
maakt de roos zo mooi', zei de vos.
De kleine prins herhaalde zachtjes deze zin.
Ze bevatte - zo vond hij - een belangrijke gedachte.
'De mensen vergeten dat domweg', zei de vos.
'Wil jij dat nooit vergeten? Je blijft verantwoordelijk voor je daden.
Jij draagt verantwoordelijkheid voor je roos.'
'Ik ben verantwoordelijk voor mijn roos', zei de kleine prins.
Daarbij hield hij zijn hand op zijn hart.

A. de Saint-Exupéry in
'De Kleine Prins'

Contents

Account

The chapters 2-4 have been or will be published in international journals.

Chapter 2.1: Kool, M.T.N. and Lenssen, E.F.A., 1996. Basal shoot formation in young rose plants: Effects of bending practice and plant density (submitted)

Chapter 2.2: Kool, M.T.N. and Van de Pol, P.A., 1993. Controlling the plant development of Rosa hybrida 'Motrea'. Scientia Horticulturae, 53: 239-248.

Chapter 3.1: Kool, M.T.N., 1996. Importance of plant architecture and plant density for rose crop performance. Journal of Horticultural Science 72: 000-000 (accepted)

Chapter 3.2: Kool, M.T.N. and Van de Pol, P.A., 1996. Long-term flower production of roses 1: The effect of rootstocks and plant type. Journal of Horticultural Science 71: 435-443.

Chapter 3.3: Kool, M.T.N., 1996. Long-term flower production of a rose crop 2: The importance of new basal shoot formation. Journal of Horticultural Science 71: 445-452.

Chapter 3.4: Kool, M.T.N., 1996. Effects of harvesting method and shoot density on production and flower performance of roses. Scientia Horticulturae 00: 000-000 (accepted).

Chapter 4.1: Kool, M.T.N., De Graaf, R. and Rou-Haest, C.H.M., 1996. Rose flower production as related to plant architecture and carbohydrate content: effect of harvesting method and plant type (submitted).

Chapter 4.2: Kool, M.T.N., Westerman, A.D. and Rou-Haest, C.H.M., 1996. Importance and use of carbohydrate reserves in above ground stem parts of rose cv 'Motrea'. Journal of Horticultural Science 71: 000-000 (accepted).

Chapter 4.3: Kool, M.T.N., 1996. Rose crop production and allocation of assimilates as affected by plant architecture and light interception (submitted).

1. General introduction

In the Netherlands the rose is the most important glasshouse cut flower; the production area is 919 ha and the auction turnover 785 million Dutch guilders (Anonymous, 1995).

Flower development and growing conditions

Rose is a perennial woody shrub. Throughout the year glasshouse roses continuously form new shoots. Each shoot is programmed to initiate a flower bud without needing a specific photoperiod or temperature (Zieslin and Moe, 1985). However, unfavourable environmental conditions such as low temperature and low light intensity (Moe, 1971; Mastalerz, 1987) may cause early abortion of flower buds (Moe and Kristoffersen, 1969; De Vries, 1977; De Vries and Smeets, 1978) leading to the formation of 'blind shoots'. The effect of the environment on growth and development of rose crops has been the focus of several studies (Moe, 1972; Post and Howard, 1976; Zieslin *et al.*, 1986; Van den Berg, 1987; Jiao *et al.*, 1991). As for other glasshouse crops, light intensity, temperature and CO_2-concentration are considered the most important factors for crop growth. Monteith (1977) has shown that for all crops yield of harvestable parts and total dry matter production are primarily related to total light interception. Therefore, in the temperate zone use of supplementary lighting of roses is increasing in order to obtain year-round production. CO_2 is usually supplemented, although optimizing its economical use in relation to crop growth, light intensity and temperature is still difficult. Temperatures of 15-20°C at night and 18-25°C during the day are considered to be optimal for most cultivars (Van den Berg, 1987). Relative air humidity is not considered to be an important factor (Harkess and Hanan, 1988) as is also the case for glasshouse vegetable crops (Bakker, 1991).

Growth and development of rose plants

Rose plants are propagated vegetatively by cutting (Dubois *et al.*, 1990), stenting (Van de Pol and Breukelaar, 1982), root grafting (Van de Pol, 1986), bench grafting (Garner, 1958), budding (De Vries, 1993) and *in vitro* culture (Short and Roberts, 1991). Plant development is more or less the same for all these methods as described by De Vries (1993) and Marcelis-Van Acker (1994c), except that *in vitro* plants often show more branching after hardening off than *in vivo* plants (Dubois *et al.*, 1988; Vijaya and Satyanarayana, 1991). Generally, the axillary bud of the scion will sprout and develop into a shoot, the so-called primary shoot, which flowers 6-12 weeks after cutting or grafting. When the apical dominance of the primary shoot is broken (often due to decapitation of the flower bud) one or more distal axillary buds of the primary shoot will sprout and grow out into lateral shoots. Bending or natural toppling over of the primary shoot promotes breaking of the basal quiescent buds (Mor and Zieslin, 1987). These buds, usually two, which become the first and second basal shoot, are already present as secondary buds in the axils of the scales of the axillary bud used in propagation (Marcelis-van Acker, 1993). Vigorous shoots growing from these buds are termed "basal shoots" or "bottom breaks". These shoots form the frame of a rose plant and their number, diameter and degree of branching mainly determine potential flower production (Zieslin *et al.*, 1973; De Vries and Dubois, 1983; Halevy, 1986).

Factors affecting crop production

Crop production is a complex phenomenon as it depends on many mutually related factors (Figure 1). It should be stated that the greater productivity achieved during the last decennia has been mainly realized through the progress in control of environmental factors (right side Figure 1) and optimization of the technical equipment (Van den Berg, 1996). These improvements required large investments which greatly increased the production costs per m^2. As a direct result, nowadays more than 40% of differences in the economic output per unit area of individual rose farms relate to differences in technical production costs as compared to fifteen years ago when only yield and auction price were involved (Benninga and Duys, 1996). Therefore, the uniformity and productivity of the smallest production unit, the individual plant, has become increasingly important. However, so far little attention has been paid to other factors than the above mentioned environmental and technical ones, to control the growth of the plant (left side Figure 1). For other woody plants, especially fruit trees, research on the relationship between production and several plant parameters was already being carried out in the 1940s (Wilcox, 1941; Pearce, 1949). The significance of

INPUT

propagation material
rootstock
cultivar
plant spacing
plant density
plant building
method of harvesting

light
temperature
carbon-dioxide
relative humidity
water/nutrition
substrate
technical equipment

GROWTH

STEM BUILDING

FLOWERS HARVESTED

Figure 1. Factors affecting rose crop production

plant structure and plant management for growth and productivity of crops such as apple and pear has been long recognized (Clayton-Greene, 1993). During the last decades improved growth control resulted in much more uniform tree stands which led to large gains in productivity.

For roses, already twenty years ago Zieslin *et al.* (1975) stated: "The life span of the woody parts of a rose plant (roots and stems) is much longer than that of the flowering shoots which appear over a relatively large number of growth cycles during the year. An interdependence exists between these two regions of the plant. The short-lived, many-leaved flowering shoots must photosynthesize sufficiently to support their own growth and also to maintain the lower, more woody parts of the plant. The latter may serve as reservoirs for the normal development of rose plants under conditions of insufficient light, and for the nutrition of the flowering shoots during their initial stages of development. Understanding the processes involved in this interdependence may contribute to the development of treatments which will raise the productivity of rose plants". However in the following twenty years, limited progress had been made in revealing the interdependence of these two regions in the plant as influenced by the factors on the left side in Figure 1. Most research has been focused on the enhancement of the number of bottom-breaks as reviewed by Fuchs (1994). Broadly speaking, the formation of basal shoots occurs when due to some growth retarding stimulus apical dominance weakens, followed by a resumption of favourable growing conditions (Zieslin *et al.*, 1975; Zieslin and Halevy, 1978; Schrock and Hanan, 1981; Khayat and Zieslin, 1982). However, in long-term experiments the effect of basal-shoot formation and plant architecture on flower production has been seldomly studied. So far the attention was limited to the influence of the number of bottom-breaks on production over a relatively short time (Kofranek and Fisher, 1949; Asen and Hamner, 1953; Zieslin *et al.*, 1976b; De Vries and Dubois, 1983 and 1984).

Although a considerable amount of rootstock research has been done, progress in this field is limited (De Vries, 1993; Fuchs, 1994). During the last decades breeding new cut rose varieties has not led to significant improvements in productivity (De Vries and Dubois, 1987; Dubois and De Vries, 1987). Assuming that there are no differences in the efficiency of leaf photosynthesis between cultivars (Daie, 1985), the slightly improved yield potential through selection and breeding must have largely been due to an increase in the proportion of accumulated dry weight that is invested in the plant parts harvested, i.e. to an increase of the harvest index (Gifford and Evans, 1981).

Analysis of crop production

It can be concluded that large and undesirable variations exist between the rose plants in a crop with respect to number and diameter of basal shoots and laterals (Kool *et al.*, 1991). Berentzen (personal communication) found large differences in number and diameter of basal shoots and their laterals in the 15 rose crops which he studied. Furthermore, rose crops are characterized by an excessive variability in number of flowers harvested and flower performance (Rejman en Wisniewska-Greszkiewics, 1986). In traditional rose bushes continuous harvesting of flowering shoots is a consequence of large variation in plant types (Kool *et al.* 1991), in factors affecting flower production per plant (Zieslin *et al.*, 1973) and in the length of time elapsing between one harvest and the next (Fuchs, 1994). Nevertheless, flowering shoots often appear in flushes due to pruning practices (Holley, 1973) or climatic conditions.

Large differences in productivity between individual growers exist (Benninga and Duys, 1996). Part of these differences originated from different environmental conditions (as summarized in Figure 1 on the right side) such as light incidence at canopy level, CO_2-concentration and temperature; the remainder must be associated with differences in technical equipment, crop conditions (water, diseases) and specific crop data (leaf area index, plant biomass). Due to these differences, analysis of the actual level of productivity is difficult. Furthermore, there is little uniformity in the description of the effects of various cultural practices, technical installations or environmental factors on production. Most common production data are number of harvestable stems, flower stem characteristics (weight, length, diameter) and economic yield. However, comparison of crop vigour by these parameters is difficult, due to differences in 1) cultivar and economic parameters (e.g. weight per stem, percentage of dry matter in stems, stem length, price), 2) light received at canopy level (global radiation, greenhouse light transmission and use of supplementary light) and, 3) other environmental factors and specific crop data. In addition, for each experiment, the potential effect of the treatment applied will vary widely, depending on the overall growing conditions. Probably the dry matter production per m^2 glasshouse is a much better parameter for crop vigour (Kool and De Koning, 1996). In that case, differences between cultivars and economic parameters are not relevant. A further improvement can be made by expressing the dry matter production per MJ photosynthetic active radiation (PAR) as has been done for such crops as tomato (De Koning, 1993; Heuvelink, 1995a) and apple (Palmer, 1989). In so doing, differences in the factor light (usually a limiting factor) are incorporated in the expression of crop vigour and only differences originating from other environmental factors or specific crop data influence the analysis of crop growth. The last step in crop growth analysis is the comparison of dry matter production with the potential production as done by Kool and De Koning (1996).

Aim of the thesis

The aim of the research was to enlarge the knowledge about the physiological basis of rose crop production under controlled environmental conditions. Firstly, it was investigated which plant factors can be used to regulate the growth and development of basal shoots and laterals during the early development of young rose plants. Secondly, it was explored to which extent some aspects of plant architecture can affect crop growth and flower quality. Thirdly, the physiological control of the influence of plant architecture on flower production was studied. The separate effects of leaf area (light interception), carbohydrate reserves and plant architecture on the production and partitioning of assimilates were unravelled. Fourthly, an effort has been made to express crop growth in more generally applicable parameters.

With a better knowledge about factors influencing rose crop production an optimal growing system might be developed. With a more uniform crop stand through improved growth control, a better approach to attaining potential yield, as being estimated by Van de Pol (1990) and Van der Meer (1995) or predicted by simulation of crop growth (Kool and De Koning, 1996), of a desirable flower quality might be possible.

Outline of the thesis

Chapter 2 deals with the evaluation of factors which control plant development. Factors studied are plant size, apical dominance, plant density, height of cutting and number of developing shoots. In Chapter 3 the importance of plant architecture with respect to long-term flower production is studied. In addition to the factors mentioned in Chapter 2, plant architecture was modified by disbudding, plant spacing and methods of harvesting.

Chapter 4 deals more in detail with the physiological background of rose crop production. The effects of plant architecture, leaf area and carbohydrate content on flower production are studied. Special emphasis is placed on the light conversion efficiency and the harvest index as two important parameters to express crop growth.

In Chapter 5 an attempt is made to integrate results of the previous chapters. This is done by defining the main physiological aspects determining optimal rose crop production. Results as found in this thesis are discussed as related to maximal production, distribution of dry-matter towards the harvestable parts and defined cut-flower quality characteristics. Special emphasis is put on evaluating the actual dry-matter production by comparing it with potential dry-matter production, calculated with a crop growth simulation model ALSIM(1.0).

2. Plant management tools

2.1. Basal-shoot formation in young rose plants: Effect of bending practice and plant density

Kool, M.T.N. and Lenssen, E.F.A., 1996. Basal-shoot formation in young rose plants: Effect of bending practice and plant density.

Abstract

To examine the relations between plant architecture and flower production, the effect of bending practices and plant densities on basal-shoot formation was studied in young rose plants. After bending the primary shoot a clear preference existed for the outgrowth of the two most basal buds which are already present as secondary buds in the axils of the scales of the axillary bud when used as a cutting for propagation. This preference came even more to the fore when bending was delayed. The source capacity of the primary shoot, mainly reflected in the leaf area index (LAI), was determined by bending time. Delayed bending increased the development rate, diameter, weight and cross sectional area (CSA) of basal shoots per plant. Plant growth rate, expressed as dry weight increment per day, was positively related with LAI and thus light interception during the early phase of basal-shoot formation although a maximum was reached at bending 28 days from T_0 (time of bending the primary shoot when the flower petals were reflexing). Outgrowth of axillary buds positioned higher on the stem strongly inhibited the outgrowth of basal shoots. Removal of competitive lateral growth increased the number and CSA of basal shoots per plant. Reducing the number of developing basal shoots strongly increased the diameter and weight of the remaining ones but hardly affected plant growth rate. The influence of plant density on basal-shoot formation of young rose plants was relatively small. However, number and cross sectional area (CSA) of basal shoots per square meter were highly positively influenced by increasing plant densities. A general concept on ways to improve plant building of young rose plants, with respect to basal-shoot formation, is discussed. Number, diameter and CSA of basal shoots, expressed per plant or per square meter, could be highly controlled using plant related factors such as time of bending of the primary shoot, removal of lateral and basal buds and by plant density.

Introduction

The importance of basal shoots with respect to a vigorous and highly productive rose-crop with a longer life-span has been stressed for a long time (Kofranek and Fischer, 1949; Zieslin *et al.*, 1976b; Van Rijssel, 1982; De Vries, 1993). A strong positive relation between the number or diameter of basal shoots and a high flower production was found (De Vries and Dubois, 1983; Van Rijssel, 1982). Various cultural practices have been tested for their ability to promote formation and development of basal shoots in established rose bushes (De Vries, 1993). Contrary to this, up to now the management of plant architecture in young rose plants has received little attention. Only Zieslin *et al.* (1976b) showed that continuously disbudding enhanced the number of basal shoots of young rose plants.

To stimulate growth of normally quiescent axillary buds in the lower part of young rose plants (Marcelis-van Acker, 1993), the outgrowing primary shoot of cuttings, stentings or graftings is bent down horizontally (90^0) after some time or may naturally topple over (De Vries, 1993). In the latter case, the number and diameter of outgrowing basal and lateral shoots vary considerably due to differences in time of emergence and competition within plants (Kool *et al.*, 1991). The effect of bud age on shoot quality may play an important role in the formation of basal shoots as suggested by Marcelis-van Acker (1994b).

Limited information is available on the influence of plant density on the plant architecture of a rose crop. In general, higher plant densities lead to an increase in LAI and dry weight production per square meter as has been demonstrated for many crops such as tomato (Papadopoulos and Ormrod, 1991), faba bean (Stützel and Aufhammer, 1991) and rose (De Vries and Dubois, 1988). However, the development of individual plants will be limited because of decreasing individual plant exposure to light as found by Crothers and Westermann (1976) and Papadopoulos and Ormrod (1991). For roses, a high plant density increased plant mortality and decreased individual plant weight combined with less structural branches and slightly smaller branch diameter after four years of culture as found by Pessala (1977).

Effects of plant density on rose flower production have been studied more often (Rupprecht, 1963; Obiol and Cardus, 1972; Steinbuch, 1985). As for many other horticultural crops, e.g. carnation (Sakashita *et al.*, 1987), increasing plant density increased productivity but decreased weight of harvestable stems.

Contrary to other horticultural crops, where the significance of plant structure and plant management on growth and productivity has long been recognized e.g. for apple (Clayton-Greene, 1993), in roses limited attention has been paid to the relation between plant architecture and flower production. In order to examine more closely the relationship between plant architecture and flower production, it is necessary to grow uniform plants of a defined shape with respect to number and diameter of basal shoots. To achieve this goal experiments were conducted to study the effect of 1) the weight and leaf area index of the primary shoot on the moment of bending 2) number and development of outgrowing basal or lateral buds 3) plant density and 4) combined effects on the process of basal-shoot formation in young rose plants. A general concept of improving plant architecture of young rose plants, with respect to basal-shoot formation, will be developed.

Material and methods

Experiment 1

On 17 September 1992, single node cuttings of *Rosa hybrida* Madelon 'Ruimeva' were dipped in talcum powder with 0.4% IBA and pricked into rockwool blocks (9x9x9 cm) for rooting. Soil and air temperature were kept at set points of 24°C D/N and relative air humidity was kept close to 100%. Supplementary lighting was given with high pressure sodium lamps (SON-T plus 70 Watt, 38.8 μmolm^{-2}s^{-1} PAR) for 16 h a day. On 7 October, 120 uniform, rooted cuttings were selected and placed on rockwool slabs in a growth chamber at a day/night temperature of 21°C and at a relative air humidity of 70%. Day length was 16 h and light intensity at plant height 164.9 μmolm^{-2}s^{-1} PAR provided by a mixture of high pressure sodium and mercury lamps (SON-T and HPI-T; both 250 and 400 Watt). Plant spacing was 50x20 cm. Plants were drip irrigated 4 times a day with a standard growers nutrient solution (EC = 1.8, pH = 5.5); length of irrigation period depended on keeping a drain percentage of 30.

Treatments consisted of 4 times of bending the primary shoot (starting when its flower bud diameter was 10 mm (T_0) and 14, 28 and 42 days later, respectively) combined with or without removal of lateral shoot growth. For each treatment 2 plants from each block were harvested destructively at the moment of bending and leaf area index and fresh and dry weight of the leaf and stem parts were measured. From the remaining plants, basal shoots and laterals (positioned higher at the bent primary shoot) were harvested when the petals opened and development time (defined as number of days from bending the primary shoot until harvesting the flowering shoot), length, diameter, number of leaves, leaf area, fresh and dry weight of leaves and flowering shoots were determined. After harvesting the last basal shoot or lateral per plant, diameter, leaf area and fresh and dry weight of the remaining primary shoot were determined. From these data, the cross sectional area (CSA; Lombard *et al.*, 1988) of shoots, leaf area index, growth rate and partitioning of dry weight over basal shoots, laterals and primary shoot were calculated.

The experimental design was a randomized block design with 3 blocks, each block consisting of 2 rows of rockwool slabs. There were 5 replicate plants per treatment. Two outermost plants per treatment were used for a destructive growth analysis at the time of bending down the primary shoot. In this way, plant density gradually decreased from 10 plants/m^2 to 6 plants/m^2. Results were statistically analyzed by analysis of variance and regression analysis with the statistical GENSTAT package. The best model was calculated out of the complete model containing blocks, bending time, lateral shoot growth and the interaction between bending time and lateral shoot growth. Only significant variables (on basis of the F-test of the individual model term ($P<0.05$) were taken into the model. The adjusted square multiple correlation coefficient (r^{2*}) is given, presenting the percentage of by regression explained variance. Mean separation was done by Students *t*-test.

Experiment 2

On 10 January, 1991, 1500 single node cuttings of *Rosa hybrida* Madelon 'Ruimeva' were dipped in talcum powder with 0.4% IBA and pricked in rockwool blocks (9*9*9 cm) for rooting. Climatic conditions were the same as described for Experiment 1. After rooting, plants were hardened off and on 13 February placed on rockwool slabs in a greenhouse area of 150 m^2. Rockwool slabs (133*15*9 cm) were transversally placed on moveable benches with discharge of drain water at one side of the bed. Plants were drip-irrigated 6 to 12 times a day depending on global radiation. Day/night temperatures were set on 19^{0}C/17^{0}C.

The following plant treatments were applied, each one combined with a plant density of 11.6, 17.4 and 23.2 (not for Treatment 1) plants/m^2, respectively (Table 1):

- *Treatment 1:* The flower bud of the primary shoot was removed in pea-bud stage. The primary shoot was then bent horizontally on 5 April when flowers of outgrowing laterals were almost in harvestable stage in order to stimulate the outgrowth of basal and lateral buds. From this moment on, new lateral bud growth within 30 cm of the base of the primary shoot was continually removed, excluding the basal shoots.
- *Treatment 2:* The same treatment as in 1 but only one basal bud was allowed to grow out after bending down the primary shoot.

Table 1. Plant spacing in Experiment 2 and 3 as influenced by plant density. Rockwool slabs were transversally placed on moveable benches.

Plant density moveable benches (plants/m^2)	Plant density greenhouse area (plants/m^2)	No. of plants/ rockwool slab	Distance between rockwool slabs (cm)
8.6	7.7^z	4	33
12.9	11.6	6	33
19.3	17.4	7	26
25.9	23.3	8	22

^{z}calculated as a result of a space utilization for this type of movable benches of 90%.

Basal shoots were harvested at the second 5-leaflet leaf counted from the base of the stem, and diameter was measured 2-3 cm above the base of the remaining stem. Number and CSA of basal shoots per plant or per square meter greenhouse were calculated.

The experimental design was a randomized block design with 4 blocks; one on each of the 4 moveable benches. Each treatment was applied on 6, 7 or 8 plants per block (Table 1) surrounded by 1 border row on each side which underwent the same plant treatment, in order to minimize edge effects.

Experiment 3

On 5 January 1993, 1500 single node cuttings of *Rosa hybrida* Madelon 'Ruimeva' were propagated as described in Experiment 2. On 11 February plants were placed on rockwool slabs in a greenhouse area of 150 m^2. For 6 weeks, supplementary lighting using high pressure sodium lamps (SON-T; 400 Watt; 36.5 $\mu mol\ m^{-2}\ s^{-1}$ PAR) was given for 20 h a day. Further growing conditions were the same as described in Experiment 2.

The following plant treatments were applied in combination with plant densities of 7.7, 11.6 and 17.4 plants/m^2 (Table 1):

- *Treatment A* - *Control:* the flower bud of the developing primary shoot was removed in the pea-bud stage. When the outgrowing laterals had reached a length of 15 cm, the primary shoot was bent for 90^0 at the base of the shoot in order to stimulate the outgrowth of basal and lateral buds. New basal and lateral shoots were harvested just above the second 5-leaflet leaf counted from the base.
- *Treatment B:* Plants were initially treated the same as the control plants. After bending the primary shoot, all lateral growth within 30 cm of the base of the primary stem was continually removed excluding basal shoots. Basal shoots were harvested just above the second 5-leaflet leaf counted from the base.
- *Treatment C:* The primary shoot was bent down 18 days later than the control plants. Only 1 basal bud and no laterals were allowed to grow out. Shoots were harvested just above the fourth 5-leaflet leaf counted from the base.

D) The primary shoot was bent down at the same time as plants from treatment C. After horizontal placement, only basal shoots were allowed to grow out as in treatment B and C. Shoots were harvested just above the fourth 5-leaflet leaf counted from the base.

- *Treatment D:* At harvesting, the diameter of the basal shoots and laterals was measured 2-3 cm above the base of the shoot which remains on the plant. Fresh weight, length, diameter and time of harvest were recorded. Number and cross sectional area of basal shoots and laterals per plant or per square meter glasshouse were calculated. The experimental design was a randomized block design with 3 blocks positioned according to the north-south orientation of the beds. Each treatment was applied on 8-14 plants (2 rockwool slabs; Table 1) surrounded by 1 border slab on each side. Results in both experiments were statistically analyzed by Analysis of Variance using the statistical SYSTAT package. Mean separation was done by Tukey-HSD test.

Results

Experiment 1

Data on primary shoot development at time of bending are shown in Table 2. Leaf area as reflected in LAI, and dry weight increased significantly with time of bending.

Table 2: Leaf area index (LAI) and plant dry weight (excluding roots: DW) at the moment of bending the primary shoots at 4 different times (n=12). Experiment 1.

Treatment (days from T_0)	LAI (m^2m^{-2})	DW ($gplant^{-1}$)	DW (gm^{-2})
0	1.0 a[z]	7.8 a	78 a
14	1.5 b	14.3 b	143 b
28	3.5 c	30.8 c	308 c
42	4.4 d	45.3 d	453 d

[z] Mean separation per column by Students t-test ($P=0.05$).

Number of basal shoots was strongly reduced by the growth of laterals on the primary shoot (Figure 1A), especially at early bending. In general, the number of basal shoots increased (Figure 1A) while development time decreased when bending was delayed (Table 3).

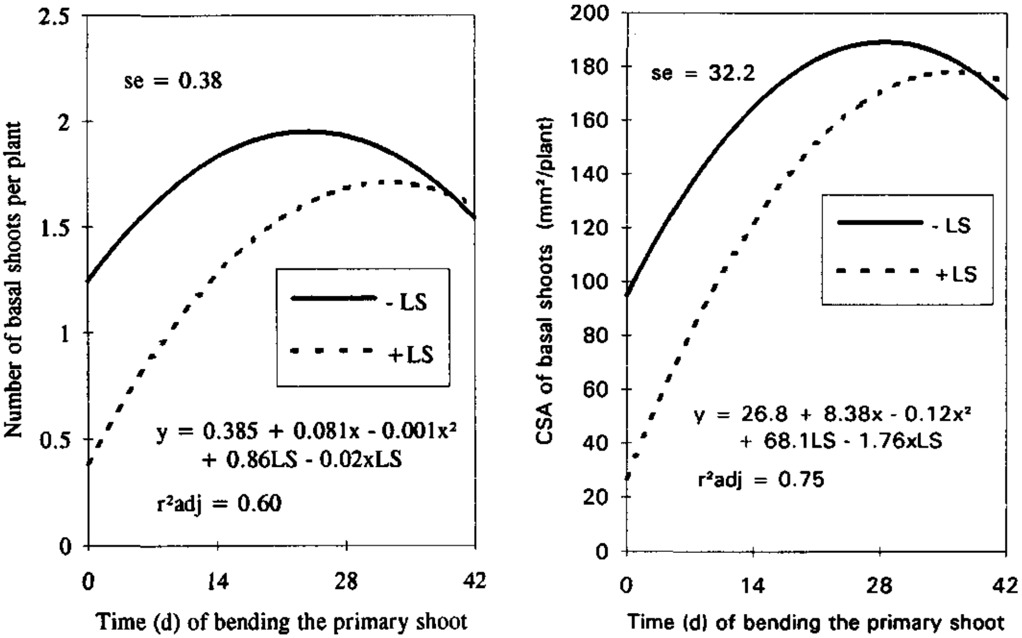


Figure 1. Relation between time of bending the primary shoot (X), combined with lateral shoot growth ($LS=0$) or without lateral shoot growth ($LS=1$) and interaction ($X*LS = 0$ or 1, respectively), on the number of developing basal shoot per plant (A) and on the cross sectional area of basal shoots per plant (B). The significant regression model ($P<0.05$) is given together with the adjusted correlation coefficient (r^2_{adj}) and the standard error (se).

Table 3. The influence of time of bending the primary shoot on development time[z], diameter and dry weight of basal shoots. Experiment 1.

Treatment (days from T_0)	Basal shoot: Development time (days)	Diameter (mm)	Dry weight (g)
0	57.3 a	9.4 a	30.3 a
14	55.6 a	9.9 ab	31.0 a
28	46.6 b	10.4 b	32.2 a
42	38.5 c	10.7 b	35.6 a

[z] time between bending the primary shoot and harvesting the basal shoots

Diameter as well as dry weight of individual basal shoots were little reduced by the growth of laterals (data not shown) and slightly increased with time of bending (Table 3). As a result, the CSA of basal shoots per plant increased with delayed bending (Figure 1B) and was lower in the presence of laterals, especially at early bending. The same patterns could be found for total fresh or dry weight of basal shoots per plant (data not shown).

Growth of laterals strongly influenced the partitioning of assimilates (Table 4). At early bending, less assimilates were allocated to growth of basal shoots. Delaying bending reduced allocation of assimilates towards growing laterals, in favour of dry weight incorporation in basal shoots. Removal of lateral growth enhanced the percentage of assimilates directed to the basal shoots. Plant dry weight, including the basal shoots, as well as the LAI also

Table 4. Influence of time of bending the primary shoot, combined with the presence (yes) or absence (no) of outgrowing laterals (LS), on the partitioning (%) of dry weight over the primary shoot, laterals at the horizontal shoot or basal shoots, calculated from the moment of bending until harvesting the basal and lateral shoots. Experiment 1.

Treatment (days after T_0)	LS	Dry weight production (%): Primary shoot	Lateral shoots	Basal shoots
0	no	37.5		62.5
14	no	39.0		61.0
28	no	27.5		72.5
42	no	12.4		87.6
0	yes	33.2	51.9	14.9
14	yes	30.9	21.6	47.5
28	yes	21.3	18.4	60.3
42	yes	25.2	4.9	69.9

Table 5: Influence of the different times of bending the primary shoot on plant dry weight, leaf area index (LAI) and growth rate. Experiment 1.

Treatment (days from T_0)	Dry weight ($gplant^{-1}$)	LAI ($6pl/m^2$) (m^2m^{-2})	Growth rate[z] ($gday^{-1}m^{-2}$)
0	71.5 a	3.8 a	6.7 a
14	100.5 b	5.2 b	8.0 b
28	114.4 c	5.9 c	8.6 b
42	116.2 c	5.7 bc	8.1 b

[z] calculated over the period T_0 until harvesting the basal shoots.

increased with time of bending (Table 5). It can be calculated that the growth rate of plants reached a maximum value of 8.6 $gday^{-1}m^{-2}$ for plants bent 28 days after T_0.

Experiment 2

Higher plant density significantly increased the number of basal shoots per m^2 (Table 6) but number of basal shoots per plant and their diameter were not significantly influenced. As a result the CSA of basal shoots increased per m^2 and decreased per plant with the higher density. Restricting the number of outgrowing basal buds to one (Treatment 2), clearly enhanced the diameter, weight and cross sectional area (CSA) of individual basal shoots as compared with the control treatment (data not shown). Number and CSA of basal shoots per m^2 increased but shoot diameter as well as CSA per plant decreased with increasing plant densities (Table 7).

Experiment 3

CSA of basal shoots was enlarged by removing the outgrowing lateral buds of the primary shoot (Table 8; treatment B vs A). The number of developing basal shoots per plant or per

Table 6: Influence of plant density on number, diameter and cross sectional area (CSA) of basal shoots. Experiment 2.

Plant density (no/m^2)	Basal shoots: Number per m^2	Number per plant	Diameter (mm)	CSA (in mm^2): per plant	per m^2
11.6	17.1 a	1.5 a	9.6 a	103 a	1194 a
17.4	22.8 b	1.3 a	9.3 a	88 b	1526 b

Table 7. Influence of plant density on number, diameter and cross sectional area (CSA) of basal shoots when only one basal shoot per plant was allowed. Experiment 2.

Plant density (no./m^2)	Basal shoots: Number (no./m^2)	Diameter (mm)	CSA (mm^2) per plant	per m^2
11.6	11.6	10.9 b	93 b	1081 a
17.4	17.4	9.7 a	74 ab	1292 ab
23.2	23.2	9.2 a	67 a	1549 b

square meter were also enhanced but a statistically significant interaction between plant type and density occurred. Harvest time, weight, length and diameter were not influenced by removing the outgrowing lateral buds (Table 8).

Delayed bending of the primary shoot (treatment D vs B) slightly enlarged the diameter and CSA of basal shoots although the differences were not significant (Table 8). Number of basal shoots was not influenced when bending was delayed. Length and fresh weight of harvested shoots were slightly less due to the height of pruning.

Restricting the outgrowth of basal buds to 1 (treatment C vs D), clearly increased the weight and diameter of basal shoots (Table 8). Shoot length and development time were not influenced. For treatments C and D, development time was delayed by 7 days as compared with treatment A en B. However, since bending occurred 18 days later for those plants, development time for basal-shoot formation was actually shortened by more than 10 days.

Higher plant densities tended to delay harvest time and to decrease fresh weight and diameter of basal shoots although the differences were not significant. On the whole, the number of basal shoots per plant decreased slightly but it increased significantly when expressed on a square meter basis except for the control treatment. CSA of basal shoots per square meter was significantly increased with density. Treatments affecting plant development combined with plant densities resulted in a wide range of plant performances concerning the basal-shoot development (data not shown). For example, the CSA of basal shoots per square meter ranged from 538 to 1410 mm^{2}m^{-2}.

Discussion

In many crops, axillary buds along the shoot grow out after bending the primary shoot (Cline, 1991), including roses (Zieslin and Halevy, 1978). In young rose plants, especially bud break of the most basal axillary buds of the primary shoot is favourable because shoots from these buds determine the potential flower production of the plant (Marcelis-van Acker, 1993). Delayed bending of the primary shoot generally promoted development rate, diameter

Table 8: Influence of plant type (control (A), removal of lateral growth (B), restricting the outgrowth of basal buds (C) or delaying the time of horizontal placement of the primary shoot (D)) and plant density (7.7, 11.6 or 17.4 plants per m²) on development time, fresh weight, length, diameter and cross-sectional area (CSA) of basal shoots as compared to the control treatment (A) in which the primary shoot was bent horizontally when the outgrowing laterals had reached a length of 15 cm. No statistical interaction occurred between treatments and density occurred for the given parameters except for number of basal shoots per plant. Experiment 3.

Treatment	Basal shoots: Harvest time^z (days)	Fresh weight (g)	Length (cm)	Diameter (mm)	CSA (mm²m⁻²)
A	83.6 a	54.3 a	85.0 a	7.6 a	586.7 a
B	84.7 a	57.3 a	84.3 a	7.7 a	979.5 b
C	90.6 b	71.5 b	77.1 a	9.7 b	915.4 b
D	90.9 b	50.4 a	75.0 a	8.1 a	1188.4 b
Plant density					
7.7	85.8 a	62.5 a	80.6 a	8.5 a	741 a
11.6	86.4 a	59.1 a	80.9 a	8.4 a	931 ab
17.4	90.0 a	53.4 a	79.6 a	8.0 a	1080 b

^{z}Time from planting until harvesting the flowering stems.

and weight of basal shoots as well as CSA which may be explained by the increase in fresh and dry weight and LAI of the primary shoot. The higher LAI resulted in a higher assimilate supply during outgrowth of the basal buds which affects shoot growth to a major extent (Marcelis-Van Acker, 1994a). Moreover, before release from bud inhibition, the increase of bud age results in an increase in number of pith cells in the subsequent shoot, indicating a greater potential diameter of the shoot (Marcelis-Van Acker, 1994b). Apart from the increased assimilate supply, a different hormone balance may influence the basal bud break as expressed by the view that nutrients and auxins mediate the influence of gravity on apical dominance (Cline, 1991). Combining these and other unpublished results it may be concluded that delayed bending generally promotes the vigour of new basal shoots as reflected in the CSA which can be due to an increase in number or diameter of developing shoots.

The increased light interception during the period of basal-shoot formation is reflected in the LAI range from time of bending until harvesting the basal shoots. As a consequence plant growth rate is increased. This is in agreement with general relations between LAI, light interception and growth (Gijzen, 1992). Plant weight as well as the development of basal shoots did not increase proportionally with time of bending because a maximum was reached in LAI, plant growth rate (Table 5) and CSA of basal shoots (Figure 1B) when bending occurred 28 days from T_0. An explanation may be that in case of a highly developed primary shoot (LAI of at least 3-3.5) in combination with a light extinction coefficient of approximately 0.7, as has been found for young rose plants (De Koning, personal communication), the light interception by the canopy already exceeded 90% (Goudriaan, 1982). A further delay in bending only resulted in leaf senescence and higher plant respiration. It may be concluded that after a certain development of the primary shoot further delay of bending is not efficient.

As time of bending the primary shoot determines its capacity as assimilate source, competition for assimilates mainly occurs through the number of outgrowing basal or lateral buds. The growth of vigorous lateral shoots strongly competes with the outgrowth of basal shoots. These lateral shoots often emerge near to the bend as has been observed by Zieslin and Halevy (1978). Removal of outgrowing axillary buds strongly favoured the outgrowth of basal buds and increased the CSA of basal shoots per plant (Figure 2). Zieslin *et al.* (1976b) and Zieslin and Mor (1981a) found that removal of outgrowing lateral buds on flower stems enhanced bottom-break formation in one and six year old rose plants. Also the removal of the axillary buds of cotton had no effect on the weight of the shoot system but altered the allocation towards alternative sinks (Nagarajah, 1975).

Furthermore, competition occurred between the outgrowing basal buds. It was shown before, that in case of an undisturbed situation, the initial diameter of basal shoots was not influenced by their number (Kool *et al.*, 1991). In that case, the variability in plant development (e.g. plant weight, leaf area) of young rose-plants probably caused differences in the number of outgrowing basal shoots while individual basal-shoot CSA was almost the same. In the case of a more uniform development of the primary shoot at the moment of bending, restriction of outgrowing basal buds strongly increase the diameter and weight of the remaining ones (Table 8). To get more than one bottom break per plant with an acceptable quality (diameter, fresh weight), the ample availability of assimilates is essential. Only delayed bending, i.e. a better developed primary shoot, resulting in an increased light interception, meets that demand.

When bending was delayed the share of assimilates spent in basal-shoot formation grew mainly at the cost of laterals, indicating a preference for the outgrowth of basal- instead of lateral shoots. Taking into account that development time from bud break until harvest amounted to 46 days (data not presented) even a spontaneous outgrowth of basal shoots before bending occurred (Table 3). The preference for the outgrowth of basal buds at a later stage of plant development was also found in rose-seedlings (De Vries *et al.*, 1986). Basal buds are already present as secondary buds in the axils of the scales of the axillary bud present on the cutting when used for propagation (Marcelis-van Acker, 1993) and are therefore older as compared to axillary buds positioned higher on the primary shoot. These basal buds continue growth, i.e. the number of leaf primordia and the number of cells in the transverse section of the pith increases with bud age, both reflecting the growth potential of the future shoot (Marcelis- van Acker, 1994b).

In general, increasing plant density result in a decrease in the individual weight and diameter of harvested rose flowers (Rupprecht, 1963; Obiol and Cardus, 1972; Steinbuch, 1985). However in the present study, small differences in plant density did not influence the formation and early development of basal shoots per plant (Tables 6 and 7). The competition for light is probably low at this early stage of plant development due to the relative low number of developing shoots. Increasing plant density, especially when combined with a controlled outgrowth of only one basal shoot per plant resulted in a gradual decrease in the diameter of basal shoots (Tables 7). An explanation may be, that in addition to an increased competition for light during the development of basal shoots, competition for light already inhibited the development of the primary shoot and as a consequence, reduced the amount of assimilates available for bud outgrowth after bending.

The observed increase in growth per square meter with plant density, as reflected in the CSA and fresh weight of basal shoots is obviously due to an increased LAI. LAI is the most important growth component for canopy photosynthesis because of its close relationship to light interception (Williams *et al.*, 1965; Shibbles and Weber, 1966; Stützel and Aufhammer, 1991). The most appropriate way to increase LAI is by increasing plant population as has been demonstrated for many different crops (Buttery, 1969; Nederhof, 1984; Papadopoulos and Ormrod, 1991). This also holds for young rose plants in our study where an increase in growth per square meter with higher plant density was accompanied by a decrease in individual plant development as reflected in the cross sectional area of basal shoots per plant. Reduced individual plant development at increasing plant density has been demonstrated for seedling roses (De Vries and Dubois, 1988), greenhouse rose crops (Pessala, 1977) and other horticultural crops such as beans (Crothers and Westermann, 1976) and tomatoes (Zahara and Timm, 1973) and have been associated with significant reductions in photosynthetic productivity per plant (Papadopoulos and Ormrod, 1988).

Table 9. Relations between some plant related factors and the formation of basal shoots in young rose plants: - - = strongly negative, - = slightly negative, ± = no clear effect, + = slightly positive, + + = strongly positive.

Factor	Number per plant	Diameter (mm)	CSA (mm^2): per plant	per m^2
Plant size at bending time	+	+ +	+ +	+ +
Competitive growth lateral shoots	-	-	- -	- -
Plant density	-	-	-	+
Restricting the number of outgrowing basal buds	- -	+ +	±	±

Based on these and unpublished results a general concept on ways to improve plant development of young rose plants with respect to the formation of basal shoots is summarized in Table 9. For example, delayed bending time of the primary shoot, in combination with removal of competitive lateral growth, low plant density and without restriction of the number of outgrowing basal buds gives a very massive plant development characterized by a high number and a large cross sectional area of basal shoots per plant. The relationships of Table 9 were successfully validated for rose varieties as *Rosa hybrida* 'Frisco' and *Rosa hybrida* 'Madelon-Ruimeva' growing under commercial conditions. The advantage of having a better management program to grow young rose plants can be at least twofold. Firstly, it creates the possibility to examine the relations between plant architecture and flower production which has been studied extensively in fruit culture (Clayton-Greene, 1993). Secondly, it opens the possibility to reduce plant variability which is a serious problem in rose research. Application of the present results in practical rose growing needs economical evaluation of this type of plant management. In that evaluation specific growing habits of cultivars with a typical plant performance should be taken into account. Finally, also the choice of a rootstock can be useful to manage the process of plant building as found before (Kool and Van de Pol, 1992).

2.2 Controlling the plant development of *R. hybrida* 'Motrea'

Kool, M.T.N. and Van de Pol, P.A., 1992. Controlling the plant development of R. *hybrida 'Motrea'. Scientia Horticulturae 53, 239-248.*

Abstract

Influencing the development of rose plants after planting has mainly been focused on manipulation of the bottom-break formation. In this experiment, the plant development of *R. hybrida* 'Motrea' could be improved by certain plant treatments considering the diameter of the harvested shoots. Early plant development was highly affected by managing the pruning height of bottom breaks and subsequent flowering cycles and by controlling the number of outgrowing laterals on the remaining stem after harvesting. As a result of the treatments applied, an increase in the stem diameter of second order flowers and a decrease in the percentage of blind shoots, from 19 to 4, could be achieved. Moreover, plant quality, defined as the sum of surface areas (mm^2) of the transverse section of the laterals at a height of 60 cm above soil level, nine months after planting, was improved by more than 50%. Bush management of distribution of assimilates over an optimal number of developing shoots is discussed. The close relation between the initial quality (diameter) of bottom breaks and plant quality nine months after planting together with the observed differences in plant development between "smaller" and "bigger" plants, stressed the importance of uniform plant material and an optimal control on the process of bottom-break formation.

Introduction

Although the results of much research on flower production in full-grown rose plants has been published, little information is available about factors influencing plant development from planting to full productivity (Zieslin *et al.*, 1976b). The rose plant is built up from the so called 'bottom breaks': vigorous structural shoots from the basal parts of rose plants (Zieslin and Mor, 1981b) and their laterals. Influencing plant canopy through manipulation of bottom-break formation has mainly been done by exposing the plants to favourable environmental conditions (Hanan, 1979; Khayat an Zieslin, 1982; Zieslin and Mor, 1981b), by special plant treatments as pinching or lateral bud removal (Zieslin *et al.*, 1976b; Zieslin and Mor, 1981a) or by application of hormones (Carpenter, 1975; Ohkawa, 1979). The importance of the number of bottom breaks and laterals for flower production was shown by Zieslin *et al.* (1976b), Van Rijssel (1982) and De Vries and Dubois (1983). In addition to number of bottom breaks and laterals, Van Rijssel (1982) also demonstrated the importance of the diameter of bottom breaks and laterals with respect to flower production. It is clear

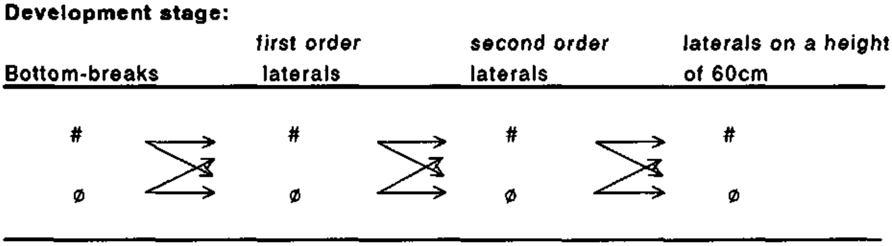


Figure 1. Interactions between the number (#) and diameter (ϕ) of flowering shoots of subsequent flowering cycles during the early plant development.

that with respect to the early plant development, both number and diameter of shoots can influence the number and diameter of shoots in the next flowering cycle (Figure 1). It is expected, that an increase in the number of flowering shoots will decrease the shoot diameter of flowers from the next cycle. Furthermore, the diameter of shoots will be positively related to both the number and diameter of outgrowing shoots from the next flowering cycle. In order to emphasize this general relations and to follow their effect in time, pruning treatments which increased the outgrowth of laterals from thick shoots and decreased the outgrowth of laterals from thin shoots after harvesting have been applied in this experiment.

In a previous paper, the number and diameter of branches at a height of 60 cm was highlighted, because this height is approximately the lowest level of pruning back in winter casu quo spring period (Kool and Van de Pol, 1992). In the present experiment an attempt was made to improve the plant development or the number and diameter of branches on a height of 60 cm, by various degrees of pruning depending on the initial diameter of bottom breaks and laterals.

Material and methods

Plant material

At the end of December, 1988, plants of *Rosa hybrida* 'Motrea' were root-grafted (Van de Pol, 1986) on *Rosa multiflora* Cathayensis 'Multic' and in the middle of February, 1989, planted in rockwool slabs, on an East-West orientated bed in a commercial greenhouse . Plant density in the 4-row bed was 12 plants/m^2. Day/night temperature set points of the glasshouse were 23^{0}C/19^{0}C. Supplementary lighting with high pressure sodium (HPS) lamps (8 Wm^{-2}) was used when global radiation inside the greenhouse decreased below 20 Wm^{-2};

day length was 20 h. In the beginning of April, 1989, at the start of the experiment, 120 plants, each having 2 bottom breaks in peabud flowering stage (85% of all plants in the bed), were selected and divided into 6 blocks of 20 plants each. In each block, 4 treatments were applied on randomized blocks of 5 plants. Plants which formed a third bottom break during the observed period were left out of the experiment.

Plant treatments

Treatments were applied in order to influence both number and diameter of developing shoots due to harvesting according to the diameter of the flowering shoots. Based on data from previous studies, a distinction was made between the diameters of "thin" (<4.0 mm), "normal" (between 4.0 and 4.8 mm) and "thick" (>4.8 mm) bottom breaks and laterals in order to get an approximately equal division of the number of bottom breaks in each diameter class. The following treatments were applied on plants with 2 bottom breaks in the same development stage of flowering.

- *Treatment 1 Control*: At the start of the experiment the bottom breaks were pruned back, leaving 4 five-leaflet leaves on the plant. At approximately 30 and 60 days after pruning the bottom breaks, flowering shoots of the first and second order laterals, respectively, were harvested leaving 2 five-leaflet leaves on the base of the shoot (Figure 2).
- *Treatment 2 Height*: At the start of the experiment the bottom breaks were pruned back depending on their diameter leaving 2 (thin shoots), 4 (normal shoots) or 6 (thick shoots) five leaflet-leaves on the base of the shoot. Flowers were harvested leaving 1 (thin shoots), 2 (normal shoots) or 3 (thick shoots) five leaflet leaves on the base of the shoot.
- *Treatment 3 Number:* At the start of the experiment the bottom breaks were pruned back leaving 4 five-leaflet leaves on the base of the shoot. At harvestable stage of first and second order laterals, flowers were harvested leaving 2 five-leaflet leaves. Each time after pruning the bottom breaks and harvesting the first and second order branches, the outgrowth of laterals was restricted depending on the diameter of the mothercane to 1 (thin shoots), 2 (normal shoots) and 3 (thick shoots). The surplus of shoots were broken away just after bud break.
- *Treatment 4 Height/Number*: Combination of treatments 2 and 3. Pruning back of bottom breaks, harvesting of laterals and restriction of the outgrowth of shoots after harvesting occurred depending on their initial diameter.

After treatments were carried out until the time that the underhook cutting procedure (Zieslin, 1981) started at the end of September (flowering shoots were harvested and pruned on second- or third order laterals in order to remove plant height), subsequent flowering shoots were harvested for all treatments on the first 5-leaflet leaf counted from below.

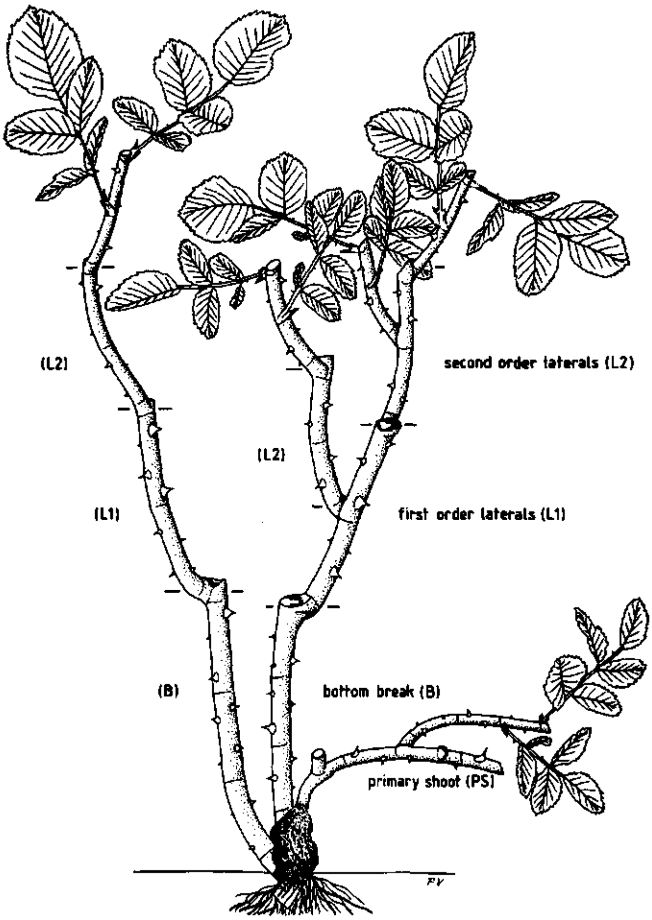


Figure 2. Plant building and development of a rose-bush, originating from the primary bud after cutting, stenting or bud-grafting. In this case, unlike treatments applied in this experiment, bottom breaks have been pruned leaving 3 5-leaflet leaves while laterals have been harvested leaving 2 5-leaflet leaves counted from the base of the shoot.

Plant measurements

At pruning the bottom breaks and harvesting the laterals of the first and second order, the diameter of bottom breaks and laterals was measured 2-3 cm above the base of the stem. Instead of using both the number and diameter of stems for certain calculations, a single parameter 'quality' has been defined as the sum of surface areas (mm^2) for all stems per plant on a certain height (Kool and Van de Pol, 1992). Plant quality is defined as the summed surface area of all laterals on a height of 60 cm above soil level, measured 9 months after planting. Stems exceeding 4.5 mm in diameter on a height of 60 cm above soil level were defined as structural laterals.

Results were statistically analyzed by Analysis of Variance followed by mean separation using Tukey's HSD-test (Table 2, 3 and 4). After classification of bottom breaks or plants according to their diameter (Table 1 and 5) results have been analyzed by mean separation using student's *t*-test.

Results

At the start of the experiment the mean bottom-break diameter for the various treatments was 4.3 or 4.4mm (not presented); the percentage of thin, normal and thick bottom breaks was 25, 55 and 20%, respectively. The various pruning treatments resulted in differences in the number of first-order laterals per bottom break (Table 1). In general the number of laterals clearly increased with bottom-break diameter (control treatment). Plant height pruning treatments (2 and 4) reduced lateral outgrowth especially in the "thin" bottom-break class. Initial diameter of laterals was not significantly affected. The observed differences between treatments were most pronounced for bottom breaks less than 4 mm (Table 1).

Following plant development, treatments 3 and 4 decreased branching of the bottom breaks up to 31% compared to the control (Table 2). Initial diameter of laterals was not significantly affected. After harvesting the flowers of the first order, differences in number and diameter of second order laterals occurred (Table 2). Treatment 3 and 4 decreased the number of laterals per plant and all treatments resulted in a significant increase of stem diameter compared to the control. Apart from treatment 3, the number of harvested flowers of the

Table 1. Development of first-order laterals after cutting the bottom breaks (B). Number and initial diameter of laterals per bottom break are shown according to their bottom-break diameter classes. Values for number or diameter of laterals separately, followed by different letters differ significantly ($P < 0.05$).

Diameter classes B	<4.0	4.0-4.8	>4.8	<4.0	4.0-4.8	>4.8
Treatment	Number first-order laterals			Diameter (mm) of first-order laterals		
Control	2.6 c	2.5 c	3.9 d	4.2 a	4.6 a	4.6 a
Height	1.3 ab	2.1 bc	3.3 d	4.4 a	4.5 a	4.9 a
Number	1.0 a	1.9 bc	2.6 bc	4.7 a	4.6 a	4.7 a
Height/Number	1.0 a	2.0 bc	2.7 bc	4.7 a	4.6 a	4.7 a

Table 2. Development of number and diameter of first- and second-order laterals per plant until harvesting the 2nd order laterals, approximately 60 days after cutting the bottom breaks. Values within a column followed by different letters differ significantly ($P < 0.05$).

Treatment	First-order laterals:		Second-order laterals:			
	Number (no./plant)	Diameter (mm)	Number (no./plant)	Diameter (mm)	Number of flowers (no./plant)	Blindness (%)
Control	5.4 a	4.5 a	9.2 a	3.9 a	7.5 a	19
Height	4.6 ab	4.5 a	8.8 ab	4.3 b	7.5 a	15
Number	3.7 c	4.7 a	6.7 b	4.3 b	6.1 b	9
Height/Number	3.9 bc	4.7 a	7.4 b	4.3 b	7.1 a	4

second order was unaffected due to differences in the percentage of blind flowers (Table 2).

Nine months after planting, no significant differences in the diameter of bottom breaks between treatments could be observed (Table 3). The diameter of first order laterals had markedly increased in all cases, the least in the control treatment (Table 2 and 3). The number of laterals on a height of 60 cm was higher increased for all treatments compared to the control while the mean diameter of laterals on a height of 60 cm was not significantly affected by treatment (Table 3). This resulted in a marked increase up to 37% in the number of structural laterals per m^2 compared to the control (Table 4). Plant quality for treatments 2, 3 and 4 was 44, 27 and 56% higher respectively, than for the control (Table 3).

By classifying plants according to bottom-break diameter at the moment of pruning irrespective of treatment, it is clearly shown that plant quality after nine months is positively

Table 3. Diameter of bottom breaks, number and diameter of first-order laterals and number, diameter and quality of laterals at a height of 60 cm, 9 months after planting. Values within a column followed by different letters differ significantly ($P < 0.05$).

Treatment	Basal-shoot	First-order laterals:		Laterals at 60 cm height:		
	Diameter (mm)	Number (no./plant)	Diameter (mm)	Number (no./plant)	Diameter (mm)	Quality (mm^2)
Control	8.5 a	5.5 a	5.7 a	5.7 a	4.4 a	94 a
Height	8.7 a	4.6 b	6.3 b	7.4 ab	4.5 a	135 b
Number	8.6 a	3.8 c	6.4 b	6.7 ab	4.5 a	119 ab
Height/Number	8.7 a	3.8 c	6.5 b	7.5 b	4.7 a	147 b

Table 4. Division of number of laterals on a height of 60 cm, 9 months after planting, according to diameter classes are shown together with number of structural laterals (>4.5 mm). Values within a column followed by different letters differ significantly at the 5% level.

Treatment	Diameter classes (mm):				Number of laterals >4.5mm:	
	<3.5	3.5-4.5	4.5-5.5	>5.5	(no./plant)	(no./m²)
Control	1.4	1.5	1.6	1.1	2.7 a	32.4 a
Height	1.3	2.4	1.9	1.8	3.7 b	44.4 b
Number	1.4	1.6	1.6	1.4	3.0 ab	36.0 ab
Height/Number	1.2	2.3	1.7	2	3.7 b	44.4 b

related with the quality (diameter) of bottom breaks for each plant at the moment of pruning (Table 5). The relative values (%) for initial bottom-break quality and final plant quality in the various classes ranged from 100-199 and 100-255, respectively. It is clear that plants in class 1 to 3 were more restricted in further development than were plants in classes 4 to 6.

Discussion and Conclusion

Plant development was highly affected by the number of outgrowing laterals dependent on the diameter of bottom breaks and laterals. The number of outgrowing laterals is positively affected by the number of 5-leaflet leaves, left behind on the mother-cane after harvesting the flowers (Table 1), as has been found before (Zieslin, 1981). Thick mothercanes also favour the formation of laterals as found in this experiment (Table 1; control). The diameter of laterals was slightly increased for treatments 3 and 4 compared to the control although no significant differences were found. Treatments 3 and 4 led to a lower number of first and second order laterals (Table 2) as could be expected. However, differences in the number of harvestable flowers of the second order were very small, due to a decreasing percentage of blind flowers. This can be explained by the lower number of second order laterals with less competition or by regulation of the position of buds which were allowed to sprout. The latter aspect is involved because the uppermost bud is less vulnerable to blindness than the second or third bud counted from the top of the shoot after harvesting the flowers (Van den Berg, 1987 and Mor and Halevy, 1984). Especially the growth and flowering potential of the third shoot from the top remain behind by the uppermost and second shoot (Mor *et al.*, 1981).

Table 5. Quality of bottom breaks at the moment of cutting back and the plant quality 9 months after planting with classification of plants according to initial bottom-break diameter. Values within a column followed by different letters differ significantly ($P < 0.05$).

Class	Number of plants	Diameter classes of bottom breaks (mm)	Quality bottom breaks (mm^2)	Quality laterals at 60 cm. (mm^2)
1	7	both <4.0	21.9 a (100)	71.5 a (100)
2	32	one <4.0 and one 4.0-4.8	26.0 a (119)	104.5 ab (146)
3	7	both 4.0-4.8	29.9 b (137)	98.7 ab (138)
4	31	one <4.0 and one >4.8	32.1 bc (147)	157.5 bc (220)
5	5	one 4.0-4.8 and one >4.8	35.3 c (161)	164.9 bc (231)
6	24	both >4.8	43.5 d (199)	182.4 c (255)

Differences in plant development between treatments became more pronounced after harvesting the second order laterals. A striking difference occurred between treatments in the number of second order laterals and laterals at a height of 60 cm above soil level, nine months after planting. For treatments 2 and especially 1, the number of laterals at a height of 60 cm nine months after planting was remarkedly smaller than the number of second order laterals. This discrepancy can be explained by both the observed higher number of blind shoots which were not further harvested in this experiment and a slightly reduced diameter of second order laterals. Shoots emerging from lateral buds on thin mothercanes are much more sensitive to 'blindness' than shoots emerging from thick mothercanes (Van den Berg, 1987). Too many laterals (control treatment) result in high production of low quality flowers (Van den Berg, 1984) and an increase in the number of blind shoots due to the competition for the limited available photosynthates (Mor and Halevy, 1984). Bush management should be directed on distribution of assimilates over an optimal number of developing branches (Zieslin *et al.*, 1973). A practical implication can be that "a grower has to sacrifice the flower count to assure future plant development" as suggested by Zieslin *et al.* (1976). However, the optimal number of (structural) laterals has yet to be examined. Van Rijssel (1982) stated that at least 40-45 structural laterals/m^2 are necessary for good flower production in a range of years. Treatment 2 and 4 satisfied this requirement. Thus, the height of harvesting the flowers on the mothercane and regulation of the number of outgrowing laterals based on the diameter of mothercanes also determines the number and diameter of (structural) laterals, in addition to the effect of rootstocks as described in a previous paper (Kool and Van de Pol, 1992).

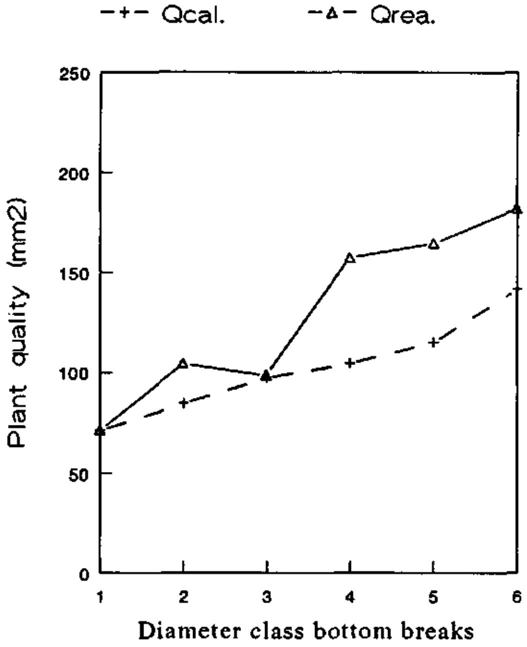


Figure 3. Plant quality as has been realized (Qrea) for the different diameter classes and has been calculated (Qcal) for all classes on the basis of an increase factor of 3.26, between quality of bottom breaks and plant quality as has been found for Class 1 (see Table 5).

A positive correlation between plant quality after nine months of growth and the initial quality of bottom breaks (Table 5) could also be shown with linear regression analysis (data not presented) as has been shown in a previous paper (Kool and Van de Pol, 1992). 'Smaller' plants, according to the initial diameter of bottom breaks, had a less vigorous plant development than 'bigger' plants as shown in Table 5. This can be expressed more clearly when calculating plant quality for all classes on a basis of an increase factor of 3.26 from initial bottom-break quality as has been found for class 1 (Table 5, 71.5/21.9).

It can be concluded that in addition to the number and time of appearance of bottom breaks (Kool *et al.*, 1991) differences in the initial diameter of bottom breaks also form a source of variation for final plant quality. Plant uniformity may be increased during the period of propagation by managing the process of bottom-break formation.

3. Effect of plant architecture on flower production

3.1 Importance of plant architecture and plant density for rose crop production

Kool, M.T.N., 1996. Importance of plant architecture and plant density for rose crop production.

Abstract

In this study, the relationships between plant architecture and flower production of rose were studied for a cropping period of 2.5 year. Four different types of plants, varying in number of basal shoots and their architecture were created, which were combined with 3 plant densities (7.7, 11.6 and 17.4 plants/m²). Plant architecture was mainly managed by manipulation of the basal-shoot formation in combination with height of pruning and de-shooting practices. The investment in stem mass significantly reduced the number and weight of flowers for the first 8 months. This was due to a delay in time of basal-shoot growth, restriction of number of outgrowing basal shoots and disbudding of shoots. However, this initial financial loss of about DFl 20,-/m² amply paid itself in the next 2 cropping years. Regression analyses showed that number and diameter of second-order laterals 8 months after planting, could explain more than 70% of the variation in number and weight of flowers harvested in more than 2 cropping years. Flower production was much less related to number and diameter of basal shoots than to number and diameter of second-order laterals. The importance of the diameter and cross sectional area of shoots of different heights with respect to assimilate storage and transport capacity is discussed in relation to flower production. Increasing plant density led to an higher biomass- and flower production per m² but to a reduced individual plant weight. Furthermore, weight and firmness of harvested flowers was reduced. The harvest index was neither affected by the applied treatments nor by plant density.

Introduction

The importance of basal shoots with respect to a vigorous and highly productive rose-crop over a longer life-span has been stressed since long (Kofranek and Fischer, 1949; Zieslin *et al.*, 1976b; Van Rijssel, 1982; De Vries, 1993). Therefore, various cultural practices have been tested to promote basal-shoot formation in established rose bushes (De Vries, 1993).

It is surprising, that apart from controlling the number of basal shoots little attention has been paid to the relation between plant architecture and flower production. In other horticultural crops the significance of plant architecture and plant management on growth and productivity have been recognized since long, e.g. in apple (Jackson, 1989; Clayton-Greene, 1993). In roses, Fuchs (1994) stressed the importance of the cross sectional area of the first-order laterals of basal shoots for flower production. For young rose plants, the height of harvesting the flowers on the parent shoot and adjusting the number of outgrowing laterals to the diameter of the parent shoots, determined the number and diameter of laterals (Chapter 2.2). Positive relationships between the cross sectional area (CSA) of laterals at a height of 60 cm and the initial number and diameter of basal shoots (Chapter 2.2) and between the CSA values of stem parts at different heights in the canopy (Kool and Van de Pol, 1992) were found. De Vries and Dubois (1983) reported a significant correlation between the girth of the root system and the number of basal shoots. Furthermore, the same authors emphasized the significance of number of basal shoots for the number of harvested shoots in the first cropping year (De Vries and Dubois, 1984).

In general, higher plant density lead to an increase in leaf area index (LAI) and dry weight production per square meter as was demonstrated for many crops such as tomato (Papadopoulos and Ormrod, 1991), faba bean (Stützel and Aufhammer, 1991) and rose (De Vries and Dubois, 1988). However, the development of individual plants will be limited owing to decreasing individual plant exposure to light as found by Crothers and Westerman (1976) and Papadopoulos and Ormrod (1991). For roses for 4 years of culture, higher plant mortality and a decreased individual plant weight, combined with less structural branches and a slightly smaller branch diameter were found at high as compared with low plant density (Pessala, 1977). In other experiments with rose it was also shown that increasing plant density increased productivity but decreased weight of harvestable stems (Rupprecht, 1963; Obiol and Cardus, 1972; Steinbuch, 1985).

Only recently a general concept on the management of plant architecture of young rose plants, with respect to basal-shoot formation was developed (Chapter 2.1). Combination of new management tools concerning basal-shoot formation as described in Chapter 2.1 with already known measures to control plant development (Zieslin *et al.*, 1976b; Chapter 2.2) should result in more uniform plants of a defined shape. A further combination of these plant management practices with plant density will create a wide range of plant performances with respect to plant architecture.

In the present study, the relation between plant architecture and flower production has been evaluated for a cropping period of 2.5 year. By applying a few plant management tools 4 different types of plants were created with respect to their architectural structure. The factor plant density (3 levels) was also involved. The economic importance of plant architecture and plant density will be involved in the discussion.

Material and methods

Plant material

In the beginning of January 1993, 1500 single node cuttings of *Rosa hybrida* Madelon 'Ruimeva' were dipped into talcum powder with 0.4% IBA and pricked into rockwool blocks (9x9x9 cm) for rooting. Soil and air temperature were kept at set points of 24°C and relative air humidity was kept close to 100%. Supplementary lighting was given by high pressure sodium lamps (SON-T plus 70 Watt, 38.8 μmolm^{-2}s^{-1}) for 16 hday^{-1}. After rooting, plants were hardened off for some days and in the middle of February placed on rockwool slabs in a 12 m x 12 m greenhouse compartment of the Department of Horticulture (Wageningen, The Netherlands, 52°N). Rockwool slabs (133x15x9 cm) were placed transversally on movable benches with discharge of drain water at one side of the bed. Plants were drip-irrigated 4 to 20 times a day depending on incoming radiation. Day/night temperatures were set on 19°C/17°C. For 6 weeks, supplementary lighting using high pressure sodium lamps (SON-T; 400 Watt; 36.5 μmolm^{-2}s^{-1}) was given for 20 hday^{-1}.

Plant treatments

- *Treatment A (Control):* The flower bud of the developing primary shoot was removed in the pea-bud stage. When the growing laterals had reached a length of 15 cm, the primary shoot was bent horizontally in order to stimulate sprouting of basal and lateral buds. Basal and lateral shoots were harvested just above the second 5-leaflet leaf counted from the base. Subsequent flowering laterals were harvested at the first 5-leaflet leaf. During winter, the underhook cutting procedure, as described by Zieslin (1981), was applied in order to reduce plant height.
- *Treatment B:* Plants were initially treated the same as the control plants. Excluding the basal shoots, all lateral growth within 30 cm from the base of the primary stem was continually removed. The harvesting procedure was similar to treatment A.
- *Treatment C:* The primary shoot was bent down 18 days later than in the control plants. Only 1 basal bud was allowed to grow which was harvested just above the fourth 5-leaflet leaf counted from the base. Only 2 uppermost lateral shoots were allowed to grow which were harvested on the second 5-leaflet leaf. The further harvesting procedure was the same as in treatment A.
- *Treatment D:* The primary shoot was bent down as in treatment C. Only basal shoots were allowed to grow; they were harvested just above the fourth 5-leaflet leaf counted from the base. Starting at the harvestable stage of the laterals on the basal shoots, half of the number of these lateral shoots were de-shooted (Zieslin and Mor, 1981a) for 3 weeks in order to stimulate the diameter increase of the basal shoot as well as sprouting and early development

of the shoots originating from the other half of the laterals that were harvested normally. The further harvesting procedure was similar to treatment A.

The above 4 plant treatments were combined with plant densities of 7.7, 11.6 and 17.4 plants/m^2 greenhouse area, as described in detail in Chapter 2.1.

The lay-out of the experiment was a randomized block design with 3 blocks positioned according to the north-south orientation of the beds. Each treatment was applied on 8-14 plants (2 rockwool slabs) surrounded by 1 border slab on each side.

Plant measurements

Time of harvest, diameter (Mitutoyo Digimatic), length and fresh weight of basal shoots were recorded. At least twice a week from May 1993 to July 1995 number and fresh weight of flowering shoots in subsequent cycles and of discarded prunings (blind shoots and pruning rests) were determined. The economical value of the flowers was calculated by using monthly average prices per class of flower length for cv Madelon as subtracted from the auction organisation. At 3 times (23 October 1993; 14 November 1994 and 10 July 1995) number and diameter of basal shoots and of first- and second-order laterals were measured. From these data, the stem cross sectional area (CSA) for different heights in the plant was calculated. At the end of the experiment (10 July 1995) plants were harvested destructively and number and weight (fresh and dry) of flowering shoots, blind shoots, leaves (weight only) and stems of fourth order laterals and higher, of third-, second-, and first-order laterals, of basal shoots and of the root collar were determined separately. The harvest index, defined as the fresh weight of harvested flowers divided by the total fresh weight production, and the firmness of the flowers, defined as the fresh weight divided by the shoot length, were calculated. Results were analyzed using the statistical SYSTAT package. Mean separation was done by Tukey-HSD test.

Results

Plant architecture 8 months after planting (October 1993) was greatly affected by both plant treatment and plant density (Table 1). Plant type B formed fewer but thicker stems than the control. In plant type C (1 basal shoot per plant) stem diameter was much greater than in the other treatments; CSA of the basal shoots was smaller than in the control but that of first- and second order laterals was much larger. System D gave a higher diameter and CSA of basal shoots than the control but their number was lower. Number, diameter and CSA of first- and second-order laterals exceeded those for the control. In all plant types number and CSA of all stems increased and the diameter declined with increasing plant density.

In november 1994, almost the same differences in plant architecture occurred between plant treatments and plant densities as found a year ago (data not shown). The increase in

Table 1: Effect of plant type and plant density on number, diameter and CSA of basal shoots, first- and second-order laterals as measured on 23 October, 1993. Different letters per column, for plant type and plant density separately, indicate significant differences ($P < 0.05$). No statistical significant interaction between plant type and plant density occurred.

Plant type	Plant density (no./m²)	Basal shoots: Number (no./m²)	Diameter (mm)	CSA (mm²/m²)	First-order laterals: Number (no./m²)	Diameter (mm)	CSA (mm²/m²)	Second-order laterals: Number (no./m²)	Diameter (mm)	CSA (mm²/m²)
A		34.1 a	8.3 a	1868 b	36.0 b	7.5 a	1585 a	45.0 a	6.5 a	1472 a
B		26.9 b	9.4 b	1831 b	31.6 c	8.3 b	1675 a	38.6 b	7.1 b	1540 ab
C		12.2 c	12.3 d	1394 a	24.4 d	10.1 c	1900 b	34.6 b	8.1 c	1729 bc
D		27.1 b	9.9 c	2077 c	43.9 a	8.5 b	2460 c	48.2 a	6.9 ab	1805 c
	7.7	19.1 a	10.4 a	1481 a	25.4 a	9.1 a	1618 a	32.7 a	7.5 a	1433 a
	11.6	25.0 b	10.0 b	1829 b	33.2 b	8.6 b	1906 b	41.9 b	7.1 b	1652 b
	17.4	31.1 c	9.4 c	2067 c	43.3 c	8.1 c	2191 c	50.2 c	6.8 c	1825 c

Table 2. Effect of plant type and plant density on number and fresh weight of basal shoots, first-and second-order laterals at the final destructive harvest (10 July, 1995). Different letters per column, for plant type and plant density separately, indicate significant differences ($P < 0.05$).

Plant type type	Plant density (no./m²)	Basal shoots:		First-order laterals:		Second-order laterals:	
		Number (no./m²)	Weight (g/m²)	Number (no./m²)	Weight (g/m²)	Number (no./m²)	Weight (g/m²)
A		27.2 c	299 a	32.0 c	251 a	42.1 bc	221 a
B		22.7 b	285 a	28.2 b	292 a	36.0 ab	252 a
C		12.3 a	395 b	23.7 a	391 b	35.7 a	251 a
D		25.0 bc	477 c	37.5 d	398 b	44.6 c	263 a
	7.7	16.6 a	310 a	23.0 a	287 a	30.0 a	211 a
	11.6	21.4 b	351 b	30.6 b	340 b	40.4 b	245 ab
	17.4	27.4 c	431 c	37.4 c	372 b	48.4 c	284 b

stem diameter resulted in higher values of CSA of especially the first- and second-order laterals despite the fact that some shoots had died.

After more than 2 years of growth still the same differences in number of stems were found between treatments (Table 2). Some basal-, first-, and second-order stems had died and only a few new ones had been formed (data not given). Treatments C and D greatly raised the weight of basal shoots and first-order laterals per m². At higher plant densities the stem weight per m² had increased but the individual weight of all stems had decreased (data not shown).

Table 3. Effect of plant type and plant density on total biomass production and on the partitioning over harvested flowers, discarded prunings, and stem mass and on the harvest index. Different letters per column, for plant type and plant density separately, indicate significant differences ($P < 0.05$).

Plant type	Plant density (plants/m²)	Biomass production (kg/m²)	Harvested flowers (kg/m²)	Discarded prunings (kg/m²)	Stem mass (kg/m²)	Harvest index (%)
A		21.0 a	17.3 a	2.13 a	1.52 b	83 a
B		22.0 b	18.3 ab	2.13 a	1.59 a	83 a
C		21.8 ab	17.9 ab	2.45 a	1.61 a	82 a
D		24.0 c	19.0 b	3.15 b	1.86 a	79 a
	7.7	19.9 a	16.6 a	1.85 a	1.46 a	83 a
	11.6	21.8 b	17.7 b	2.51 b	1.62 a	81 a
	17.4	25.1 c	20.2 c	3.03 c	1.87 a	80 a

Table 4. Effect of plant type and plant density on number, fresh weight and economic value of flowers harvested for 2 cropping periods (period 1: week 17 until week 40, 1993; period 2: week 41, 1993 until week 28, 1995). Different letters per column for plant type and plant density separately, indicate significant differences ($P < 0.05$).

Plant type	Plant density (no./m²)	Flower production period 1: Number (no./m²)	Weight (g/m²)	Value (fl/m²)*	Flower production period 2: Number (no./m²)	Weight (g/m²)	Value (fl/m²)*
A		137 a	4841 b	68.2	411 a	12409 a	201
B		110 b	4667 b	58.2	446 ab	13653 a	224
C		86 c	3999 a	43.2	457 ab	13771 ab	231
D		89 c	3869 a	48.1	503 b	15083 b	254
	7.7	87 a	3774 a	45.6	403 a	12787 a	204
	11.6	107 b	4422 ab	55.1	438 a	13262 a	245
	17.4	123 c	4835 b	62.4	521 b	15138 b	283

* no statistical analysis possible

At the end of the experiment total biomass production, fresh weight of flowers harvested, weight of discarded prunings as well as total stem mass was higher for plant type D than for the control (Table 3). Plant type B and C usually occupied an intermediate position. Higher plant densities resulted in a higher biomass production, number of harvested flowers, weight of discarded prunings and stem mass. The harvest index was neither influenced by plant treatment nor by plant density.

Table 5. Effect of plant type and plant density on number, weight, shoot length, shoot firmness and economic value of flowers harvested over the whole experimental period. Different letters per column for plant type and plant density separately, indicate significant differences ($P < 0.05$).

Plant type	Plant density (no./m²)	Flower production: Number (no./m²)	Weight (g)	Length (cm)	Firmness (g/cm)	Economic value (fl/m²)*
A		548 a	31.5 a	71.4 a	0.42 a	270
B		556 a	33.0 a	72.1 a	0.44 b	282
C		543 a	32.7 a	71.9 a	0.45 b	274
D		592 b	32.0 a	73.3 b	0.42 a	302
	7.7	491 a	33.7 b	73.1 b	0.45 a	250
	11.6	545 b	32.5 ab	71.8 a	0.43 b	300
	17.4	643 c	31.1 a	71.9 a	0.42 b	345

* no statistical analysis possible

Table 6. Regression analysis between parameters of flower production (FP: weight of harvested flowers (g/m^2); NF: number of harvested flowers (no./m^2); FW: flower weight (g) and both number (N) and diameter (D) of basal shoots (BS), first-order laterals (1o) and second-order laterals (2o) as present 8 months after planting. Only significant models are presented together with the square multiple correlation coefficient (r^2) and the mse.

Flower production parameter	Model		r^2	mse
FP	FP =	- 5104.5 + 260.7 * NBS + 1537.6 * DBS	0.27	1945
	FP =	- 964.4 + 196.9 * N1o + 1281.3 * D1o	0.49	1616
	FP =	- 1549.8 + 276.0 * N2o + 2905.0 * D2o	0.74	1159
NF	NF=	- 221.6 + 10.4 * NBS + 50.1 * DBS	0.38	62.1
	NF =	- 47.3 + 7.1 * N1o + 29.0 * D1o	0.60	49.8
	NF =	- 323.1 + 9.1 * N2o + 67.4 * D2o	0.71	42.2
FW	FW =	33.9 - 0.110 * NBS + 0.015 * DBS	0.33	1.62
	FW =	26.0 - 0.041 * N1o + 0.771 * D1o	0.40	1.53
	FW =	20.1 - 0.011 * N2o + 1.622 * D2o	0.41	1.52

In the first 8 months, number, fresh weight and economic value of the flowers harvested was much lower for plant type C and D than for the control (Table 4). For the next cropping period production parameters were higher for all treatments as compared to the control. For both periods, number, weight and value of the flowers harvested increased with higher plant density.

For the whole experimental period, number of harvested flowers was higher and flowers were longer for plant type D than for the other types (Table 5). Shoot firmness was slightly improved by plant type B and C. The economic value of the flowers harvested was highest for plant type D and lowest for the control. Number of flowers and their economic value increased and flower weight, flower length and shoot firmness decreased with increasing plant density.

When the data for all treatments were taken together, regression analyses showed significant positive correlations between the number and diameter of stems, and the number and weight of flowers harvested (Table 6). Flower weight was positively correlated with stem diameter but negatively with number of stems. Much higher correlation coefficients were found when stems positioned higher in the plant were considered.

Furthermore, total biomass production during the experimental period was positively related with final stem mass (Figure 1). The separate correlation coefficients (r^2) for plant type B and D were 0.79 and 0.88, against for plant type A and C, 0.18 and 0.32, respectively.

Table 7. Relationships between the cross sectional area (CSA), measured at the level of the basal shoots (BS), first-order laterals (1o) and second-order laterals (2o) for 3 successive years. Only significant models are presented together with the square multiple correlation coefficient (r^2) and the mean square error (mse).

Year	Model		r^2	mse
1993	CSA1o =	656.3 + 0.697 * CSABS	0.36	354.7
	CSA2o =	1086.4 + 0.307 * CSABS	0.19	245.3
	CSA2o =	681.0 + 0.502 * CSA1o	0.67	156.3
1994	CSA1o =	569.3 + 0.812 * CSABS	0.52	303.1
	CSA2o =	883.8 + 0.634 * CSABS	0.45	272.0
	CSA2o =	604.4 + 0.702 * CSA1o	0.70	201.6
1995	CSA1o =	660.3 + 0.76 * CSABS	0.57	280.0

The CSA of stem parts at different heights in the plants were also closely related (Table 7). Correlation between the CSA of first- and second-order laterals was higher than between basal-shoots with first-order laterals. The correlations coefficients increased in successive cropping years.

Discussion

Plant architecture

Plant architecture with respect to number, diameter and CSA of basal-, first- and second-order laterals was mainly controlled by management of basal-shoot formation. The effect of a delayed bending of the primary shoot (treatment C and D), removal of competitive lateral growth (B), reduction in number of developing basal shoots (C) and plant density on basal-shoot formation of young rose plants confirmed results of Chapter 2.1. As was also reported by Zieslin (1981) and Kool and Van de Pol (Chapter 2.2), the number of outgrowing laterals was positively affected by the number of 5-leaflets leaves left behind on the parent shoot after harvesting the flowers as found in our experiment (Table 1: for type C and D, 2.0 and 1.6, respectively, against for type A and B, 1.1 and 1.2, respectively). This effect was most likely due to the positive effect of the number of remaining leaves on light interception and assimilate production. De-shooting (type D), i.e. the continuous removal of sinks, enhanced the diameter increase and storage of assimilates in experiments of Morisot *et al.* (1996) and Zieslin and Mor (1981a). Furthermore, it stimulated the branching after cutting as also found

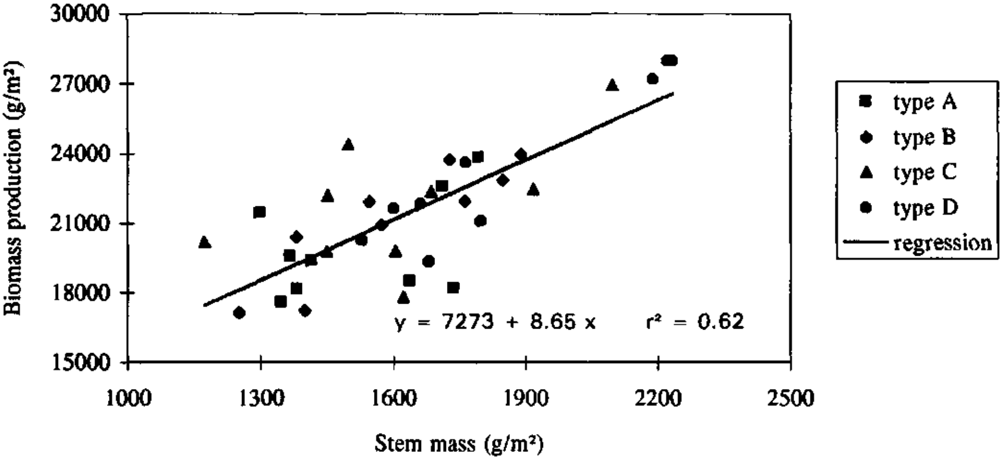


Fig. 1: Relationship between final stem mass (g/m²) and total biomass production (g/m²) as influenced by plant type. The regression line is given together with the square multiple correlation coefficient (r²).

by Zieslin et al. (1976b).

Initially, the investment in stem mass led to a clear reduction in number and weight of flowers for the first 8 months due to a delay of bending (type C and D), restriction of outgrowing shoots (B, C and D) or disbudding of shoots (D). However, this, in financial terms, investment of about Dfl 20,- (excluding labour costs) amply paid itself in the next 2 cropping years. Most attention is usually given to the number of basal shoots with respect to a vigorous and highly productive crop (Asen and Hamner, 1953; Kofranek and Fischer, 1949; Zieslin *et al.*, 1976b; Van Rijssel, 1982; De Vries, 1993). However, Van Rijssel (1982), Kool and Van de Pol (1992) and Fuchs (1994) also stressed the importance of the diameter of basal shoots. Moreover, Fuchs (1994) showed that in the long run flower production was related to number and diameter of the first-order laterals rather than to number and diameter of basal shoots. In our study, regression analyses showed that number and diameter of second-order laterals present after 8 months, could explain more than 70% of the variation in number and weight of flowers harvested in the whole experimental period (Table 6). Flower production was hardly related to number and diameter of basal-shoots. The minor importance of basal shoots is also shown by Kool (Chapter 3.3) who found that a twofold increase in number of basal shoots hardly influenced flower production during the first 4 years of growth. Basal shoots compete with each other as shown by a reduced diameter increase (Kool *et al.*, 1991; Chapter 3.3), by a higher mortality rate for old basal shoots (Fuchs, 1994; Chapter 3.3) and a reduced flower weight (Chapter 3.3).

Parameters of higher positioned stems were closer related to flower production than those of lower positioned ones (Table 7). This suggests that number and diameter of still higher positioned stems such as those on the height of cutting the flowers might be even more important for flower production as already emphasized by Kool and Van de Pol (Chapter 2.2) and Fuchs (1994). The number of stems may be an indication of the potential flower production because new shoots originate from cut shoots and, therefore, are highly important during periods of high light intensity (Fuchs, 1994) but less important during periods of low light intensity due to an increased risk of becoming "blind". Thick parent shoots bear heavier buds (Marcelis-Van Acker, 1994c) and produce thicker and heavier shoots (Byrne and Doss, 1981). In addition, the diameter or CSA of shoots is also important in view of their role in the storage of reserves and transport of nutrients (Lieth and Pasian, 1991; Fuchs, 1994). Since bud development and shoot growth are highly promoted by assimilate supply (Marcelis-Van Acker, 1994a), easiness of bud break is greater and the time required for flower development is shorter when shoots emerge from thick parent shoots (Byrne and Doss, 1981; Fuchs, 1994). The importance of stems in their transport and storage function is furthermore shown by the close relationship between stem mass and biomass production over the experimental period (Figure 1). In addition, the positive correlation between CSA of basal and upper parts indicates a close relationship between diameter increase at different plant heights for the first 3 cropping years, and not only for the first year as reported by Kool and Van de Pol (1992). Such close biometrical relations between different parts of a plant have been reported for several deciduous fruit crops such as sweet cherry (Maurer, 1971) and apple (Moore, 1978).

Plant density

In general, LAI is the most important controlling factor of canopy photosynthesis because of its close relationship to light interception (Williams *et al.*, 1965; Shibbles and Weber, 1966; Stützel and Aufhammer, 1991). The most appropriate way to increase LAI is by increasing plant population as has been demonstrated for many different crops (Buttery, 1969; Nederhof, 1984; Papadopoulos and Ormrod, 1991). It is, therefore, not surprising that the increase in LAI with plant density resulted in an increase in biomass production. However, individual plant development was reduced at higher density which is in agreement with results found for seedling roses (De Vries and Dubois, 1988), greenhouse rose crops (Pessala, 1977) and other horticultural crops such as beans (Crothers and Westermann, 1976) and tomatoes (Zahara and Timm, 1973). The significant reduction in flower quality parameters as weight, shoot length and shoot firmness at increasing plant density is in line with other results for rose (Rupprecht, 1963; Obiol and Cardus, 1972; Steinbuch, 1985). In the present study only flower length has been taken to calculate the economical value of the crop but other quality parameters are also important. Reductions of almost 10% in weight and firmness of harvested flowers, as actually found during periods of low light, may result in an unacceptable low quality.

Despite large differences in plant density and plant treatments, the harvest index was not influenced. Heuvelink (1995b) already concluded for fruit vegetables as tomato and cucumber that differences in assimilate supply per plant, brought about by plant density, season or irradiance levels did not affect dry matter distribution to the fruits. It may be concluded that a very constant relation exists between total dry matter production and dry weight of harvested parts as reported for several crops by Challa and Heuvelink (1993).

3.2 Long-term flower production of a rose crop 1: The influence of planting system and rootstock clone.

M.T.N. Kool and P.A. Van de Pol, 1996. Long-term flower production of a rose crop 1: The influence of planting system and rootstock clone. Journal of Horticultural Science 71, 435-443.

Abstract

The effect of planting system and rootstock clone on plant development and flower production of *R. hybrida* 'Motrea' was studied for more than 4 years. Initially, rootstock 'Ludiek' gave the highest number of flowering shoots as compared to the rootstocks 'Multic' and 'Moonlight'. However, the decline in flower production for 'Ludiek' after 2 years of culture was more severe than for the other rootstocks. Plants on 'Moonlight' out-yielded those on the other rootstocks during the third and fourth year of culture and this result is discussed in relation to their high renewal cane production. Death of basal shoots during 4 years of culture were mainly due to competition between numerous shoots. No influence of rootstocks on longevity of rose plants could be detected during this period. Comparison of basal-shoot formation during the early period of plant development in single-stemmed plants at double plant density with two-stemmed plants at normal plant density showed that intra-plant competition between basal shoots was stronger than inter-plant competition. During subsequent years of production no differences in basal shoot competition between or within plants occurred, as reflected in equal total flower fresh weight production, number of new basal-shoot formation and number of dead basal stems. However, higher plant densities increased the number of harvested flowering shoots and decreased individual shoot weight.

Introduction

Rose crops reach the highest production and economic yield already in the second year. In subsequent years, production stabilizes or slowly decreases (Rupprecht, 1963; Obiol and Cardus, 1972; Pessala, 1977). In the Netherlands, the economic life-span of a rose crop is usually 4 to 7 years which, however, is much lower than its potential longevity (Nooden and Leopold (1988). Data on long-term rose crop production are scarce and little attention is paid to the factors which determine longevity of a rose crop. The importance of shoots originating from the basal part of the rose bush and their laterals for flower production and life-span of the plants has often been stressed (Kofranek and Fisher, 1949; Zieslin *et al.*, 1976b). A strong positive relation between number or diameter of basal shoots and flower production was found by Van Rijssel (1982) and De Vries and Dubois (1983). However, data were only obtained during a limited cropping period. The general idea of 'the more basal shoots the better' has been questioned by Kool *et al.* (1991), who clearly demonstrated competition in secondary thickening between basal shoots on the same plant. This could be an argument for designing a plant system with only one basal shoot per plant and a uniform, controlled branching pattern. Recently, in a long-term experiment, no clear relation could be found between flower production and number of basal shoots (Chapter 3.3). Plant architecture is not only affected by basal-shoot development. Van Rijssel (1982) stressed the importance of an optimal number of laterals at a height of 60 cm for good flower production over a number of years. Later on the importance of both number and diameter as reflected in the cross sectional area (CSA) of stems at a certain plant height were emphasized by Kool and Van de Pol (Chapter 2.2) and Fuchs (1994). The CSA of laterals at a height of 60 cm could be manipulated by pruning strategy (Chapter 2.2) and by choice of rootstock clones (Kool and Van de Pol, 1992; De Vries, 1993; Fuchs, 1994).

In the present study, the effect of planting system and rootstock clone on plant development and flower production of the cv 'Motrea' was followed over more than 4 years. The rootstock clones *R. hybrida* 'Moonlight', *R. multiflora* Cathayensis 'Multic' and *R. multiflora* 'Ludiek' were chosen for the excellent branching capacity and flower productivity induced in the scion cultivar (Van de Pol *et al.*, 1988; Kool and Van de Pol, 1991; Kool and Van de Pol, 1992). The possibility of early rootstock screening on the basis of plant vigour, expressed in plant development as suggested by De Vries and Dubois (1990) and Kool and Van de Pol (1992), was tested in this 4-year production trial. Three planting systems were compared in order to find out whether competition between basal shoots on the same plant was stronger than between basal shoots of neighbouring plants.

Material and methods

On 21 November, 1989, 3 scion-rootstock combinations of the small-flowered cut rose 'Motrea' on *Rosa hybrida* Cathayensis 'Multic', *Rosa hybrida* 'Moonlight' and *Rosa hybrida* 'Ludiek' were propagated by stenting (Van de Pol and Breukelaar, 1982). On 6 February 1990, the plants were planted into soil in a 12 m x 12 m greenhouse compartment at the Department of Horticulture (Wageningen, the Netherlands, 52°N). Temperature set-point was 20°C during day and 18°C during night. Ambient carbon dioxide concentrations were maintained. From September until April supplementary lighting, using high pressure sodium lamps (SON-T; 400 Watt; 36.5 μmolm^{-2}s^{-1} PAR), was given when global radiation dropped below 100 Wm^{-2} outside the greenhouse. Day length was 18 h.

Treatments

The 3 scion-rootstock combinations were grown in combination with the following planting systems:

- *Treatment A (control):* Primary shoots were bent horizontally 6 weeks after planting, while all new laterals within 30 cm of the base of the primary shoot were continually removed with the exception of the most basal shoots. These shoots were harvested at the fourth 5-leaflet leaf from the base of the stem. Higher-order laterals were harvested at the second 5-leaflet leaf. The harvesting and pruning regime commonly adopted in the Netherlands was followed.
- *Treatment B:* The same as in treatment A but only 2 basal shoots per plant were allowed to grow out.
- *Treatment C:* Only 1 basal shoot per plant was allowed to grow out, combined with a doubled plant density as compared to treatments A and B (see experimental design).

From February 1991 onwards, new basal-shoot formation was inhibited for half of the plants (3 beds on the West-side of the greenhouse compartment) by continuously removing shoots emerging within 30 cm from the base of the plant. Results concerning this treatment are described in Chapter 3.3.

Experimental design

Plants were grown in four-row beds with a spacing of 0.25 m x 0.33 m for treatment A and B and 0.25 m x 0.17 m for treatment C, resulting in a density of 12 and 24 plant per m^2 bed, respectively. Between the beds a path of 0.6 m width was maintained. The experimental design consisted of 6 north-south orientated beds (blocks), each containing a random distribution of 9 plots of 1 m^2 (viz. 12 or 24 plants) for each combination of rootstock and planting system. All together 864 plants, excluding border plants, were involved.

Measurements

Flower production (number and fresh weight) and weight of blind shoots and of other discarded prunings were recorded per square meter bed at least twice a week from April 1990 until June 1994 (except for the period of April 1990 until October 1990 and July 1991 until October 1991 when only the number of flowers was measured). Total flower fresh weight production was calculated per month. Plant architecture as characterised by the number and diameter of basal stems, first- and second-order laterals and laterals at a height of 60 cm above the base of the plant, was measured in October 1990 and subsequently once a year at the end of winter. The cross-sectional area (CSA) of these stems was calculated and summed per square meter bed. Number, diameter (as measured on a height of 3 cm from the base of the shoot) and date of emergence of new basal shoots were recorded each year.

Results according to planting system and rootstock were statistically analyzed as a randomized block design with nine treatments (planting system (3) x rootstock (3)) by analysis of variance with the statistical Genstat package. Mean separation was done by Tukey's HSD-test.

Results

In February 1991 planting system A had greater numbers of both basal shoots and laterals than systems B and C (Table 1A) whereas their diameter was smaller. Furthermore, system A increased the CSA of basal shoots. Thick basal shoots were produced by system C. Independent of the system, 'Moonlight' induced more basal shoots and laterals than 'Multic'. Thick basal shoots and a lower number of second-order laterals were produced by 'Multic', while 'Moonlight' gave thin laterals. The CSA of second-order laterals was improved by rootstock 'Ludiek'.

Table 1. Influence of planting system and rootstock clone on plant architecture after 1 (A) or 3 (B) years of culture of rose cv Motrea. Planting date was February 1990. Different letters per column for planting system, rootstock and year separately, indicate significant differences ($P<0.05$). No significant statistical interaction between planting system and rootstock was found.

A Plant architecture February, 1991:

		Basal shoots:			Second order laterals:		
Planting system	Root-stock	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)
A		27 b	8.9 a	1651 b	71 b	5.3 a	1592 a
B		23 a	9.2 b	1521 a	64 a	5.6 b	1590 a
C		23 a	9.6 c	1582 ab	67 ab	5.5 b	1627 a
	MC	23 a	9.4 a	1593 a	64 a	5.5 b	1558 a
	ML	25 b	9.2 ab	1585 a	70 b	5.3 a	1571 a
	LU	25 ab	9.1 b	1579 a	69 b	5.5 b	1680 b

B Plant architecture February, 1993:

		Basal shoots:			Laterals at 60 cm height:		
Planting system	Root-stock	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)
A		35 b	9.4 a	2416 a	102 a	4.7 a	1905 a
B		32 a	9.6 a	2315 a	99 a	4.7 a	1830 a
C		34 ab	9.6 a	2399 a	115 b	4.4 b	1940 a
	MC	29 a	9.9 c	2254 a	102 a	4.8 a	1956 a
	ML	42 b	9.2 a	2713 b	114 b	4.4 b	1952 a
	LU	31 a	9.5 b	2214 a	100 a	4.6 ab	1774 b

Table 2. Influence of planting system and rootstock clone on the formation of new basal shoots during the second and third year of culture of cv. Motrea for plants in which basal-shoot formation was not restricted. Different letters per column for planting system and rootstock clone separately, indicate significant differences ($P < 0.05$).

Planting system	Root-stock	Number (no./m^2)	Diameter (mm)
A		16.8 a	8.4 a
B		15.1 a	8.3 a
C		19.7 a	7.5 b
	MC	10.9 a	8.4 a
	ML	26.2 b	8.1 ab
	LU	13.8 a	7.8 b

After 3 years, in February 1993, the greatest number of basal shoots was found in planting system A (Table 1B). System C resulted in more second-order laterals with a smaller diameter. No differences in CSA of basal and lateral shoots with respect to planting systems were observed. Independent of the system, 'Moonlight' induced the highest number of basal shoots and laterals with reduced diameters. The CSA of basal shoots was highest on 'Moonlight' while the CSA of laterals was lowest on 'Ludiek'.

Basal-shoot formation during the second and third year was significantly increased by rootstock 'Moonlight' as compared to the other rootstocks (Table 2). Planting system C and rootstock 'Ludiek' gave rise to thinner basal shoots.

Planting system had no significant effect on the number of stems which died during 4 years of culture (Table 3). Rootstock 'Moonlight' significantly increased the number of dead 'Motrea' basal shoots. This was even more clear when basal-shoot treatment is taken into

Table 3. Influence of planting system and rootstock clone on the number of stems that died during 4 years of culture of Rose cv. Motrea. Planting date was February, 1990. Different letters per column separated for planting system and rootstock clone indicate significant differences ($P < 0.05$).

Planting system	Root-stock	Basal shoots* (no./m^2)	First-order laterals** (no./m^2)	Second-order laterals (no./m^2)
A		5.1 a	11.7 a	12.0 a
B		2.9 a	10.8 a	11.3 a
C		3.0 a	11.5 a	16.8 a
	MC	1.5 a	9.8 a	14.6 a
	ML	6.4 b	12.0 a	10.6 a
	LU	3.1 ab	12.5 a	14.9 a

* including first- and second-order laterals on these basal shoots
** including second order laterals on these first-order shoots

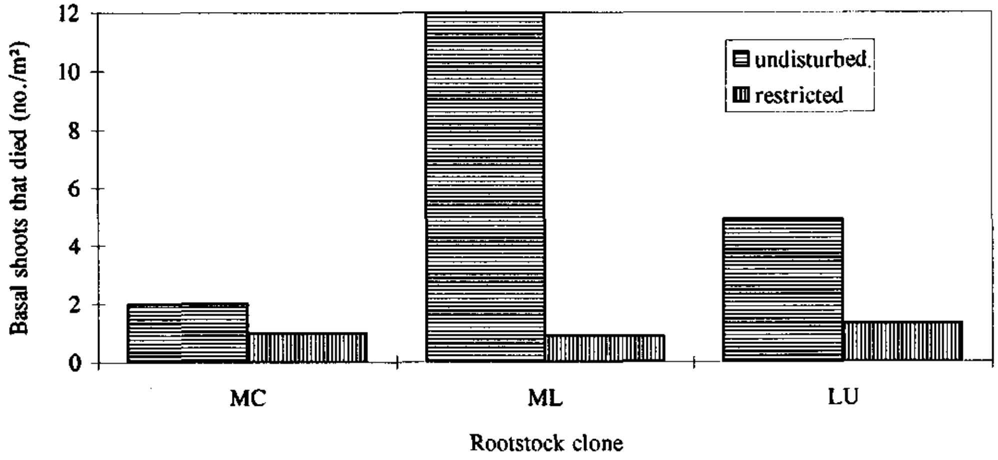


Figure 1. Influence of rootstock clone (MC = 'Multic'; ML = 'Moonlight'; LU = 'Ludiek'), combined with undisturbed or restricted basal-shoot formation on the number of 'Motrea' basal shoots that died during 4 years of culture. Planting date was February, 1990.

account (Fig. 1). As shown in Figure 2, total number of harvested flowers increased in the second year with 15% but gradually decreased in the next 2 years. That decrease was much more pronounced on rootstock 'Ludiek' than on 'Moonlight'. Flower production of plant system A, B and C were more or less the same.

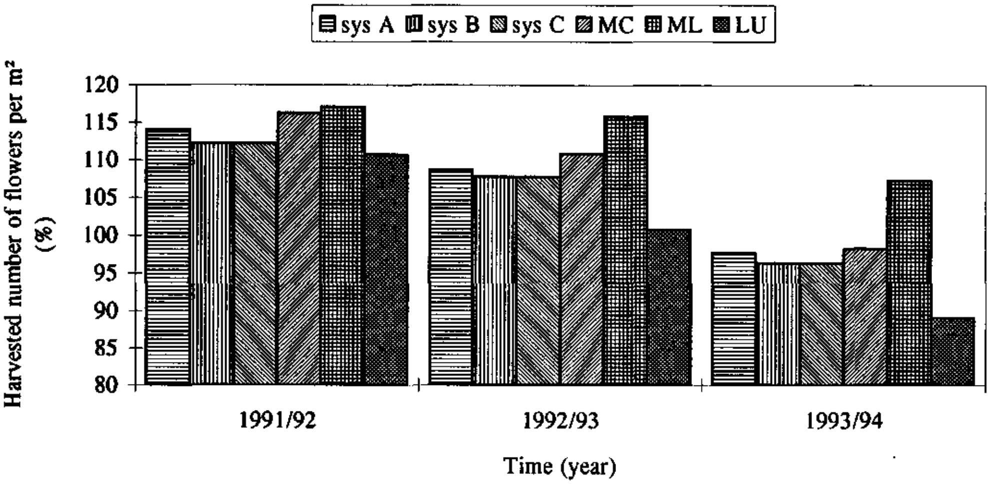


Figure 2. Number of harvested flowering shoots of rose cv. Motrea per year (July-June) expressed as a percentage of the first cropping year (1990/91 = 100%) and as influenced by planting system (A, B and C) and rootstock clone (MC, ML and LU).

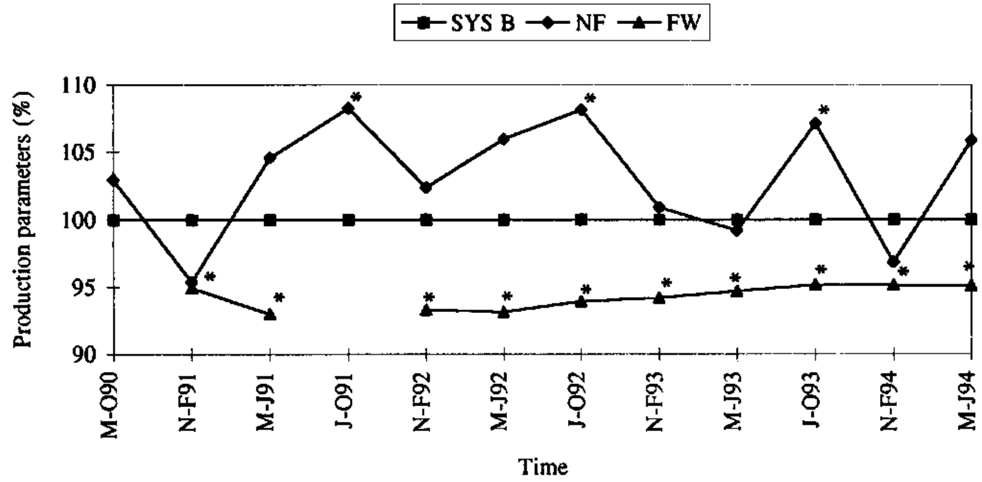


Figure 3. Number of harvested flowering shoots per m² bed (NF) and fresh flower weight in g (FW) in planting system C expressed as a percentage of the values in system B (=100%) in successive periods of 4 months (November-February 1991; March-June 1991; ...until March-June 1994) during 4 years of culture of rose cv. Motrea. Planting date was February, 1990. Significant differences between planting systems are indicated by an asterix.

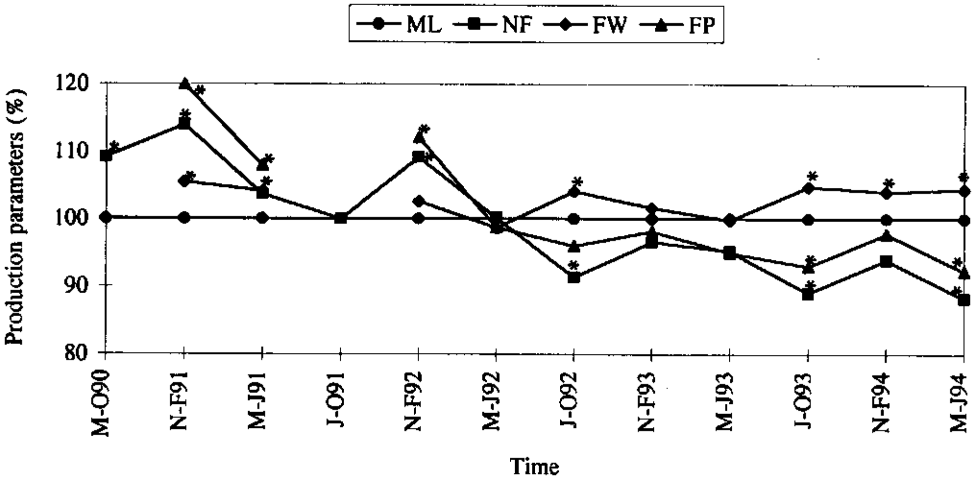


Figure 4. Number of harvested flowering shoots (NF; per m² bed), flower fresh weight (FW: in g) and total fresh weight flower production (FP: gm^{-2} bed) for rootstock clone Ludiek expressed as a percentage compared with 'Moonlight' (ML) in successive periods of 4 months (November-February; March-June 1991;... until March-June 1994) during 4 years of culture of rose cv. Motrea. Planting date was February, 1990. Significant differences between rootstock clones are indicated by an asterix.

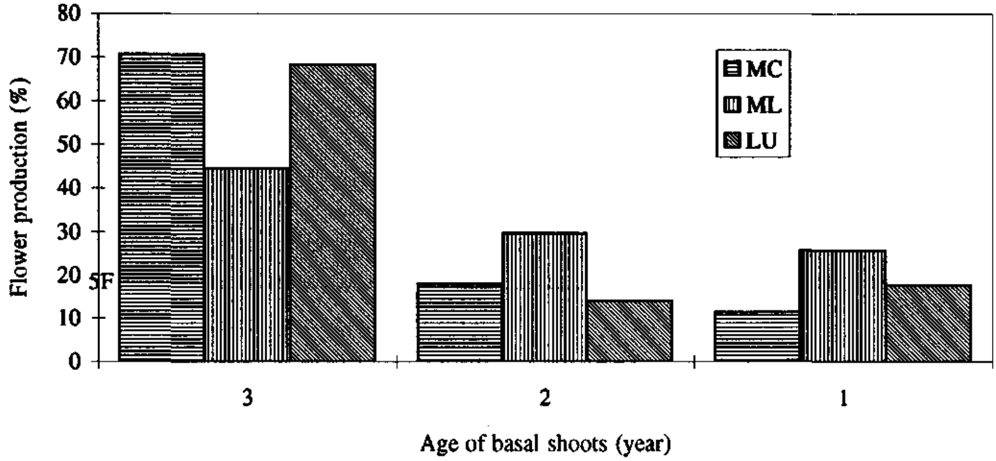
Table 4. Influence of planting system and rootstock clone on number of harvested flowering shoots (NF) and total fresh weight flower production (FP) per period of 4 months (November-February; March-June; July-October) as averaged over the period of November, 1991 until June, 1994 for rose cv. Motrea. Planting date was February, 1990. Different letters per column for planting system and rootstock clone separately, indicate significant differences ($P<0.05$).

		Nov - Feb:		Mar - Jun:		Jul - Oct:	
Planting system	Root-stock	NF (no./m^2)	FP (g/m^2)	NF (no./m^2)	FP (g/m^2)	NF (no./m^2)	FP (g/m^2)
A		161 a	2027 a	209 a	2872 a	253 a	2647 a
B		166 a	2107 a	214 ab	2950 a	249 a	2585 a
C		166 a	1986 a	222 b	2883 a	267 b	2632 a
	MC	165 a	2074 a	215 a	2928 a	255 a	2654 ab
	ML	164 a	1993 a	221 a	2956 a	271 b	2684 b
	LU	164 a	2042 a	210 a	2822 a	245 a	2533 a

Planting system C combined an increase in number of harvestable flowers with a significant decrease in individual flower weight in comparison with system B (Fig. 3). Total flower fresh weight production was less affected (data not given).

During the first 2 cropping years, the number of flowers, weight per flower and total fresh flower weight on rootstock 'Ludiek' were on average 10% higher than on 'Moonlight' (Fig. 4). From March 1992 onwards a gradual decline in number and fresh weight production of harvested flowers occurred. However, flower weight was still significantly higher on 'Ludiek'. Flower production on rootstock 'Multic' was more or less intermediate between that on 'Moonlight' and 'Ludiek' (data not given).

Figure 5. Influence of rootstock clone on the distribution (percentage) of total fresh flower weight over basal shoots of different age groups; data for September and October 1993.



The number of harvested flowering shoots was higher for planting system C during the spring, summer and autumn periods (Table 4) than for systems A and B. Total fresh weight of flowers tended to be lower in winter for system C due to a lower individual shoot weight. Independent of planting system, plants on 'Moonlight' yielded more flowers, with an increase in total fresh weight of shoots, than the others during the autumn period. During the other periods of the year no significant differences in flower production as induced by rootstocks were observed.

Three year old plants on 'Moonlight' produced more than 50% of total flower weight on basal shoots which had been formed in the second and third year after planting (Fig. 5). This was much higher than found for 'Multic' and 'Ludiek'.

Discussion

The number and diameter of basal shoots and laterals formed by roses within a year after grafting may be important selection criteria for plant vigour, as reported by De Vries and Dubois (1990) and Kool and Van de Pol (1992). However, the significant decline in flower production on the initially vigorous rootstock *R. multiflora* 'Ludiek' as found in this study stresses the need to test promising rootstocks for a longer period. Hardly any information is available about the influence of rootstocks on ageing and longevity of rose plants. The number of basal stems that die in the course of a certain cropping period might be indicative for the effect of rootstock on longevity as is generally supposed in woody crops (Nooden and Leopold, 1988). In our study, the highest number of basal shoots died on rootstock 'Moonlight' when basal-shoot formation was not restricted. However, these plants also produced the highest number of flowers in the fourth year. Moreover, where basal-shoot formation was restricted, plants on 'Moonlight' had the lowest number of dead basal shoots over 4 years. Yerkes (1934) compared 14 rose rootstocks and concluded that number of dead plants during his 5-year trial was too low to test longevity. Furthermore, Fuchs (1994) found much higher percentages of dead basal shoots (up to 54%) of *Rosa hybrida* 'Varlon' during 3 years of culture; he related this to an increased competition in view of their initial high number as described in terms of xylem connection and transport by (Marcelis-Van Acker, 1993; Marcelis-Van Acker *et al.*, 1993). It may be concluded that, in agreement with Fuchs (1994), dying back of basal shoots during 3 to 4 years of culture is mainly due to competition for nutrients and assimilates and probably has limited value as a selection criterion for the longevity of stock-scion combinations.

Many authors have stressed the importance of basal shoots with respect to a vigorous and highly productive rose-crop over a longer life-span (De Vries, 1993; Kofranek and Fisher, 1949; Van Rijssel, 1982; Zieslin *et al.*, 1976b). Leemans (1967) classified different types of rootstocks according to their growth habit. He concluded that rootstock types that produce many renewal canes from the base of the plant were more promising than the ones that hardly renew their basal stems. This agrees with our results for rootstock 'Moonlight', where a high productivity after 4 years was associated with a great number of renewal canes. However, in the long run the number of renewal canes is not the only factor determining productivity. Kool (Chapter 3.3) reported that in rose doubling of the number of basal shoots during the first 3 years did not influence flower production. Furthermore, in the present study flower production on rootstock 'Multic' declined less than 'Ludiek' in later years, although the plants produced fewer renewal canes.

The decline in productivity of the 'Motrea' crop on rootstock 'Ludiek' after a couple of years might be due to a decrease in leaf area i.e. photosynthetic capacity. This decrease in leaf area could have resulted from a decrease in number of harvested shoots (Fig 4) and in weight of blind shoots and other discarded prunings (10% less for 'Ludiek' than for 'Multic'; data not given). The photosynthetic surface area and its efficiency in capturing light account for most of the variation in productivity of woody crops (Cannell *et al.*, 1987).

The increased number of harvested flowers on rootstock 'Moonlight' as compared to 'Ludiek', especially in spring, summer and autumn, might be due to the higher number of laterals (Table 1B) on 'Moonlight'. The excellent branching induced by 'Moonlight' and its positive effect on flower production was confirmed by observations of Kool and Van de Pol (1992) and Fuchs (1994), and is probably the main factor leading to a high flower production (De Vries, 1993).

Winter productivity was very much the same for all 3 rootstocks, which might indicate that the advantage of a higher number of laterals as induced by 'Moonlight' is limited due to the underhook pruning practice as this decreases the number of laterals. The small differences in winter production found in this study deviate from previous findings of Pollock (1983), Miller (1986) and Fuchs (1994), showing that differences between rootstocks were most pronounced during winter. In winter, rootstock differences might come to the fore where rootstocks of sub-tropical origin are compared with the more winter-hardy rootstocks originating from temperate zones, as suggested by Pollock (1983). Such a comparison was not made in this study.

With respect to the question whether competition between basal shoots on the same plant differs from competition between basal shoots on neighbouring plants, Kool *et al.* (1991) suggested that in a plant system with only 1 basal shoot per plant competition between stems is less, resulting in a more homogeneous, prolific crop. In the present study it was found that the diameter of basal shoots was larger in single-stem plants at double plant density (Table 1A). This is in agreement with Kool and Lenssen (Chapter 2.1) who found that restricting the number of basal shoots per plant strongly increased their diameter, almost independently from plant density. It might be concluded that during the period of basal shoot formation with a low number of developing shoots and a low leaf area index, competition between basal shoots on the same plant is stronger than on adjacent plants, as already suggested by Kool *et al.* (1991). With respect to the long-term flower production, no difference in competition between basal shoots on the same plant or on different plants could be observed as reflected in an almost equal total fresh flower weight. Moreover, no significant differences in number of renewal canes during the successive years of production, nor differences in number of dead stems in the course of 4 years were observed with respect to plant density. However, single-stemmed plants at double density produced more flowers with a lower individual weight as compared to planting system B. Higher plant densities generally increase the number of branches per square meter rose bed and reduce average flower weight (Rupprecht, 1963; Obiol and Cardus, 1972), due to an increased competition for assimilates; this applies to many horticultural crops, e.g. carnation (Sakashita *et al.*, 1987). The number of root systems may also influence cytokinin production which will affect bud break, however, cytokinins were not determined.

3.3 Long-term flower production of a rose crop 2. The importance of new basal-shoot formation.

Kool, M.T.N., 1996. Long-term flower production of a rose crop 2. The importance of new basal-shoot formation. Journal of Horticultural Science 71, 445-452.

Abstract

The importance of new basal-shoot formation for plant development and flower production of *Rosa hybrida* 'Motrea' was studied for more than 4 years. After 1 year, new basal-shoot formation was either restricted or undisturbed. In both treatments, fresh weight production decreased after the second year which is discussed in relation to an increase in respiration as a result of an increase in stem biomass. Limiting the number of new basal shoots increased flower weight and slightly enhanced flower production during the second year as compared to leaving all renewal canes on the plant. In the latter case, the number of basal stems was almost twice as high after 3 years. New basal shoots may compete with existing ones as indicated by the limited diameter increase and the higher mortality rate for old basal shoots in comparison with the treatment in which basal-shoot formation was restricted. Furthermore, the weight of flowers harvested from new basal shoots was clearly higher than from older shoots. However, restricted basal-shoot growth had hardly any significant effects on total number of harvested flowers and average flower weight as compared to the undisturbed situation. In the fourth year a slightly decreased flower production in the case of restricted basal-shoot formation was observed. It may be concluded that there is no clear relation between the number of basal shoots and flower production over a series of years.

Introduction

In the Netherlands, the economic life-span of a rose crop usually is between 4 to 7 years. In general roses reach their highest production and economic yield already in the second year, which is fast as compared to other cultivated woody plants, such as fruit crops (4-12 years: Wagenmakers, 1994) or forest crops (12-35 years: Kozlowski *et al.*, 1991). After the second year flower production stabilizes or starts to decrease (Rupprecht, 1963; Obiol and Cardus, 1972; Pessala, 1977). Net biomass production commonly increases to a maximum near the time of full canopy closure and usually declines thereafter.

Data on long-term rose crop production are scarce. Moreover, factors affecting the length of the (economic) production period have seldom been studied. Many authors stressed the importance of basal shoots for a vigorous and highly productive rose-crop having a longer life-span (Kofranek and Fisher, 1949; Zieslin *et al.*, 1976b; Van Rijssel, 1982; De Vries, 1993). Therefore, many experiments have been carried out in order to promote basal-shoot formation of established rose bushes (De Vries, 1993) and a positive relation between the number of basal shoots and flower production often occurred (De Vries and Dubois, 1983; Schrock and Hanan, 1981; Van Rijssel, 1982). However, in none of these studies the relationship between basal shoots and flower production was followed over a range of years. Furthermore, no attempt has been made to separate the effects of new basal shoots from already existing ones on plant development and flower production. Kool *et al.* (1991) already demonstrated competition between diameter growth of basal shoots during the first year of cultivation. A hypothesis was put forward by Marcelis- van Acker *et al.* (1993) that later developing basal shoots may influence the growth of earlier ones by the formation of a new ring of xylem vessels in the root collar around those serving the older shoots and so restricting their secondary growth. In the present study, the effects of undisturbed basal-shoot formation as compared to restriction of the number of emerging basal buds on plant development and biomass production were observed in detail over a cropping period of more than 4 years.

Material and methods

On 21 November, 1989, plants of *Rosa hybrida* 'Motrea' were stented (Van de Pol and Breukelaar, 1982) and on 6 February, 1990, planted into soil in a 12 m x 12 m greenhouse compartment which was part of the multi-span Venlo-type greenhouse of the Department of Horticulture (Wageningen, the Netherlands, 52°N). Temperature set-point was 20°C during the day and 18°C at night. From September until April, supplementary lighting using high pressure sodium lamps (SON-T; 400 Watt; 36.5 μmolm^{-2}s^{-1} PAR) was given when global radiation outside the greenhouse dropped below 100 Wm^{-2}. Day length was 18 h.

Treatments

Three scion-rootstock combinations were grown in combination with 3 planting systems as described in detail by Kool and Van de Pol (Chapter 3.2). From February 1991 onwards, basal-shoot formation for half of the plants was restricted by continuously removing new sprouting buds emerging within 30 cm from the base of the plant. In the other half of the plants basal-shoot formation occurred undisturbed. Flower stems were cut on the first 5-leaflet leaf counted from the base of the stem at least twice a week. During winter the underhook cutting procedure was applied (Zieslin, 1981) in order to reduce plant height.

Experimental design

Plants were grown in 4-row beds with a spacing of (0.25 m x 0.33 m or 0.25 m x 0.17 m as dependent on planting system (Chapter 3.2). Between the beds a path of 0.6 m width was maintained. The experimental design consisted of 6 north-south orientated beds (blocks). Restriction of basal-shoot formation was applied to 3 beds on the West-side of the greenhouse, while on the other beds basal-shoot formation occurred undisturbed. All together 864 plants, excluding border plants, were taken into account.

Measurements

Flower production (number and fresh weight) and weight of blind shoots and other discarded prunings were recorded at least twice a week from April 1990 until June 1994. However, between April 1990 and October 1990 and between July 1991 and October 1991 only flower counts were done. Total fresh biomass production (weight of harvested flowers, blind shoots and other prunings) was recorded per month. Number and diameter of basal stems, first and second order laterals and laterals at a height of 60 cm above the base of the plant were measured in October 1990 and furthermore at the end of each winter. The cross sectional area (CSA; Lombard *et al.*, 1988) of the stems per square meter bed was calculated. Number, diameter and date of appearance of new basal shoots were recorded and new stems were labelled according to year of appearance. During January and February 1992 and September and October 1993, number and weight of harvested flowers were recorded according to year of appearance of basal shoots.

Results were analyzed as a randomized block design with 9 treatments (3 planting systems x 3 rootstock clones) by analysis of variance with the statistical Genstat package as described by Kool and Van de Pol (Chapter 3.2). Mean separation was done by Tukey's HSD-test. This HSD-value was used in order to evaluate significant differences in the effect of restricted as compared to undisturbed basal-shoot formation with an experimental lay-out of 3 blocks per treatment with 9 replications each. Regression models were calculated between fresh weight flower production over a period of time and the CSA of basal shoots. Only significant models ($P < 0.05$) are presented together with the correlation coefficient.

Results

In October 1990, before the treatments with respect to undisturbed or restricted basal-shoot formation were applied, no significant differences in plant architecture were observed (Table 1A). Two years later, almost 20 new basal shoots per square meter bed had formed (Table 1B), with a somewhat smaller diameter than the already existing ones. CSA of basal shoots was much higher for undisturbed than for restricted basal-shoot formation (Table 1B).

Table 1. Influence of undisturbed or restricted basal-shoot formation on the development of basal shoots and laterals at a height of 60 cm of Rose cv. Motrea before the start of basal-shoot restriction in 1990 (A) and after 3 years later in 1993 (B). In 1993 a division was made between shoots formed in 1990 (3 years old) and total number of shoots formed in 3 years. Different letters per column indicate significant differences ($P < 0.05$).

A: Plant building October, 1990.

	Basal shoots:			Laterals:		
Basal shoot treatment	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)
Undisturbed	23.2 a	9.2 a	1545 a	75.6 a	4.6 a	1231 a
Restricted	23.0 a	9.1 a	1478 a	75.1 a	4.7 a	1278 a

B: Plant building February, 1993.

	Basal shoots:			Laterals:		
	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)	Number (no./m^2)	Diameter (mm)	CSA (mm^2/m^2)
Undisturbed (total)	42.5 a	9.0 a	2764 a	108.3 a	4.6 a	1986 a
Undisturbed (formed in 1990)	25.4 b	9.5 b	1864 b	78.5 b	4.5 a	1329 b
Restricted (total)	23.7 b	10.1 c	1960 b	102.0 a	4.5 a	1792 c

Number, diameter and CSA of branches at a height of 60 cm was only slightly affected by treatments. Restricted basal-shoot formation resulted in a larger diameter and CSA of 3-year-old basal shoots as compared to the treatment with undisturbed basal-shoot formation (Table 1B). The number of basal shoots and first-order laterals that died in the course of 4 years of cultivation was significantly higher on plants with undisturbed than with restricted basal-shoot formation (Table 2).

Table 2. Influence of undisturbed or restricted basal-shoot formation on the number of stems that died during 4 cropping years of rose cv. Motrea. Planting date was February, 1990. Different letters per column indicate significant differences ($P < 0.05$).

Basal shoot treatment	Basal-shoots* (no./m^2)	First-order laterals** (no./m^2)	Second-order laterals (no/m^2)
Undisturbed	6.3 a	12.2 a	12.9 a
Restricted	1.1 b	10.4 b	13.9 a

* including first- and second-order laterals

** including second-order laterals

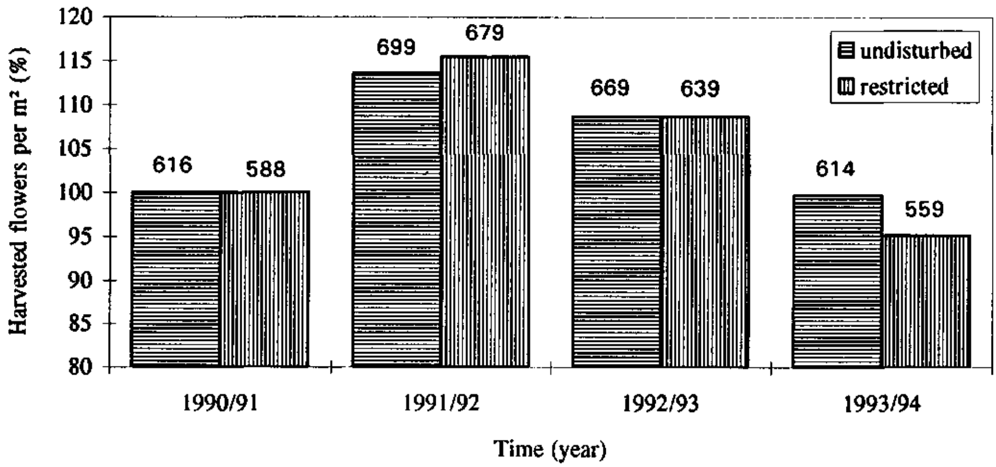


Figure 1. Numbers of harvested flowers of rose 'Motrea' per year (July-June) as influenced by undisturbed or restricted basal-shoot formation, expressed as a percentage of the first full-productive year (1990/91 = 100%). Absolute numbers of harvested flowers (no./m²) for each year are given above the column.

Total number of flowers increased in the second year by 15% as compared to the first year but gradually decreased in the following years (Figure 1). Restricted basal-shoot formation slightly decreased the number of flowers harvested during the fourth year; this was the only noticeable treatment effect. Total biomass production decreased by 3 - 4% per year in the period 1992 until 1994 (data not given).

From March 1991 until February 1993 restricting basal-shoot formation enhanced number of flowers, weight per flowering shoot and total flower fresh weight (Figure 2) as compared to the undisturbed treatment although some fluctuations per period of four months were observed.

Individual flower weight was much larger for restricted basal-shoot growth during the spring of the second year. From February 1993 onwards, the small positive effect had disappeared and from July 1993 until June 1994 even a negative effect on number of harvestable flowers could be noticed (Figure 2). Total fresh weight of flowering shoots during this latter period was much the same as in the control because superior weight of flower compensated for the inferior number of flowers.

In September and October in 1993 most flowers were still harvested from the original, 3-year-old, basal shoots (Figure 3). However, flowers borne on these basal shoots clearly weighted less. Restricting basal-shoot formation had no significant effect on average number and weight of harvested flowers during these 2 months. Similar results were obtained over January and February 1992, when plants were 2 years old (data not given).

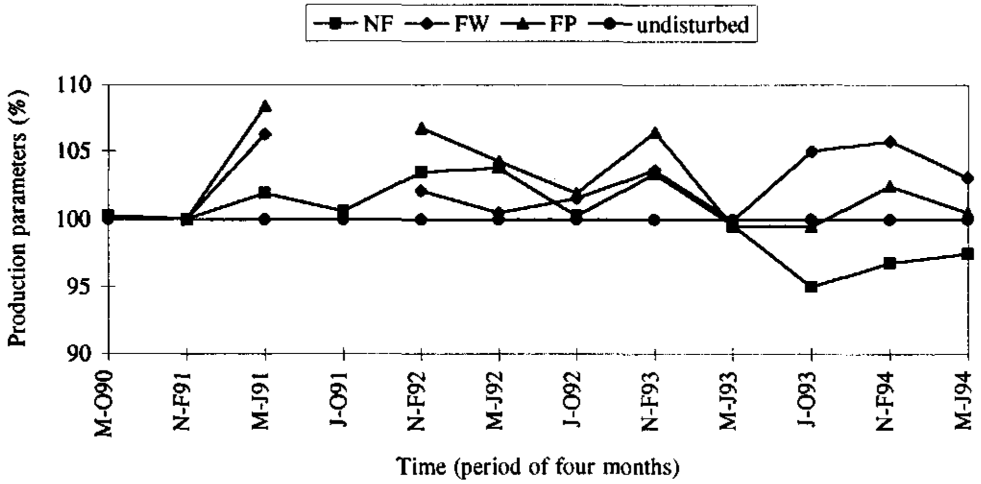


Figure 2. Numbers of harvested flowers (NF per m² bed), flower stem weight (FW in gram) and total flower production (FP in gram fresh weight per m² bed) in successive periods of four months (November-February 1991; March-June 1991; ... until March-June 1994) of 'Motrea' rose with restricted basal-shoot formation expressed as percentage of the values for the control treatment. In the case of restricted basal-shoot formation, data on NF, FW and FP have been adjusted by taking the period of November 1990-February 1991 (before treatments affecting basal-shoot formation were applied) as a reference period (=100%).

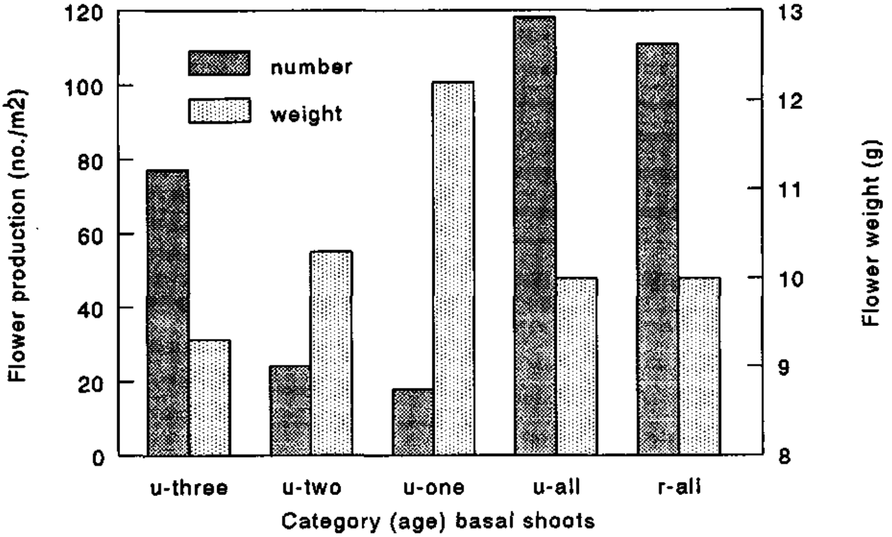


Figure 3. Number and weights (g) of flowers harvested in September and October 1993 from plants with undisturbed (u) or restricted (r) basal-shoot formation, for the former treatment also specified according to age class (one, two and three years old) of the basal shoots.

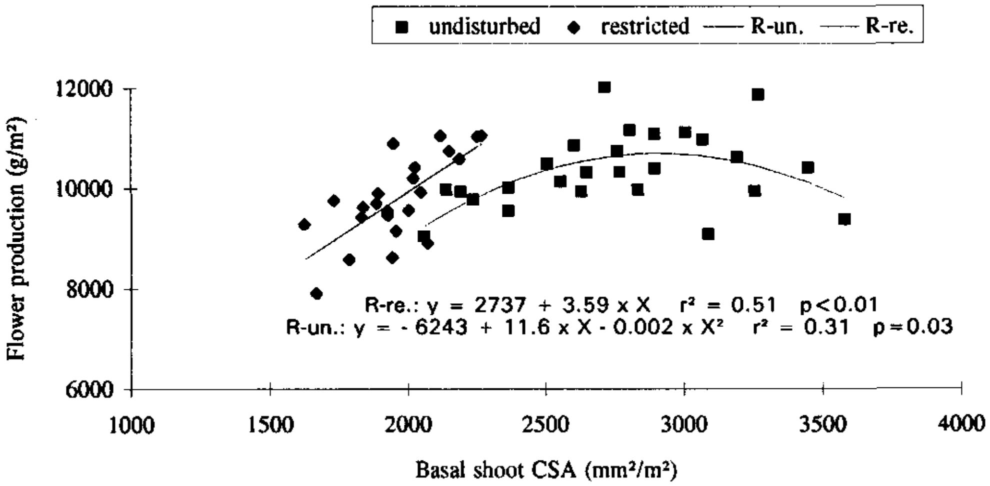


Figure 4. Regression analysis on basal shoot CSA (February 1993) and flower production (March 1993-June 1994) for rose cv. Motrea as influenced by undisturbed and restricted basal-shoot formation.

For 3-year-old plants with restricted formation of basal shoots a linear relationship was found between the CSA of basal shoots and flower production in the period of March 1993 until June 1994 (Figure 4). In the case of undisturbed basal-shoot formation an optimum was found at CSA of 2900 mm²m⁻².

Discussion

Flower production reached a maximum already in the second cropping year (Figure 1). Generally, maximum growth is reached at canopy closure at a leaf area index of approximately 3 (Gijzen, 1992) which for rose already occurs a few months after planting (Chapter 2.1). However, the number of flowering shoots is more in particular related to the number of supporting stems (Van Rijssel, 1982) which is probably still too low in the first year of growth and may not reach its optimum until the second year.

From the second year onwards, a gradual decrease of 4 to 8% per year in flower production was observed, which is in the range of values reported by Obiol and Cardus (1963), Rupprecht (1963) and Pessala (1977). This decrease is probably related to the significant increase in stem biomass, as reflected in the increase in CSA of approximately 50% in less than 3 years. Since plant height also slightly increased over the years total plant biomass increase will have exceeded 50%. As recently discussed by Kool and De Koning (1996) this leads to considerably more assimilates being needed for maintenance respiration of roses, resulting in a reduced net biomass production. However, other factors related to ageing, such as a decrease in the transport function of the xylem pathway (Zimmerman, 1983), the increasing distance between shoot apices and roots (Maggs, 1964), an overall decrease in meristematic activity due to stronger competition for available nutrients in complex plants (Moorby and Wareing, 1963) and other factors as summarized by Nooden and Leopold (1988) may also be involved.

During the second year of growth, formation of new basal shoots had no or a negative effect on crop production. By February 1993 the number of basal shoots had almost doubled, but still no clear effect on flower production could be observed. This is contrary to the positive effect of number of basal shoots on flower production as reported by others (De Vries and Dubois, 1983; Schrock and Hanan, 1981; Van Rijssel, 1982). However, in these studies relations between flower production and basal-shoot formation only covered the first year of rose production (De Vries and Dubois, 1983) or just concerned a momentarily observation of basal shoots (Van Rijssel, 1982). Schrock and Hanan (1981) also supplied only short-term data, reporting the direct effect of the applied treatment on basal-shoot formation and flower production. Positive effects of number of basal shoots on flower production might only hold for a short time or else be obtained under circumstances of an open canopy (young crops or sub-optimal growing conditions). In such cases new basal shoots are able to intercept more light and as a consequence biomass production will increase. In the case of a more homogeneous crop with an almost closed canopy, new basal shoots compete for assimilates with developing shoots at the top of the canopy. In this reasoning it is not surprising that new basal shoots reduce the diameter increase and branching capacity of existing shoots (Table 1) as was indeed found for an one-year-old rose crop (Kool *et al.*, 1991). In the present experiment stems of old basal shoots hardly showed secondary thickness growth in later years, which might be due to the formation of a new ring of xylem vessels around the former ones as shown by Marcelis-van Acker *et al.* (1993). Due to gradually dis-functioning of xylem vessels (Zimmerman, 1983) shoots originating from these old basal stems may be less able to obtain water and minerals, leading to a decrease in branching capacity (Table 1B) and an increase in shoot mortality (Table 2). Competition between basal shoots of different ages was further shown by the much higher weight of the flowers harvested from new basal shoots (Figure 3).

Decrease in production after the second year was faster in the case of restricted as compared to undisturbed basal-shoot formation. Without new shoots sprouting from the base of the plant, open spaces in the canopy which might occur due to dying back of basal stems can not easily be filled. A major reason for differences in productivity of woody crops is still the photosynthetic surface area and its efficiency in light capture (Cannell *et al.*, 1987). The observed small positive effect of undisturbed as compared to restricted basal-shoot formation on flower production over the 4 years might be even less for other varieties, because 'Motrea' characteristically forms more new basal shoots than most other varieties.

Waring and Schlesinger (1985) have shown in their review that in many woody plants relatively stable relationships are maintained between leaf area, stem diameter, sapwood CSA and root biomass due to an internal control exerted by water, carbohydrates, nitrogen supply and hormone levels. Already in 1934 Yerkes reported for rose a positive correlation between annual weight of stem wood and number of harvested flowers. More recently, a positive relation between CSA of basal and upper stem parts was found by Kool and Van de Pol (1992) and between the number of bottom-breaks and the girth of the root system by De Vries and Dubois (1983). However, biometrical relations between biomass accumulation and stem biomass, as reported for deciduous fruit crops such as sweet cherry (Maurer, 1971) and apple (Moore, 1978) might be disturbed for roses by the continuous harvesting practice. Nevertheless, even for 3-year-old plants a positive relation between stem cross sectional area and subsequent flower production was found in this study (Figure 4) although when new basal-shoot formation was not restricted, flower production declined at extremely high CSA values. This may point to the negative effect of an increased biomass (via respiration of photosynthates) on flower production as already discussed. In that case, the positive effect of renewal canes may be improved by eliminating increases in stem biomass through cutting out of older stems as soon as their photosynthesis approaches the compensation point, as suggested by Kozlowski *et al.* (1991).

In this study restricted basal-shoot formation only slightly affected flower production over a 4-year period. In commercial growing systems differences in flower production of more than 50% have been observed between individual crops (Berentzen, 1995; personal communication) already in the second year. Further research already discovered the importance of plant architecture with respect to flower production (Chapter 3.1 and 5.3). Therefore, it seems logical to focus research on plant architecture, mainly achieved during the first year of development, rather than on basal-shoot formation during later years of growth.

3.4. Effects of harvesting method and flowering shoot density on production and performance of roses

Kool, M.T.N., 1996. Effects of harvesting method and flowering shoot density on production and performance of roses. (submitted).

Abstract

The effect of continuous versus flush harvesting and flowering shoot density on the production of assimilates and flower performance was studied under controlled conditions in climate chambers. Continuous harvesting as compared to flush harvesting reduced the number of developing shoots while it increased the amount of intercepted photosynthetic active radiation. As a result, continuous harvesting and the lower shoot density had a positive effect on flower performance (weight, length, firmness and dry weight percentage). Furthermore, the time from cutting until harvesting a flower was shortened by an increased assimilate supply. Distribution of dry matter towards flowers harvested (harvest index) was not influenced by method of harvesting or shoot density which is in line with previous experiments with rose and some vegetable fruit crops. All treatments seem equally efficient in converting PAR into dry weight of harvested flowers.

Introduction

The rose is a polycarpic, self-inductive plant which initiates flowers without needing a specific photoperiod or temperature (Zieslin and Moe, 1985). In a traditional rose crop, flowering shoots have to be cut daily due to the large variation in plant types (Kool *et al.*, 1991), factors affecting flower production per plant (Zieslin *et al.*, 1973) and the length of time between one harvest and the next (Fuchs, 1994). Nevertheless, shoots often appear in peaks due to pruning practices (Holley, 1973) or climatic conditions. By using specific cultural practices such as pinching and deshooting rose production can be timed in order to meet high demand periods (Jones and Hartley, 1978). Hardly any information is available concerning the physiological differences between continuous versus flush harvesting of roses. It may be that by harvesting all shoots at the same time at the same height, the number of new sprouting buds might be enhanced due to increase of the photon flux density and of the red/far-red ratio (R/FR) (Mor and Halevy, 1984). However, removal of many flowering shoots (and leaves) over a short period might increase root death and delay in root regrowth (Fuchs, 1986). Furthermore, it wwould be difficult to maintain an leaf area index of approximately 3 as assumed to be optimal for the growth of greenhouse crops (Gijzen, 1992).

The aim of this study was therefore to determine the effect of continuous versus flush harvesting on number as well as quality of flowers of harvested shoots, and on light interception, total assimilate production and allocation towards harvestable flowers. Higher shoot or plant densities increase dry weight production per area but decrease the individual shoot or plant development in many horticultural crops (Heuvelink, 1995b) including roses (Chapter 3.1 and 3.3). The possible role of shoot density on yield potential was therefore also examined.

Material and methods

In the middle of January 1994, cuttings of *Rosa hybrida* Madelon 'Ruimeva', rooted in rockwool blocks (7*7*7 cm), were placed on rockwool slabs in 2 growth chambers of 16 m^2 each. In each chamber 2 beds each with 6 rows of rockwool slabs existed. Plant density was 12 plants/m^2 (0.25 m between slabs * 0.30 m within slabs). Between beds the distance was 0.5 m. Temperature was 20°C, day length 16 h. Lighting was provided by fluorescence tubes (type TL-D/50Watt/84-F) giving an irradiance of 32.8 Wm^{-2} at plant level. Four weeks later, the primary shoots were bent horizontally in order to promote basal shoot formation. Only 1 basal shoot per plant was allowed to develop. At the harvestable stage, the basal shoot was pruned above the third 5-leaflet leaf counted from the base. Subsequent flowering shoots were pruned above the second 5-leaflet leaf.

Plant treatments

Two densities i.e. 24 and 48 shoots per m^2 were maintained. At 24 shoots/m^2, after harvesting the basal shoot, the 2 uppermost buds on the remaining stem were allowed to develop. After harvesting those 2 first-order laterals, bud break was restricted to 1 bud per stem. At 48 shoots/m^2 the procedure was equal to 24 shoots/m^2 except that after pruning the 2 first-order laterals, bud break was restricted to 2 buds per stem.

At each density, flowering shoots were harvested in flushes or continuously. For flush harvesting, the first-order laterals with a flower bud in the harvestable stage were topped and de-shooted until 75% of the shoots had reached this stage. At that moment, all first-order laterals were pruned back to the second 5-leaflet leaf counted from the base of the stem. Second order laterals were cut at the same time when 50% of the flowering shoots had reached the harvestable stage. Third and fourth order flowering laterals were cut at their harvestable stage. For continuous harvesting, the uppermost shoot of the first-order laterals was cut at the second 5-leaflet leaf at the harvestable stage. At the same time, the lowermost shoot was topped and de-shooted for 3 weeks and then cut at the second 5-leaflet leaf. Second-, third-, and fourth-order flowering laterals were cut at the harvestable stage.

Plant measurements

Number, development time (time from cutting until harvesting) and quality (length, diameter, fresh and dry weight) of basal shoots harvested and of the shoots of the 4 successive flowering cycles were recorded and shoot firmness (g/cm), shoot growth rate (presented as g/day and cm/day) were calculated. At harvesting the flowers of the fourth cycle, plants were pruned back to second order stems. After all flowers of the fourth cycle had been harvested, plants were analysed destructively and fresh and dry weight (60°C in ventilated oven for at least 48 h) were determined. The crop harvest index of flowers was calculated by dividing fresh weight of flowering shoots harvested by total fresh weight. The photosynthetic active radiation (PAR) was measured at weekly intervals at 3 places above the canopy and at 6 places below the lowest leaves using a 75 cm long quantum response tube PAR sensor (TFDL-Wageningen, The Netherlands). From these data, light interception (%) and amount of intercepted PAR were calculated.

Each treatment was replicated in separate growth chambers with 9 plants per treatment plot, surrounded by border plants. Data were expressed per m^2 bed or per shoot. Results were statistically analysed by Analysis of Variance using the package of SYSTAT. Mean separation was done by Tukey's-HSD test ($p<0.05$).

Results

Number of flowers harvested over the whole experimental period was reduced by continuous harvesting especially at the higher shoot density (Figure 1) but the production expressed as fresh weight was more or less the same in the 2 methods of harvesting (Figure 2). Flower performance was highly affected by harvesting method and shoot density (Table 1). Shoot weight, length, firmness, dry weight percentage and growth rate were all reduced by flush harvesting and were also lower at the higher shoot density. Moreover, the time from cutting until harvesting a shoot was significantly extended by flush harvesting. Despite the differences in number and performance of harvested flowers, the harvest index was not influenced by harvesting treatment and shoot density (87-88% for all treatments). Plant weight at the end of the experiment was almost the same for all treatments (data not given).

The method of harvesting also affected crop light interception (Figure 3). Light interception in the flush harvesting treatment fluctuated between 40 and 98% but only between 70 and 90% for continuous harvesting (Figure 3). A linear relationship was found

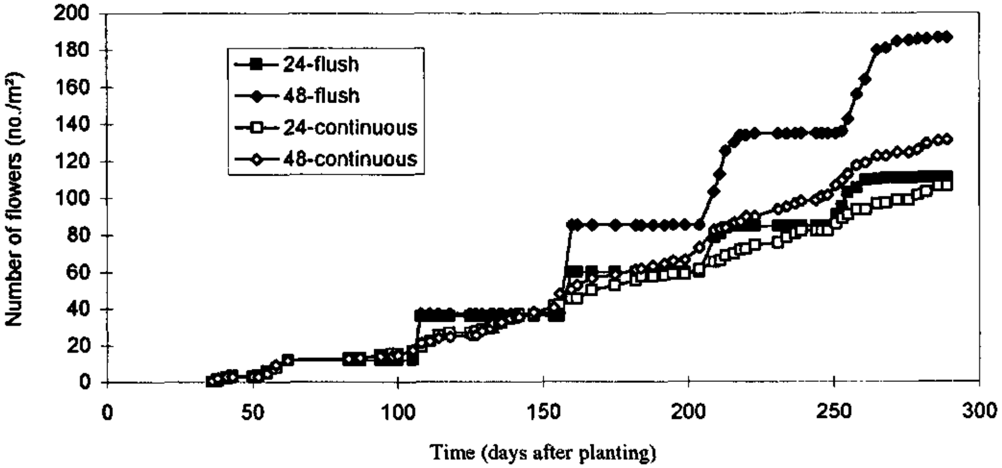


Figure 1. Influence of harvesting method (flush versus continuous) in combination with shoot density (24 and 48 shoots /m²) on the cumulative number of flowers of cv. Madelon for five subsequent flowering cycles.

between flower production and intercepted PAR (Figure 4). It could be calculated from these data that continuous harvesting increased the daily intercepted photosynthetic active radiation (PAR) to 1.49 MJ/m²day versus 1.18 MJ/m²day for flush harvesting. Furthermore, continuous harvesting increased the daily dry weight flower production (6.09 g/m²day versus 5.22 g/m²day for flush harvesting) over the last 3 flowering cycli.

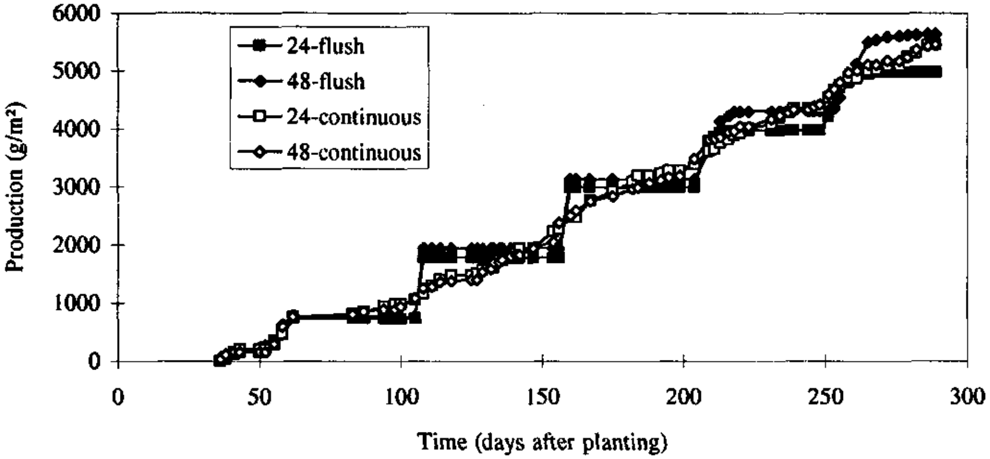


Figure 2. Influence of harvesting method (flush versus continuous) in combination with flowering shoot density (24 and 48 shoots/m²) on the cumulative weight of the flowers produced of cv. Madelon for 5 subsequent flowering cycles.

Table 1. Influence of harvesting method (flush or continuous) and shoot density (24 or 48 shoots/m²) on some parameters of flower performance as averaged over the second until the fourth flowering cycle. Different letters per column indicate significant differences. Significance of the main effects of harvesting method or shoot density as indicated by the F_p of the Analysis of Variance, are given by the bottom line (ns = not-significant; * = $F_p<0.05$; ** = $F_p<0.01$).

	Flower performance:					Growth rate:	
Treatment	Time* (days)	Weight (g)	Length (cm)	Firmness (g/cm)**	Dry weight (%)	(cm/day)	(g/day)
24-flush	49.2 ab	42.6 bc	83 ab	0.12 bc	23.2 ab	1.68 b	0.20 b
48-flush	51.6 b	24.8 a	73 a	0.08 a	22.6 a	1.41 a	0.11 a
24-continuous	47.9 a	51.0 c	89 b	0.14 c	24.3 b	1.85 c	0.26 c
48-continuous	47.7 a	37.9 b	84 ab	0.11 b	23.7 ab	1.76 bc	0.19 ab
Harvesting	*	**	*	**	*	**	**
Shoot-density	ns	**	*	**	ns	*	**

* time from cutting until harvesting
** calculated as gram dry weight per cm.

Discussion

In this study, continuous harvesting reduced the number of new developing shoots (Figure 1) as also found by Kool *et al.* (Chapter 4.1) over the 1.5 year duration of the experiment with the cultivar 'Frisco'. The reason may be that mutual shading effects especially occurring in the continuous harvesting treatment lead not only to a reduction in irradiance at the height in the canopy where bud break occurs, but also to a reduction of the red/far-red ratio (R/FR)

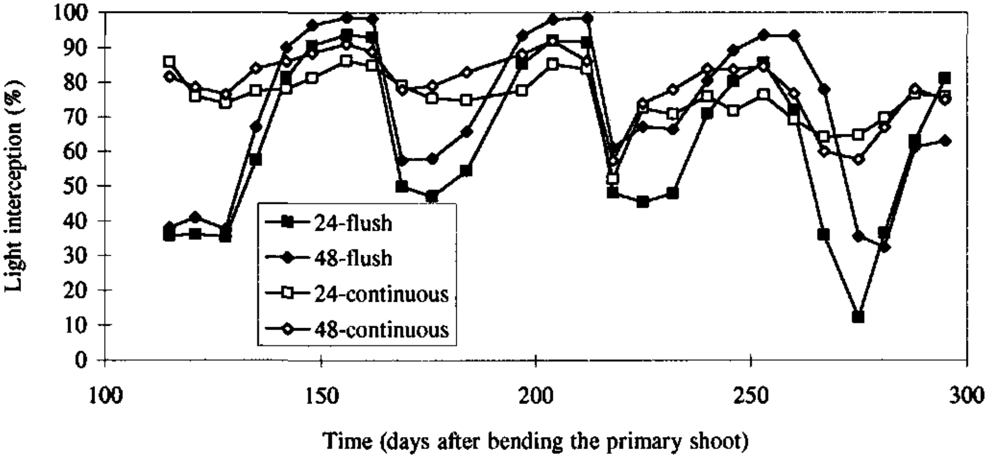


Figure 3. Influence of harvesting method (flush versus continuous) and shoot density (24 and 48 shoots/m²) on light interception of the canopy for 3 flowering cycles.

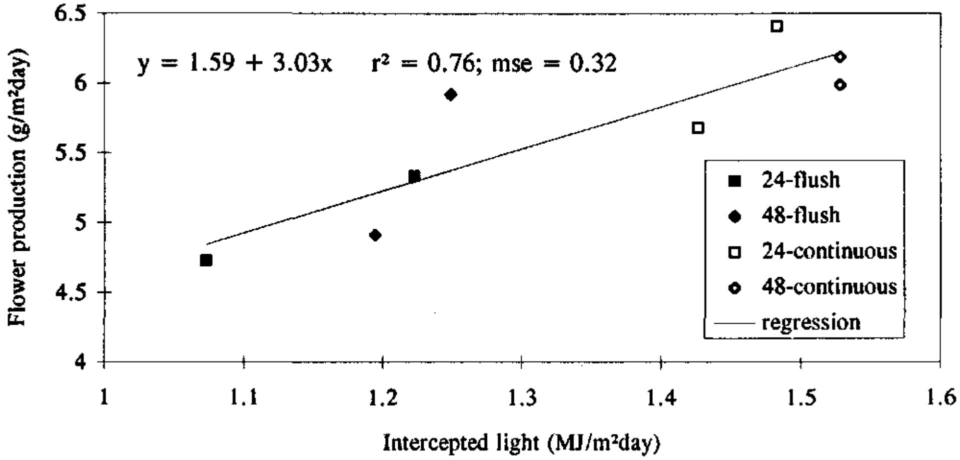


Figure 4. Relation between daily intercepted PAR and dry weight of the total number of flowers harvested in the third-, fourth- and fifth flowering cycle. The regression coefficients of the fitted line are given together with the adjusted square correlation coefficient (r^2) and the standard error (mse).

in the transmitted light (Deregibus *et al.*, 1983). As reviewed by Cline (1991) red light (R) weakens apical dominance whereas far-red (FR) light strengthens it. Mor and Halevy (1984) found for roses that self-shading, associated with dense planting, suppressed lateral bud outgrowth and branching. An additional reason for the lower number of developing shoots in case of continuous harvesting might be a shift in the sink-source relations during harvesting the first-order laterals. Deshooting of the lowermost first-order laterals for 3 weeks after harvesting the uppermost first-order lateral may have resulted in an extra source of assimilates promoting bud break and shoot growth on the uppermost shoot as found by Breugem (personal communication). After 3 weeks of development, under the conditions of the present experiment, these new developing shoots did not show any visible terminal flower bud which may indicate that they still act as strong sinks (Mor and Halevy, 1979). As a result bud break on the lowermost first-order lateral was often restricted to only 1 which reduced the total number of second-order laterals as compared to flush harvesting.

The most obvious effect of flush harvesting was its negative effect on shoot performance probably due to the increased competition for assimilates by the higher number of developing shoots. In addition, since daily intercepted PAR was lower for flush than for continuous harvesting the amount of PAR received per flower probably was much lower in the flush harvesting treatment than in the continuously harvesting treatment, which may explain the difference in shoot weight, length, firmness, growth rate and dry weight percentage between the 2 harvesting methods. Marcelis-van Acker (1994c) who manipulated the assimilate supply in rose by varying the number of 5-leaflet leaves supporting a new shoot, found similar results. Furthermore, she found that a higher assimilate supply shortened the period between bud break and harvesting. In the present experiment we did not record the time of bud break. However, since assimilate supply is probably not influencing the rate of bud break as found by Zieslin *et al.* (1976b) and Marcelis-van Acker (1994c) flush harvesting might have extended the time from cutting until harvesting (Table 1) due to a lower growth rate. Moreover, Byrne and Doss (1981) found that thick shoots shortened the time from cutting until harvesting for the next flowering cycle. They suggest that thick stems may be able to store and translocate more assimilates for new developing shoots. In our study, continuous harvesting gave heavier and firmer flowering shoots (Table 1) with a greater diameter (data not shown) which may have had a similar positive effect on development time of the next flowering cycle. In this respect, it is interesting to notice that in a simulation study in rose by Lieth and Pasian (1991) the simulated growth of a shoot originating from thick mothercanes was under-estimated.

In this study, the higher shoot density as compared to the lower one, resulted in the same negative effect on flower performance as found for flush harvesting due to a reduced assimilate supply per developing shoot. Both shoot density and harvesting system did not influence the percentage of dry matter distributed towards the flowers harvested (harvest index). The harvest index was not influenced by large differences in plant density (7.7 - 17.4 plants/m^2) and plant management systems (Chapter 3.1 and 5.3) although in the latter experiment some seasonal fluctuations could be found due to the method of harvesting. Heuvelink (1995b) already concluded for tomato that differences in assimilate supply per plant, brought about by plant density (Heuvelink, 1995a) or season (Heuvelink, 1995a) did not affect dry matter distribution to the fruits. It may be concluded that a very constant relation exists between total dry matter production and dry weight of harvested parts as reported for several crops by Challa and Heuvelink (1993).

The linear relationship between flower production and intercepted PAR (Figure 4) indicates that light interception is the main factor for assimilate production as in agreement with previous results of Kool (Chapter 5.3). Both harvesting systems seem equally efficient in converting PAR into dry weight of flowers. A possible negative effect of root death, occurring when too many leaves are removed at once as in the case of flush harvesting as found by Fuchs (1986), could not be detected.

It can be summarized that flush harvesting stimulates bud break but due to the reduced overall light interception, total assimilate supply and hence crop growth and flower performance are reduced. Under less controlled circumstances, blind shoots can be bent into the canopy in order to intercept more light. Further research has to reveal whether, if all shoots are in the same stage of development, climate conditions, nutrient supply and disease control can be optimized for that stage while at the same time labour productivity, through mechanization and planned production can be enhanced (Van den Berg, 1996).

4. Physiological background of rose flower production

4.1 Rose crop production as related to plant architecture and carbohydrate content: Effect of harvesting method and plant type

Kool, M.T.N., De Graaf, R. and Rou-Haest, C.H.M. 1996. Rose crop production as related to plant architecture and carbohydrate content: Effect of harvesting method and plant type. (submitted).

Abstract

The dependence between flowering cycles and woody stem parts of a rose crop was studied, with respect to plant architecture and carbohydrate content. Two harvesting methods ("control" versus "flush") and 2 plant types ("control" versus "one-stemmed") were compared. Crop growth and partitioning of dry matter were studied as influenced by crop management during 18 months of culture. For a full-productive year, flush harvesting generally promoted bud break as compared to continuous harvesting but at the same time, also due to a lower light interception, blind-shoot formation was enhanced and the individual flower weight reduced. Number of basal shoots was hardly related to flower production over a full cropping year. Flower production was much more sensitive to the number and diameter of branches at the height of cutting the flowers. The applied treatments did not affect carbohydrate allocation in the plant. Total carbohydrate storage was much too low to argument a clear role for the possible use of movement of carbohydrate reserves towards new growth. Maximum starch level was found in the beginning of summer and gradually dropped to a minimum in December whereafter it increased again to a spring maximum. A cold treatment did increase the total non-structural carbohydrate (TNC) level but no positive influence on new basal-shoot formation was observed. No starch gradient was found in basal stem parts.

Introduction

During the life-span of a rose crop, year-round production is dependent on the architecture of the basal, woody frame of the plant, and understanding the processes involved will contribute to the development of treatments that raise plant productivity (Zieslin *et al.*, 1975). So far, research on the relations between plant architecture and flower production has been mainly focused on bush renewal through the stimulation of basal-shoot formation (Schrock and Hanan, 1981; Khayat and Zieslin, 1982). Only recently, Kool and Lenssen (Chapter 2.1) developed a general concept on ways to improve and manage plant building of young rose plants with respect to basal-shoot formation. They found that reducing the number of developing basal shoots strongly increased the diameter and weight of the remaining ones. Kool *et al.* (1991) already reported that in a commercial rose crop stems of plants having only 1 basal shoot showed the greatest increase in diameter and xylem area during the first 1 months of growth. The observed competition between basal shoots on the same plant might be an argument for developing a plant system with only 1 basal shoot per plant.

Several authors suggested that plant treatments like pruning, pinching, flower removal and disbudding have their main effect on storage of carbohydrates in lower parts of the plants (Byrne and Kohl, 1972; Zieslin *et al.*, 1975; Morisot *et al.*, 1996). For year-round rose flower production, the woody stem parts may serve as a reservoir for the normal shoot development under adverse conditions (Zieslin *et al.*, 1975). Storage and mobilization of carbohydrate reserves in perennial parts play an essential role in winter survival and spring regrowth of perennial plants (Oliveira and Priestley, 1988; Loescher *et al.*, 1990).

Plant treatments such as pinching and de-shooting can also be used to aim production at periods of high demands (Jones and Hartley, 1978). Kool (Chapter 3.4) studied the effect of continuous versus flush harvesting on the production and partitioning of assimilates and flower performance in rose under controlled environmental conditions. He found that flush harvesting stimulated bud break but had a negative influence on crop growth rate and flower performance.

In view of the importance of plant architecture as well as carbohydrate reserves in stems for flower production in rose, it may be assumed that:

1) The number of basal-shoots is often found to be positively correlated with flower production (Van Rijssel, 1982; De Vries and Dubois, 1983).

2) Flush harvesting increases the number of buds that break and develop into a shoot but decreases the individual shoot weight (Chapter 3.4).

3) Plant treatments like de-shooting affect flower production by influencing carbohydrate allocation. Carbohydrate storage plays an important role in flower production (Byrne and Kohl, 1972; Zieslin *et al.*, 1975; Morisot *et al.*, 1996).

4) Seasonal patterns of carbohydrates (high during the autumn and low during spring) and a gradual increase of starch for lower plant parts, especially roots (Loescher *et al.*, 1990; Haddad *et al.*, 1995), as usually found for perennial woody plants, are similar for rose.

The goal of the present study was to test these assumptions. Therefore, growth and development of 3 treatments are compared i.e. a 'normal' crop where basal-shoot formation was not restricted, a 'normal' crop having only 1 basal-shoot per plant, and a flush harvested crop in which each flowering cycle is harvested in a short time. The influence of these treatments on crop performance was studied for more than 1.5 years.

Material and methods

At the end of January 1992, single node cuttings of *Rosa hybrida* 'Frisco' were propagated on rockwool blocks (9x9x9 cm). One month later, rooted plants were placed on rockwool slabs (100x15x9 cm) in 3 greenhouse compartments of 250 m^2 each with 4 plants per rockwool slab. The rockwool slabs were placed transversally on the bed with discharge of drain water at one side of the bed. Distance between the slabs was 30 cm (13.3 plants/m^2); distance between beds was 60 cm. Plants were drip irrigated automatically with the aid of an irrigation calculation model, developed by PBG-Naaldwijk (De Graaf, 1988). Day/night temperature was set at 19/17°C but from the middle of November until the middle of January at 12/12°C.

Plant treatments

Two harvesting methods ('control' versus 'flush') and 2 plant types ('control' versus 'one-stemmed') were compared.

- *Treatment continuous harvesting (Control):* The primary shoot was bent horizontally 6 weeks after planting and new basal and lateral shoots were harvested above the first or second 5-leaflet leaf counted from the base of the stem. In subsequent flowering cycles, flowers were harvested on the first 5-leaflet leaf. During winter the underhook cutting procedure was applied as described by Zieslin (1981).
- Treatment flush harvesting: Primary shoots were treated as in the control treatment. New basal and lateral shoots were decapitated, de-shooted for 4 weeks and then removed by cutting above the second 5-leaflet leaf counted from the base of the stem. Subsequent 2 flowering cycles were harvested above the first 5-leaflet leaf. The shoots of the third cycle were again decapitated and de-shooted for 2 weeks and thereafter removed by cutting above the second 5-leaflet leaf. In the middle of January, after the low temperature treatment, shoots were bent horizontally at a height of 40 cm in order to allow a simultaneous development of new sprouting buds.
- Treatment one-stemmed: As in the control treatment but the primary shoot was bent down 2 weeks later. Only 1 basal shoot was allowed to sprout which was harvested at the third five-leaflet leaf. Only 2 first-order laterals were allowed to develop and these were harvested above on the second 5-leaflet leaf. Further harvesting was done as for the control.

Measurements

From April 1992 until September 1993, flower production (number, length and fresh weight) and weight of blind shoots and other discarded pruning were recorded 3 times a week. Shoots which were decapitated and de-shooted were recorded as flowering shoots. Destructive measurements were conducted at 9 times during the experimental period, i.e. on

18 June, 29 July, 7 September, 26 October and 25 November 1992 and on 18 January, 11 March, 12 May and 30 September 1993. Each time, per treatment 4 plants per rockwool slab per compartment were taken (4*3*3 = 36 plants). Empty spaces were filled by plants of the same size. Number and diameter of basal shoots and of their first, second and third order laterals were determined. Leaf area (Licor Model 3100 Area Meter) and weight (fresh and dry; ventilated oven, 60°C for at least 48 h) of leaf and stem parts were measured separately for the root collar, primary shoot, basal stems, first-order stems, second-order stems, third-order stems, flowering shoots, and blind shoots. The harvest index (HI) was defined as the fresh weight of harvested flowering shoots divided by the total fresh weight production. Except for the flowering and blind shoots, carbohydrates analyses was done in all stem types. Pieces of 1 cm were cut from every 10 cm stem, frozen in liquid nitrogen, freeze dried and stored at -18 °C. Freeze dried material was ground and extracted with 80% ethanol. Sucrose, glucose and fructose were analyzed by HPLC (Interaction CHO620 column) using water as eluent at a flow rate of 0.5 ml/min at 90 °C. The extraction residue, containing starch, was hydrolysed enzymatically by amyloglucosidase (Boehringer Mannheim) into glucose which was analyzed by HPLC. Total non-structural carbohydrates (TNC) were determined by summing the concentrations for total sugar and starch.

Experimental design

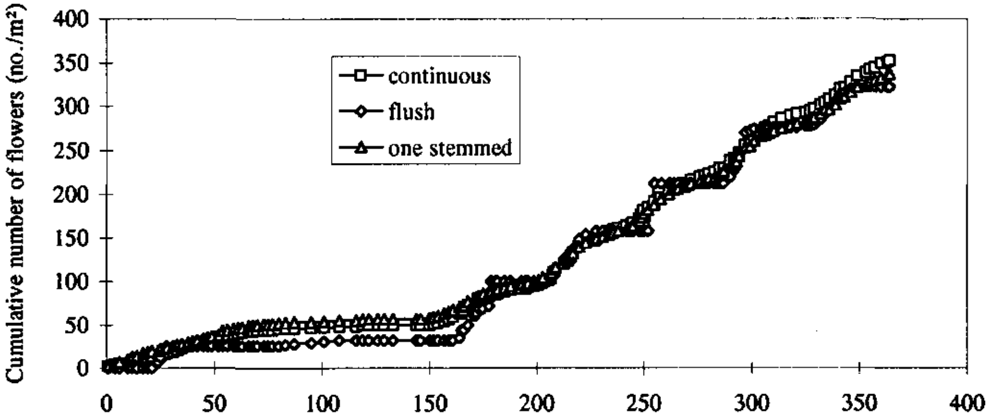
All treatments were randomized in double plots of approximately 12 m^2 bed in each of the 3 greenhouse compartments of 150 m^2. Data were averaged per treatment per compartment and expressed per m^2 bed. Results were statistically analyzed as a randomized block design by Analysis of Variance using the package of SYSTAT. Mean separation was done by Tukey's-HSD test.

RESULTS

Flower production

Cumulative number of flowers, flowering shoot weight and biomass production were reduced by flush harvesting and in the one-stemmed plant type as compared to the control treatment (Table 1). Flower weight was highest for the one-stemmed plant type. Flush harvesting resulted in an increased number of blind shoots (data not shown) and a lower harvest index (Table 1).

For a full-productive year, number of harvested flowers was not significantly affected by treatments (Figure 1). However, cumulative weight of flowering shoots was clearly reduced by flush harvesting (Figure 2) due to a strong decrease in individual shoot weight (Table 1). The one-stemmed plant type resulted in heavier flowering shoots as compared to the control especially during spring and early summer (data not shown).

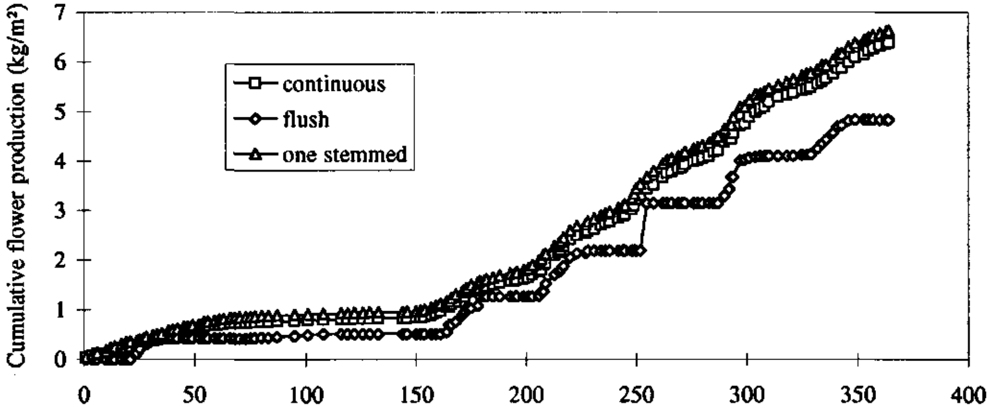


Time (days from 2 October 1992)

Figure 1. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on the number of flowers during a full productive year ranging from 2 October, 1992 until 1 October 1993.

Plant architecture

Flush harvesting slightly increased the number of basal shoots (Figure 3; only significant for the destructive harvest 2 and 4) and first- and second-order laterals (data not shown) as compared to the control treatment but hardly any differences in diameter were found (Figure 4). Basal shoots were much thicker in the one-stemmed plant type than in the control (Figure 4). The same holds for the first- and second order shoots (data not shown). Number of third-order laterals was the same in the 3 treatments with the exception that in the flush treatment almost no third-order stems remained just after bending the stems horizontally at a height of



Time (days from 2 October 1992)

Figure 2. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on the fresh weight of flowering shoots produced during a full productive year ranging from 2 October, 1992 until 1 October, 1993.

Table 1. Influence of harvesting system ('flush' versus 'continuous') and plant type ('control' versus 'one-stemmed') on the cumulative flower production in number and weight (total and average), total biomass production and harvest index for the period from the time of planting (28 February, 1992) until 1 October, 1993. Different letters per column indicate significant differences.

Treatment	Flower production: Number (no./m²)	Weight (g/shoot)	Production (kg/m²)	Biomass Production (kg/m²)	Harvest index (%)
Control	565 a	17.9 b	10.1 c	12.9 c	78 b
Flush	488 b	14.0 a	6.9 a	9.9 a	69 a
One-stemmed	453 b	19.7 c	8.9 b	11.6 b	77 b

40 cm (after the low temperature period). Flush harvesting generally tended to give thinner third-order laterals but no significant differences were found (Figure 4). During winter and spring the number of third-order laterals was lower for the one-stemmed plant type (Figure 3). In all treatments plant dry weight increased during the first year of culture, stabilized during winter and increased again during the second year of growth (Figure 5). In the flush harvesting treatment plant weight was slightly higher then in the other treatment except for the spring period.

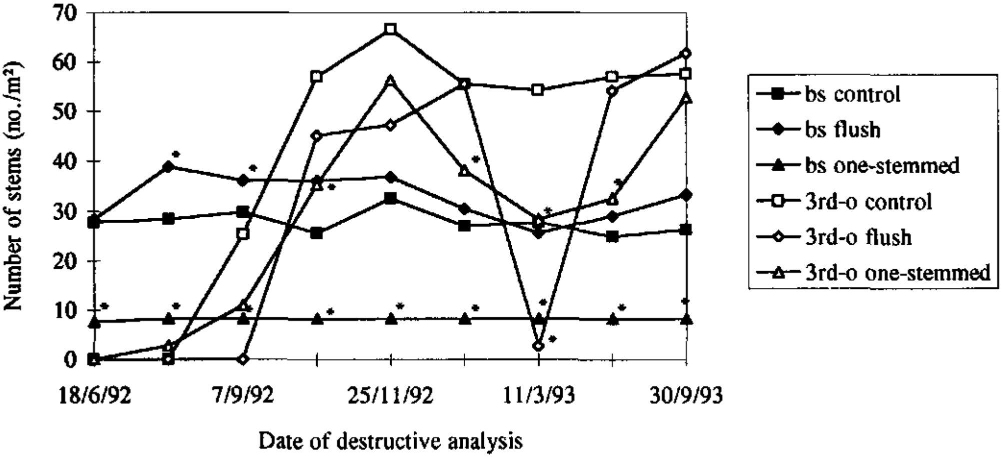


Figure 3. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on number of basal shoots (bs) and third-order laterals (3^{rd}-o) over the experimental period. Values which are significantly different from the control are indicated with an *.

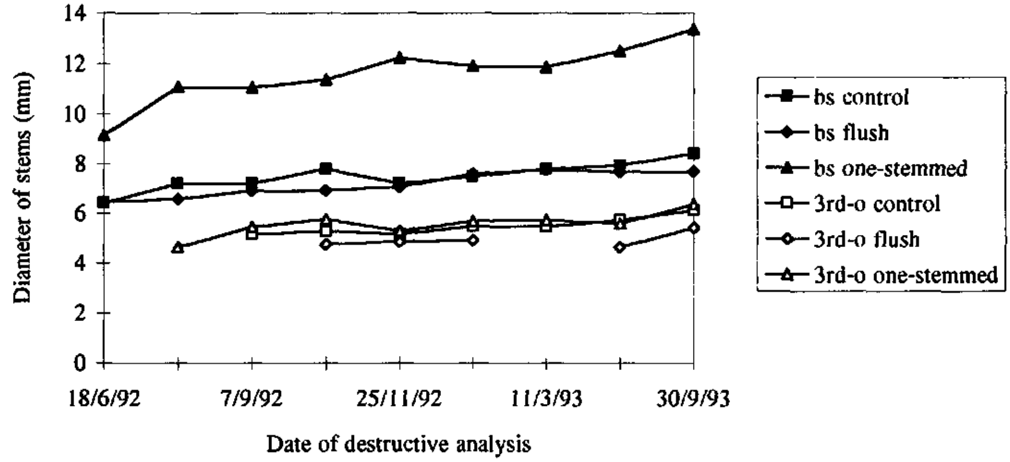


Figure 4. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on the diameter of basal shoots (bs) and third-order laterals (3^{rd}-o) over the experimental period.

Carbohydrates

Generally, total non-structural carbohydrate concentration (TNC) differed little between treatments. Throughout the trial it fluctuated between 10 and 20 mg/g dry weight but a peak occurred just after the low temperature treatment (Figure 6). Exception form the high values for one-stemmed plant type and for flush harvesting at the first and third destructive harvest,

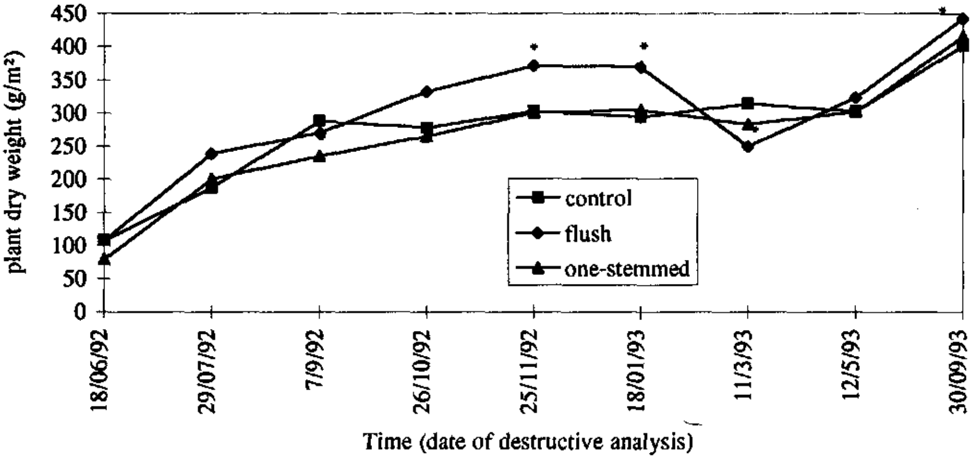


Figure 5. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on the plant weight, as measured from the root collar up to the third-order laterals, over the experimental period. Values which are significant different from the control are indicated with an *.

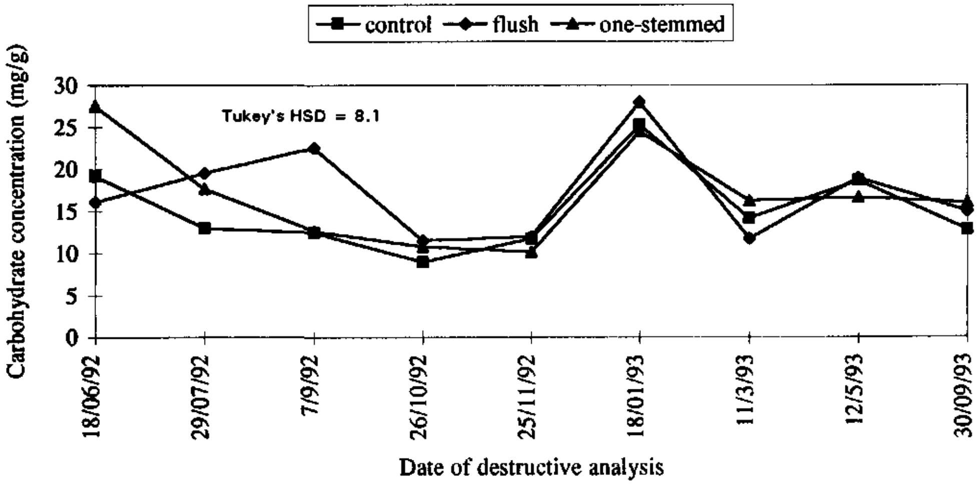


Figure 6. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on the carbohydrate concentration (TNC) of stems as averaged for the different parts over the experimental period. A significant interaction occurred between date of destructive harvest and plant treatment. Therefore, the value of Tukey's HSD holds for all dates.

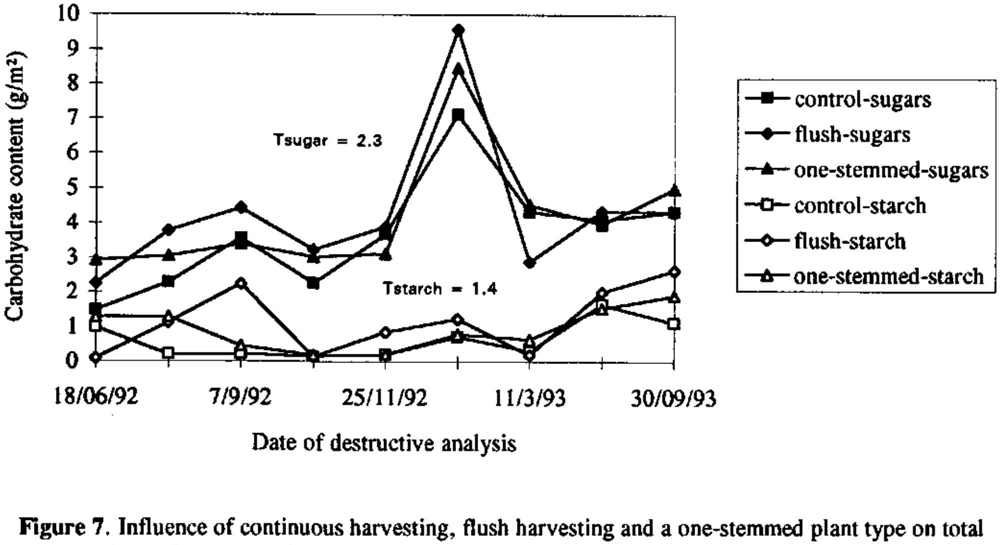


Figure 7. Influence of continuous harvesting, flush harvesting and a one-stemmed plant type on total sugar and starch contents in plant parts over the experimental period. A significant interaction occurred with respect to both sugar and starch content between date of destructive harvest and plant treatment. Therefore, Tukey's HSD values for both sugar (Tsugar) and starch (Tstarch) respectively, holds for all dates.

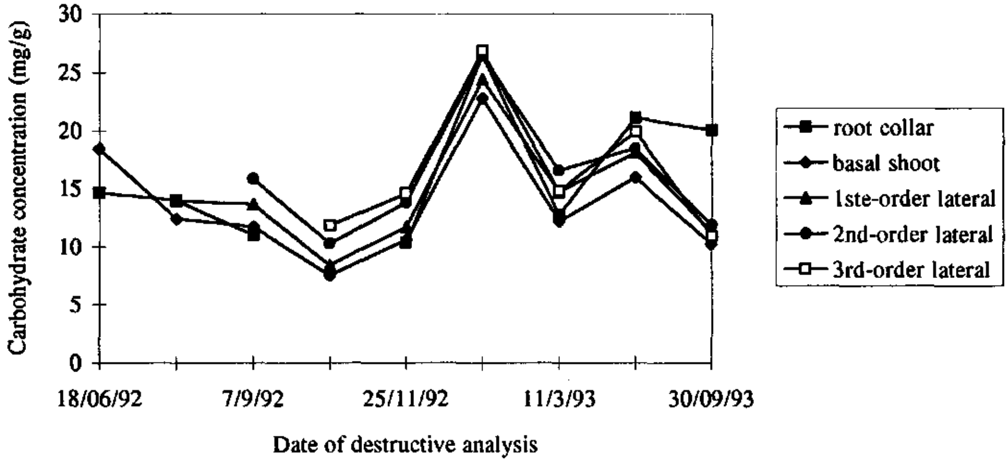


Figure 8. Partitioning of total non-structural carbohydrates over several plant parts as averaged for all treatments from root collar up to third-order laterals over the experimental period.

respectively. TNC contained 50-80% sucrose, 5-15% glucose and fructose, and 5-30% of starch (data not shown). No other carbohydrate compounds could be detected. The separate sugars roughly followed the same pattern as TNC but starch was low from the late autumn until early spring. Total sugars and starch were also not much affected by treatments (Figure 7). As time progressed, a gradual increase in reserves up to 7 g/m², could be detected for sugars and starch but just after the winter period a peak of 10 g/m² was found. No clear differences in carbohydrate concentrations were found with respect to the height of the various stem parts within the plant (Figure 8), except for the higher concentration in the root collar in the last sample.

Discussion

Harvesting method

As was also found by Kool (Chapter 3.4) flush harvesting stimulated bud break in each flowering cycle. However, due to the simultaneous sprouting of a high number of buds that will act as strong sinks during the first 3 weeks of their development (Mor and Halevy, 1979; Marcelis-van Acker, 1994c) competition for assimilates resulted in an increased number of blind shoots, a lower harvest index and a reduced individual flower weight. A reduction of flower weight probably due to the simultaneously development of shoots was also found by Kool (Chapter 3.4), Marcelis-van Acker (1994c) and Mor *et al.* (1981). Since number of harvested flowers over a full productive year was not affected in this study, a clear reduction in the cumulative production weight by flush harvesting occurred. This reduction in may be explained by (1) total weight of decapitated flower heads and removed laterals during deshooting (see M&M) were not taken into account, (2) removal of many leafy shoots in a short time might have enhanced root dying and delayed root regrowth (Fuchs, 1986), and (3) flush harvesting results in a reduced light interception just after harvesting the entire flush, which reduces biomass production (Chapter 3.4). Since hardly any differences in plant architecture, total plant weight, and biomass partitioning (data not shown) were found between the flush and continuous harvesting, the observed differences in flower production remain unexplained by these aspects. Furthermore, differences in level of individual or summed compounds of non-structural carbohydrates were not found between flush or continuous harvesting indicating that carbohydrate storage or partitioning did not respond to these treatments.

Plant type

The one-stemmed plant type reduced the number and total weight of harvested flowers over the experimental period. However, this reduction completely occurred early in development because for a full-cropping year no differences in flower production or plant weight were found as compared to the control treatment. The importance of basal shoots for a vigorous and highly productive rose-crop have been stressed since long (Kofranek and Fisher, 1949; Asen and Hamner, 1953) and a positive relation between the number of basal shoots and flower production was often reported (Van Rijssel, 1982; De Vries and Dubois, 1983). However, although in the present study number of basal shoots was more than 3 times lower for the one-stemmed plant type, flower production was not affected over a full-productive year. A similar result was observed by Kool (Chapter 3.2) in a long-term production experiment. In this latter experiment, it was shown that new basal-shoots directly competed with already existing ones.

During the first months of culture, light interception for the one-stemmed plants and as a direct result biomass gain was reduced probably due to the much lower number of basal-, first- and second-order shoots. However, their diameter had markedly increased which agrees with results of Kool and Lenssen (Chapter 3.1) who clearly demonstrated competition between developing basal shoots. Flowering shoot weight was significantly higher in the one-stemmed plant especially during the spring period. During that period, the underhook cutting procedure was applied, i.e. harvested flowers were cut back on second or third-order laterals (Zieslin, 1981). These laterals were thicker than in the other treatments which might have had a positive influence on the development of new shoots. Byrne and Doss (1981) found for rose a positive influence of the parent shoot diameter on the diameter and weight of daughter shoots. Similarly, Lieth and Pasian (1991) concluded from a simulation study, that in thick stems translocation of assimilates towards new developing shoots is more marked.

It might be concluded from these results that flower production for a full cropping year is hardly influenced by number of basal shoots but depends on the number of branches at the height of cutting the flowers as stressed by Van Rijssel (1982) and Kool and Van de Pol (Chapter 2.2) as well as the branching capacity which seems to be influenced by the diameter of the parent shoot.

Carbohydrates

Treatments hardly affected the non-structural carbohydrate concentration (TNC) of stem parts during a full-productive year. An increase in TNC was observed for the one-stemmed plant type at the first destructive harvest, probably due to the low number of developing shoots in combination with high light intensity. Another peak was found for flush harvesting in the third sample which must be a direct response to de-shooting (Chapter 4.2). However, apart from a possible treatment effect, total carbohydrate storage was much too low to be of much significance for new growth, which is in contrast to the opinion of Byrne and Kohl (1972), Zieslin *et al.* (1975), Zieslin and Mor (1981a) and Morisot *et al.* (1996). The theoretically maximal biomass gain from stored carbohydrates can be calculated (Chapter 4.2) and just after the winter period amounted to only about 30 gram of fresh weight per m^2 which is equivalent to 2 flowering shoots. Therefore, it can hardly be argued that in the present situation carbohydrate reserves play an essential role for flower production, even more so since the observed differences in TNC between treatments had already disappeared after 1 flowering cycle.

The general trend for starch in different parts of a rose plant as occurred in the present study is similar to that for other woody plants species (Priestley, 1970). However, in our study, the starch level was maximal in the beginning of summer instead of in the autumn and gradually dropped to a minimum in September-December probably due to the higher temperature and metabolic activity inside a glasshouse. Thereafter, it increased again to a maximum in spring. Carbohydrate content increased during the low-temperature period of 8 weeks at 12^0C which is in accordance with results of Schrock and Hanan (1981) who subjected 'Samantha' and 'Cara Mia' roses to 3 periods of low temperature. However, in the present study no positive effect of stored carbohydrates on new basal-shoot formation was found which disagrees with results of Schrock and Hanan (1981) and Zieslin and Mor (1981b).

Although all perennial organs of a woody plant may have a storage function, the highest concentrations of carbohydrates are usually found in root tissues (Loescher *et al.*, 1990). A decreasing gradient of starch from the basal to upper plant parts is often found as reported for rose by Menoud *et al.* (1991) and Kool (Chapter 4.2) and for plane trees by Haddad *et al.* (1995). In the present study no such starch gradient could be shown. An explanation might be that pruning disturbs the gradient by creating new sinks resulting in depletion of reserves as also occurs in other regularly cut crops like forage and pasture crops (Spague and

Sullivan, 1950), tea plants (Tubbs, 1937) and plane trees (Haddad *et al.*, 1995).

With respect to the assumptions put forward in the introduction, it is concluded that:

- The number of basal-shoots is hardly related to rose flower production over a full cropping year.
- Flush harvesting increases the number of developing shoots but at the same time, also due to a lower decrease in light interception, blind shoot formation is enhanced and individual flower weight reduced.
- The applied treatments did not affect carbohydrate allocation in the plant. Furthermore, there were hardly any arguments that differences in carbohydrate storage play an important role in rose flower production
- The seasonal pattern of carbohydrates, as generally found in woody plants grown outside is somewhat disturbed in the case of glasshouse crops, due to the high autumn temperature in the glasshouse. The gradual decline of starch from plant base to the top was not found which might be due to the continuous cutting practice.

4.2 Importance and use of carbohydrate reserves in above ground stem parts of rose cv. Motrea

Kool, M.T.N., Westerman, A.D. and Rou-Haest, C.H.M., 1995. Importance and use of carbohydrate reserves in above ground stem parts of rose cv Motrea. Journal of Horticultural Science, 71, 000-000 (accepted).

Abstract

The effect of deshooting of flowering stems of rose cv Motrea as compared to a normal harvesting procedure was studied with respect to carbohydrate storage and subsequent flower production after an underhook cutting of flowering shoots. Growth analyses in 2 periods of time were conducted in order to calculate total biomass production and partitioning. Analyses of soluble sugars and starch in samples of the stem taken at several heights in the plant were also carried out. In general, starch concentrations increased and sugar concentrations decreased from upper to lower stem parts. Deshooting resulted in an increase in total non-structural carbohydrates, mainly caused by starch. The stored carbohydrates were used during a subsequent flowering cycle. Total extra carbohydrate reserves due to the deshooting practice could explain the resulting increase in fresh weight production. Biomass production was not influenced by treatments over the experimental period but deshooting greatly reduced flower production and enhanced the weight of discarded prunings. It is concluded that treatments primarily directed on redistribution of carbohydrates are probably of little use to improve the management of a rose crop.

Introduction

To manage a rose crop during successive years of culture, several strategies with respect to pruning, pinching, detopping, disbudding and other practices, have been developed. Byrne and Kohl (1972) suggested that in this way the carbohydrate storage in lower parts of the plant is affected. Zieslin *et al.* (1975) found that pinching treatments, encouraging the growth of inhibited buds, had a negative effect on carbohydrate storage in rose stems. However, if the new laterals were also removed the movement of assimilates was directed towards lower plant parts and subsequent flower production was improved, depending on cultivar (Zieslin *et al.*, 1976b). Zieslin *et al.* (1975) suggested, that stored carbohydrates serve as a reservoir for the normal development of flowering shoots especially under insufficient light. Recently, Morisot *et al.* (1996) developed a new method of flower harvesting based on the assumption that deshooting enhances storage of carbohydrates for future use. There is no doubt that stored carbohydrates are essential especially in woody plants (Loescher *et al.*, 1990) but their role is probably restricted to the initial stages of development (Hansen, 1971). The greater part of the reserves are used in maintainance respiration rather than for new building material (Hansen and Grauslund, 1973; Tromp, 1983). The implications of the importance of reserves in relation to management practices, are only beginning to be realised (Loescher *et al.*, 1990). Up to now experimental data showing that stored carbohydrates are used for increased flower yield are lacking for rose. Therefore, in this study, 2 experiments were conducted to determine the storage capacity of rose stems and the importance of carbohydrate reserves for flower production. The first experiment was carried out in winter in a 2 year old crop of Rose cultivar 'Motrea' while the second experiment was conducted in summer and autumn in a 4 year old crop of the same cultivar.

Material and methods

Experiment 1

In February 1990, scion-rootstock combinations of *Rosa hybrida* 'Motrea' stented on *Rosa hybrida* 'Multic', *Rosa hybrida* 'Moonlight' and *Rosa hybrida* 'Ludiek' were planted into soil in 2 rows, one on the east and the other on the west side of a 12 m x 12 m greenhouse compartment. Plant distance was 16.7 cm. Plant treatment was normal for Dutch rose culture as described in detail by Kool and Van de Pol (Chapter 3.2). Temperature set-point was 20°C during the day and 18°C at night. From September until April during the day supplementary lighting by high pressure sodium lamps (SON-T; 400 Watt; 36.5 μmolm^{-2}s^{-1}PAR) was given when global radiation dropped below 100 W m^{-2} outside the greenhouse. Day length was 18 h.

Treatments

Starting at 12 October 1992, 2 treatments were compared for a period of 8 weeks. In the 'control' treatment flowers were continuously harvested at the second 5-leaflet leaf counted from the base of the shoot. In the 'de-shooting' treatment, all flower heads and subsequent sprouting buds were removed. On 9 December, for both treatments, all stems were pruned above the lowest 2 leaves per stem counted from the base of the plant, approximately at a height of 40 cm above soil level (see Figure 1). New shoots were harvested on the first 5-leaflet leaf counted from the base of the flowering shoot.

Experimental design

The 2 border rows were divided into 4 blocks of 16 plants each. From each block 8 randomly chosen plants were used for destructive carbohydrate measurements and the remaining plants for estimating flower production.

Measurements

Number and fresh weight of harvested flowers and blind shoots per plant were recorded from 18 January - 22 February 1993. Carbohydrate analyses were done at 1, 4, 8, 10, 12, 14 and 19 weeks after the start of the experiment from samples of the stem taken from the lowest 30 cm of 4 plants. Pieces of 1 cm stem material were cut from every 10 cm of the stem, weighted, frozen in liquid nitrogen, freeze dried and stored at -18°C. Freeze dried material was ground and extracted with 80% ethanol. Sucrose, glucose and fructose were analysed by HPLC (Interaction CHO620 column) using water as eluent at a flow rate of 0.5 ml/min at 90°C. Sugar concentrations were calculated in gram per gram dry weight of stem material. The residue from the ethanol extraction, which contains starch was enzymatically hydrolyzed with amyloglucosidase (Boehringer Mannheim) into glucose which was analysed by HPLC. The amount of starch was calculated as gram glucose per gram dry weight material. Total non-structural carbohydrates (TNC) were determined by summing the concentrations for total sugar and starch. Results were analysed statistically as a randomized block design using the Genstat package. Mean separation was by Students *t*-test ($P<0.05$).

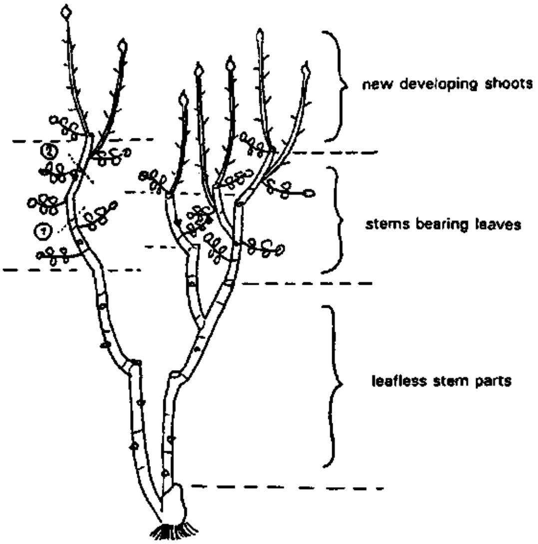


Figure 1. Diagram of a rose plant indicating the 3 parts of the plant analysed separately in experiment 2. The sites of pruning the stems downward is indicated by 1 or 2 for experiment 1 and 2, respectively.

Experiment 2

In this experiment, in 1994, a four and a half year old rose crop of *Rosa hybrida* 'Motrea' stented on 3 rootstocks was used. Plants were planted in 4-row beds at a density of 12 (0.25 m x 0.33 m) or 24 (0.25 m x 0.17 m) plants per m^2 bed as described in detail by Kool and Van de Pol (Chapter 3.2). Climatic conditions were as described for Experiment 1 except that on 1 September supplementary lighting was stopped (day of pruning back the plants by the underhook cutting procedure, see below) in order to increase the possible effect of treatments on redistribution of stored carbohydrates.

Treatments

Two treatments were applied which were similar to those in the first experiment:

- *Treatment 'Control':* Flowering stems were harvested from 1 August 1994 until 1 September 1994. On 1 September all developing shoots were pruned downwards by an underhook cut (Zieslin, 1981) on the first bud below the leaf-axis where the developing shoot originated from (see Figure 1). From 10 October onwards, the new cycle of flowering shoots was harvested at the first 5-leaflet leaf counted from the base of the flowering shoot. From 22 November onwards, the second cycle of flowering shoots was again pruned downwards.
- *Treatment 'De-shooting':* Starting at 1 August, flowering stems were topped and all subsequent lateral shoot growth removed. On 1 September, all disbudded shoots were pruned downwards as described for the 'control' treatment. Subsequent harvest practice was the same as for the control treatment.

Measurements

Number and weight of harvested flowers and the discarded prunings, defined as total weight of blind shoots, shoots which were detopped and stem parts due to the cutting procedure, were recorded. At 4 times during the experiment (1 Augustus, 1 September, 16 September and 10 October) from 12 plants of each treatment, fresh and dry weight of stems and, if present, leaves and leaf area (Licor Model 3100 Area Meter) were measured separately from: 1) the most basal leafless stem part, 2) the stem part bearing leaves, and 3) the developing new shoots. Stem biomass partitioning, growth rate, flower production and weight of discarded prunings were calculated for 3 specific periods: 1 August until 10 October (the period of conducting the treatments until the time of harvesting the first flowering cycle after pruning the stems downwards); 10 October until 22 November (period of harvesting the first flowering cycle); 22 November until 11 January (period of harvesting the second flowering cycle). In stem tissue, analysis of soluble sugars (sucrose, glucose and fructose) and starch was done as described for Experiment 1. The absolute carbohydrate amounts expressed as g per m^2 were calculated.

Experimental design

The experiment is designed as a split plot scheme with the 2 treatments of 3 m² bed each randomized over a bed of 6 m² in 4 replicates. The 3 plants that were used for destructive growth analyses at each of 4 times during the experiment, were randomized as subplots. Only inner row plants were used for growth and carbohydrate analyses.

Interaction with previous treatments as described by Kool (Chapter 3.3) and Kool and Van de Pol (Chapter 3.2) was allowed for by taking rose yield of a full-productive year just preceding the start of the experiment as a co-factor in analyses of treatment effects on flower production. Flower production was calculated per m² bed corrected per period of time for missing plants used for destructive analyses. Analysis of variance was done according to a randomized split plot scheme with the statistical Genstat package. Mean separation was done according to Students *t*-test ($P<0.05$).

Results

Experiment 1

During the 8 weeks of de-shooting sucrose and starch were slightly higher than in the control

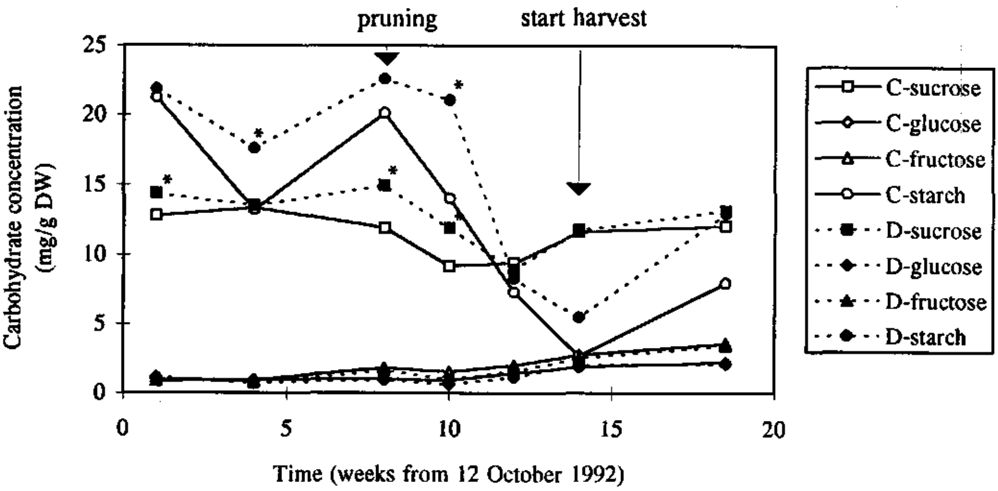


Figure 2. Time-course of soluble carbohydrate concentrations and starch in basal stem parts as affected by the control (C) and deshooting (D) treatment. Significant differences for $P<0.05$ are indicated by an asterix.

Table 1. Effect of plant treatments on flower production of *Rosa hybrida* 'Motrea' between 18 January and 22 February, 1993. Different letters per column indicate significant differences ($P<0.05$).

Treatment	Biomass production (g/m²)	Flower production (g/m²)	Discarded prunings (g/m²)	Growth rate (g/day)
Control	2980 a	1990 b	989 a	18.2 a
Deshooting	3038 a	1449 a	1590 b	18.5 a

treatment (Figure 2). After pruning, starch concentration in both treatments dropped in the next 6 weeks but increased thereafter. Sucrose was only little reduced during the 4 weeks after pruning but later it reached again the original level. The concentrations of glucose and fructose were low as compared to sucrose and starch. It slightly increased towards the end of the experimental period.

Treatments did not significantly influence number and total weight of harvested flowers and blind shoots (Table 1). However, de-shooting increased the weight of flowering shoots by more then 15%.

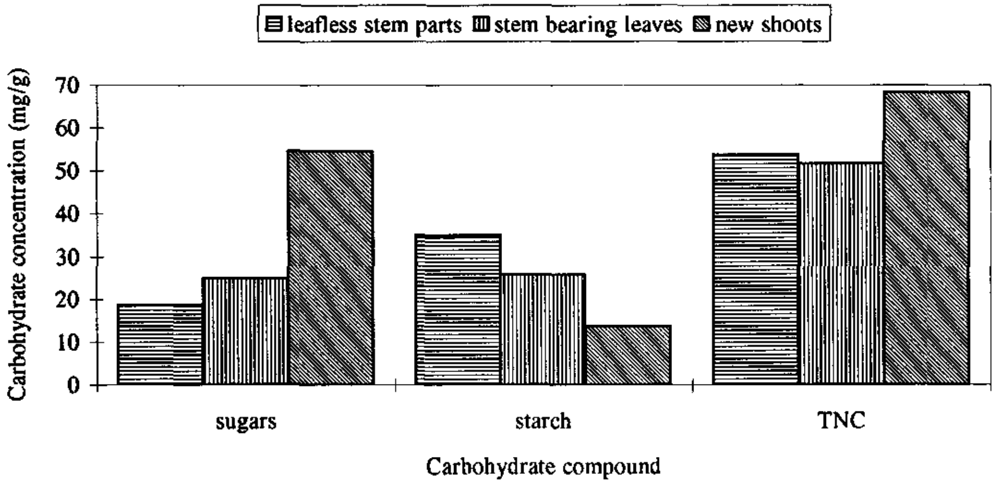


Figure 3: Sugars, starch and total non-structural carbohydrate concentrations (TNC), expressed in mg dry weight of stem tissue as affected by plant height and averaged over the experimental period.

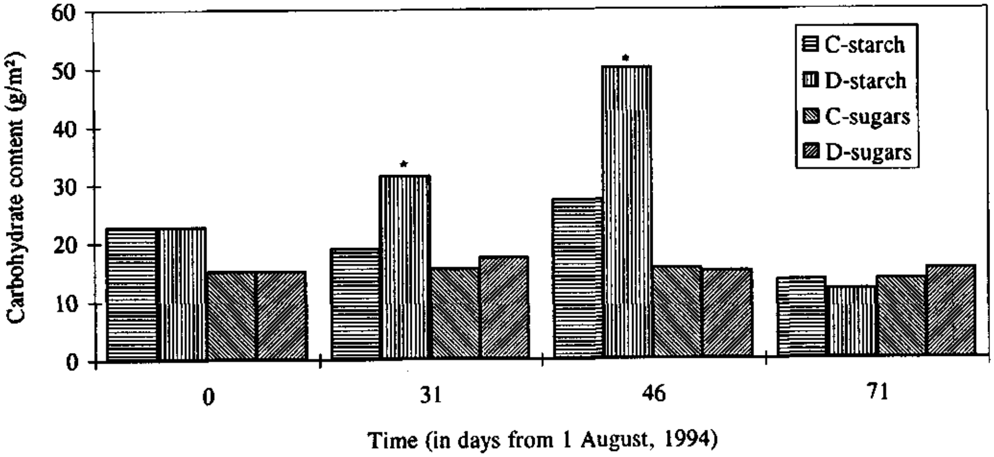


Figure 4. Influence of plant treatment (C = 'Control' and D = 'Deshooting') on soluble sugars and starch (g/m²) in the above ground stem in relation to time. Significant differences for $P<0.05$ are indicated by asterix.

Experiment 2

On average, 70% of stem biomass was found in the most basal leafless stem parts of the plant (data not presented). From the basal towards upper stem parts, soluble sugars increased and starch decreased (Figure 3). Total non-structural carbohydrate concentration was highest in the new shoots. The concentrations of glucose and fructose were only about 10% of that

Table 2. Effects of plant treatment on biomass production and partitioning between 1 August 1994 and 11 January 1995 of *Rosa hybrida* 'Motrea'. Different letters per column indicate significant differences ($P<0.05$).

Treatment	Biomass production (g/m²)	Flower production (g/m²)	Discarded prunings (g/m²)	Growth rate (g/day)
Control	2980 a	1990 b	989 a	18.2 a
Deshooting	3038 a	1449 a	1590 b	18.5 a

Table 3. Effect of plant treatments on biomass production and partitioning for *Rosa hybrida* 'Motrea' for 3 periods of time (period 1; 1 August - 10 October 1994; period 2; 10 October - 22 November 1994 and period 3; 22 November 1994 - 11 January 1995). Different letters per column indicate significant differences ($P<0.05$).

Period	Treatment	Biomass production (g/m²)	Flower production (g/m²)	Discarded prunings (g/m²)	Number of flowers (no./m²)	Flower weight (g)	Flower length (cm)
1	Control	1568 a	721 b	847 a			
	Deshooting	1526 a	88 a	1438 b			
2	Control	767 a	734 a	32 a	90 a	8.1 a	32.7 a
	Deshooting	852 b	817 b	37 a	87 a	9.4 b	33.6 a
3	Control	648 a	535 a	112 a	61.6 a	8.5 a	42.7 a
	Deshooting	648 a	544 a	105 a	65.4 a	8.4 a	41.9 a

of sucrose in the most basal stem parts and up to 40% in the flowering stems (data not given).

De-shooting positively affected the starch content of the above ground stem tissue as compared to the control (Figure 4). Two weeks after underhooking (day 46) starch content had further increased in both treatments. At the beginning of harvesting the next flowering cycle (day 71) it was again low. Contents of soluble sugars were relatively stable throughout the experiment.

Leaf area per square meter bed (LAI) was not much affected by treatments during the experimental period (data not given). Four weeks after the start of the experiment (1 Sept.), underhooking resulted in a sharp decrease of the LAI which dropped from 3 to 1. Thereafter LAI rose again until values around 3.

Biomass production and growth rate were the same for both treatments over the experimental period (Table 2). However, deshooting resulted in a much lower flower production and a higher weight of discarded prunings. Biomass production and growth rate were not significantly influenced by plant treatment before flower harvest of the first cycle (from 11 October onwards) (Table 3). However, deshooting enhanced the weight of discarded prunings at the expense of flower production.

Flower production and biomass production were higher for the deshooting treatment during the period of harvesting the first flowering cycle after pruning downwards (10 October to 22 November, Table 3). Deshooting produced heavier flowers but number and length of shoots were not affected. Treatments hardly affected biomass production and partitioning over flowering shoots and discarded prunings during the second cycle of flower production (22 November 1994 - 11 January 1995, Table 3). Furthermore, there were no differences in number, weight or length of the flowers harvested.

Discussion

Although some authors ascribe a clear role to carbohydrate reserves in rose growing (Zieslin *et al.*, 1975; Byrne and Kohl, 1972) especially after deshooting (Zieslin and Mor, 1981a; Morisot *et al.*, 1996) most studies on deshooting confirm the present data (Table 2), that deshooting reduced flower production over a period of time. The investment (a deshooted flower is not saleable anymore) is too high. However, our study shows that removal of flower heads and subsequent lateral growth for a period of time enhance storage of carbohydrates, mainly starch, as previously suggested by Byrne and Kohl (1972) and Morisot *et al.* (1996). Moreover, the pattern of sugar and starch in Figures 2 and 4 shows that carbohydrate reserves in basal stem parts were used again as suggested for rose by Zieslin *et al.* (1975). The positive effect of deshooting on subsequent biomass and flower production as compared to the control treatment suggests a direct positive effect of stored carbohydrates on subsequent growth of flowering shoots. The extra amount of stored carbohydrates, mainly starch, in the deshooting treatment (Figure 4) had completely disappeared at the beginning of the harvesting period (day 71) indicating that carbohydrates reserves had been used for flower production. Extra carbohydrate reserves for the deshooting treatment as compared to the control amounted to 22.3 gram per m^2 bed, equivalent to 69.3 g of fresh material if a growth conversion efficiency of 1.4 is assumed (Kool and De Koning, 1996) and dry weight content is 23%. Deshooting enhanced rose production directly after pruning by 85 gm^{-2} as compared to the control treatment (Table 3) so roughly it can be stated that all stored carbohydrates were used again. This situation is unlike that for woody perennials as fruit trees where stored carbohydrates play only a role during the earliest stages of development (Hansen, 1971) and, apparently, most of the reserves are used in maintainance respiration rather than for new building material (Hansen and Grausland, 1973; Tromp, 1983). Also for roses, no direct relation between the total amount of carbohydrates accumulated during cold storage before lifting and the root regeneration potential was found (Menoud *et al.*, 1991). Schrock and Hanan (1981) concluded that a minimum carbohydrate requirement was necessary for renewal cane production. However, both Menoud *et al.* (1991) and Schrock and Hanan (1981) did not try to quantify absolute carbohydrate storage and new grown material.

Carbohydrate concentrations were expected to be highest just after the period of deshooting and decrease sharply as bud break and shoot growth started. By that reasoning, the high carbohydrate concentrations 2 weeks after pruning the plants (Figure 4, day 46) is quite unexpected. Several factors may be involved. Firstly, root carbohydrate reserves could have been effective. Although not determined, starch concentrations could have been high in root material as indicated by Figure 2. For roses, Zieslin *et al.* (1975) and Menoud *et al.* (1991) found highest starch concentrations in the roots which is in agreement with the distribution of carbohydrate reserves usually found in woody plants (Loescher *et al.*, 1990). Summer pruning experiments in fruit trees as reviewed by Saure (1987) showed that late-season defoliation always results in smaller carbohydrate reserves in especially the roots. Secondly, although the pruning back of stem parts decreased leaf area, as in this experiment, and carbon fixation (Mika, 1986; Saure, 1987) it should be realized that, at least temporary, sinks are also removed which may have redirected allocation (Loescher *et al.*, 1990). Thirdly, a compensatory increase in photosynthetic activity in the remaining leaves after summer pruning may have occurred as found for mulberry (Satoh *et al.*, 1977) and peach (Rom and Ferree, 1985).

The most remarkable effect of deshooting practice as compared to the control was the significant increase in weight of flowers in the subsequent period (Table 1 and 3). Marcelis-Van Acker (1994a, 1994c) studied the effect of assimilate supply as varied by differential defoliation on axillary bud development and subsequent shoot growth in roses. She found that although the increase in assimilate supply had already increased the number of leaves and leaf primordia in the bud slightly, shoot growth after its release from inhibition was to a major extent dependent on the assimilates available during growth. In the present study, the positive effect of deshooting on flower weight disappeared during the second flowering cycle after pruning, which is a strong argument for the positive role of carbohydrate content during shoot development on the weight of harvestable shoots as found for the first flowering cycle.

Resuming, it could be concluded from this study that it is doubtful whether the control of carbohydrate storage in organs of rose plants will ever contribute to a better management and increased production of established rose bushes.

4.3 Rose crop growth and allocation of assimilates as affected by plant architecture and light interception

Kool, M.T.N., 1996. Rose crop growth and allocation of assimilates as affected by plant architecture and light interception. (submitted).

Abstract

Long-term effects of the woody stem parts and leaf area on rose crop performance of cv Madelon were studied. Four plant types were established, combining 2 levels of stem weight and 2 levels of leaf area. Crop growth rate and dry-matter partitioning between stems, flowers harvested and discarded prunings, including blind shoots, were analyzed over 5 successive periods within a 2-year experiment. A high leaf area enhanced weight of harvested flowers and discarded prunings as a result of a higher light interception but the number of harvested flowers was less resulting in an increase in weight of flowering shoots. The positive effect of a high stem weight on flower production stresses the physiological importance of the stem in its transport and storage function. A linear relationship between crop dry weight increase and intercepted photosynthetically active radiation (PAR) by the canopy was observed. Average light conversion efficiency (LCE) was 2.5 g/MJ PAR. LCE was slightly higher in winter than in summer and decreased with crop age. The percentage of dry matter distributed to harvested flowers (HI) was on average 79%. Values were somewhat higher in winter than in summer which could be explained by the way of harvesting. Bending shoots into the canopy to increase light interception reduced HI.

Introduction

Glasshouse roses are perennial woody shrubs which continuously form new shoots which are harvested daily for at least 4 to 7 years. Despite this long cultivation period, long-term flower production trials are scarce and have the limitation of providing information which is not easily generalized. To enable making inferences from such long-term experiments requires a more fundamental understanding of the principles involved in rose crop performance.

During the life-span of a rose crop, an interdependence exists between the number of flowering cycles throughout the year and the structure of the woody part of the plant (Zieslin *et al.*, 1975). Number and diameter of first- and second-order laterals measured after 8 months of cultivation, either influenced by rootstock (Fuchs, 1994) or specific crop management (Chapter 3.1), can largely explain the variation in number and weight of flowering shoots in the next cropping years. The woody stem parts of a rose plant may affect flower production by its effect on (1) transport and storage of water, nutrients and carbohydrates (Fuchs, 1994; Chapter 4.2), (2) bud break and shoot development (Marcelis-van Acker, 1994), and (3) the maintenance respiration (Gijzen, 1992).

A major principle in crop production science is the close relation between total dry matter production and amount of intercepted light (Monteith, 1977; Robinson and Lakso, 1991). Since light interception is primarily dependent on leaf area, the optimal leaf area index (LAI) should be maintained (Gijzen, 1992). For roses, information on crop light interception is lacking and only a few experimental data are available on canopy photosynthesis (Hand and Cockshull, 1975; Jiao *et al.*, 1991).

Besides light interception, crops should be evaluated for their efficiency in converting total light energy intercepted into dry matter as well as for the efficiency of partitioning assimilates towards harvestable parts which has been done for crops such as apple (Palmer, 1989; Robinson and Lakso, 1991), tomato (Heuvelink, 1995a) and rose (Kool and De Koning, 1996). Knowing the light interception and dry matter production of a crop can more specifically explain the effects of the treatments applied by calculating the light conversion efficiency (LCE) and the percentage of assimilates partitioned towards harvestable flowers (harvest index; HI).

The objectives of this study were to determine the separate effects of leaf area (light interception) and plant structure on (1) seasonal biomass production and allocation over stems, flowers and discarded prunings, and (2) the light conversion efficiency. Four plant types were established as a combination of 2 levels of stem weight and 2 levels of leaf area. Flower production as well as plant architecture were recorded for 5 periods during a 2 year cropping period.

Material and methods

Growing conditions and plant material

On 18 January 1993, 1500 single node cuttings of rose cv Madelon 'Ruimeva' were dipped into a mixture of talcum powder and IBA 0.4% and pricked into rockwool blocks (9x9x9 cm) for rooting. Soil and air temperature set points were 24^{0}C day and night and relative air humidity was kept close to 100%. Supplementary lighting was given by high pressure sodium lamps (SON-T plus 70 W, 38.8 μmolm^{-2}s^{-1}) for 16 h per day. A dark period of 8 h was kept. After rooting, plants were hardened off for some days and on 24 February placed on rockwool slabs in a 12.8 m x 12 m compartment of the multi-span Venlotype glasshouse at the Department of Horticulture (Wageningen, The Netherlands, 52^{0}N). Rockwool slabs were transversally placed on moveable benches with discharge of drain water at one side of the bed. Four plots per treatment were used, each one consisted of 4 rockwool slabs (Figure 1).

Each plot was surrounded by 1 border row which underwent the same treatment. Plant density was 13.7 plants/m² or 12.3 plants/m² taking into account a space utilization of 90% for this type of moveable benches. Plants were drip-irrigated 4 to 20 times a day depending on global radiation outside the glasshouse. Day/night temperatures were set on 19°C/17°C.

Treatments

Four treatments, combining 2 levels of stem weight and 2 levels of leaf area were applied. In the low stem weight treatment, the flower bud of the primary shoot was removed in pea-bud stage. When the most distal laterals had reached a length of 15 cm, the primary shoot was bent horizontally in order to stimulate the growth of basal and lateral buds. At the harvestable stage, these and subsequent flowering shoots were pruned just above the first 5-leaflet leaf counted from the base. During winter, the underhook cutting procedure (Zieslin, 1981) was applied. In order to develop a high stem weight, the promotion of thicker basal shoots and laterals was stimulated according to methods described by Kool and Lenssen (Chapter 2.1). The primary shoot was bent 3 weeks later than in the low stem weight treatment, while after horizontal placement all lateral growth within 30 cm from the base of the primary shoot was continually removed excluding basal shoots. Basal shoots were harvested just above the third 5-leaflet leaf. At the harvestable stage of the first-order laterals, half of them were decapitated and de-shooted for 3 weeks in order to stimulate the diameter increase of the basal shoot as well as sprouting and early development of the second-order laterals originating from the other half of the laterals which were harvested normally. Further flowering cycles were harvested as in the low stem weight treatment but the underhook cutting procedure in winter was less severe.

A high leaf area was aimed at through regularly bending of blind shoots and small, unsaleable flowers horizontally inside the canopy. When the leaf canopy was relatively thin, flowering shoots were cut on the second 5-leaflet leaf instead of on the first 5-leaflet leaf, especially after the winter period with underhook cutting. For a low leaf area all shoots, including blind and small shoots were continuously harvested.

Measurements

The number and fresh weight of flowers and blind shoots and weight of discarded prunings were determined at least twice a week from April 1993 until July 1995. Weekly, light interception of the canopy was estimated from simultaneous measurements of the photosynthetic active radiation (PAR) under overcast sky conditions, using a 75-cm long quantum response tube PAR sensor (TFDL, Wageningen, The Netherlands) at 1 place above each plot and at 11 places in the canopy just above the rockwool slabs (Figure 1). PAR was calculated by multiplying the estimated light interception with the PAR incident. The latter one was calculated by multiplying the daily global radiation outside the greenhouse, as

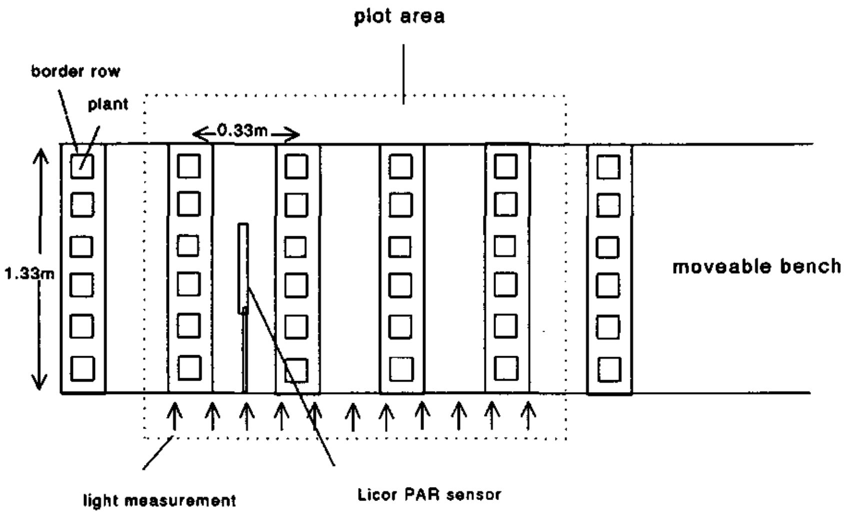


Figure 1. A plot area consisting of 24 plants. The arrows indicate where weekly light measurements at the base of the plants were done.

obtained from the Department of Meteorology at about 800 m distance, with the glasshouse transmission for diffuse radiation (0.62: Heuvelink *et al.*, 1995) and ratio between PAR and global radiation (0.47: Gijzen, 1992).

On 6 occasions i.e. 31 August 1993, 30 December 1993, 25 April 1994, 30 August 1994, 28 February 1995 and 3 July 1995, 6 plants on 1 rockwool slab per plot were measured destructively. Empty spaces were filled with equally treated spare plants out of the same compartment. Number and diameter (Mitutoyo Digimatic) of root collar, basal shoots and first-, second-, and third-order laterals were measured. From these data, the stem cross sectional area (CSA) at different plant heights were calculated. Leaf area (LICOR Model 3100 Area Meter) and fresh and dry weights (ventilated oven at 60°C for at least 48 h) of leaves and of stems from flowering shoots, blind shoots (including bent shoots), structural shoots and root collar were determined. From these data, biomass production and partitioning were calculated for 5 periods (September - December, 1993; January - April, 1994; May - August, 1994; September, 1994 - February, 1995; March - June 1995). The light conversion efficiency (LCE) defined as dry-matter production per MJ PAR intercepted and the harvest index (HI) defined as the percentage of dry-matter production in harvested flowers relative to total above ground dry-matter production were calculated for the 5 periods. Results were analyzed as a random block design by Analysis of Variance using the statistical Systat package. Mean separation was done by Tukey-HSD test ($p<0.05$).

Results

No statistically significant interactions were found between the stem weight treatment and the leaf area treatment. Stem weight was significantly higher for the high than for the low stem weight treatment (Table 1). Initially, leaf area treatment did not affect stem weight but already from the third harvest onwards a significant increase in stem weight was found for the higher leaf area treatment. Stem weight increased with time. Diameters of root collar, basal shoots and first- and second order shoots were higher at the high stem weight treatment whereas the number of basal shoots and second-order laterals were lower (data not shown). After more than 2 cropping years, hardly any basal and first-order laterals had died in the high leaf area treatment whereas almost 25% of first-order laterals in the low leaf area treatment had died (data not shown).

Light interception by the canopy ranged from 85 to 95 % for the high and from 75 up to 90 % for the low leaf area treatment (Figure 2). In each period the percentage of light intercepted by the canopy was 5 to 8 % higher in the high than in the low leaf area treatment

Table 1. Influence of stem weight (SW) and leaf area (LA) on (A) the average plant weight (excluding flowering and blind shoots: in gm^{-2}) and (B) daily intercepted PAR (MJm^{-2}) for 5 periods (1 = 31 August - 30 December, 1993; 2 = 31 December, 1993 - 25 April, 1994; 3 = 25 April - 30 August, 1994; 4 = 30 August, 1994 - 28 February, 1995; 5 = 28 February - 3 July, 1995). Different letters for each period within a column indicate significant differences ($p<0.05$). No statistically significant interaction between stem weight and leaf area was observed.

A plant weight (gm^{-2})						
Treatment		Period:				
SW	LA	1	2	3	4	5
High		384 a	356 a	403 a	445 a	456 a
Low		271 b	269 b	351 b	388 b	369 b
	High	326 a	325 a	430 a	482 a	478 a
	Low	329 a	300 a	324 b	351 b	347 b
B Daily intercepted PAR ($MJm^{-2}day^{-1}$)						
High		1.23 a	1.54 a	4.14 a	1.09 a	3.45 a
Low		1.26 a	1.55 a	4.18 a	1.09 a	3.46 a
	High	1.29 a	1.61 a	4.27 a	1.13 a	3.56 a
	Low	1.19 b	1.48 b	4.04 b	1.05 b	3.35 b

Table 2. Influence of the combined treatments with respect to stem weight (SW) and leaf area (LA) on the allocation of dry matter to stems, flowering shoots and blind shoots + discarded prunings (DP), on total biomass production, and on the light conversion efficiency (LCE) for different periods of time. The percentage of total dry-matter production is given between brackets. Different letters within a column indicate significant differences ($p<0.05$). No statistically significant interaction between stem weight and leaf area was found.

Treatment SW	LA	Stems (g/m^2)	Flowers (g/m^2)	DP (g/m^2)	Total growth (g/m^2)	LCE (g/MJ)
Period 0: 12 April - 31 August, 1993						
High		378 a (26)	691 a (48)	368 a (26)	1437 a	-
Low		257 b (18)	995 b (68)	205 b (26)	1457 a	-
	High	311 a (22)	827 a (58)	287 a (26)	1424 a	-
	Low	325 a (22)	860 a (59)	286 a (19)	1470 a	-
Period 1: 31 August - 30 December, 1993						
High		12 a (3)	322 a (85)*	43 a (11)	377 a	2.6 a
Low		26 a (6)	344 a (79)	64 b (15)	433 a	2.9 a
	High	30 a (8)	295 a (75)	67 a (17)	391 a	2.6 a
	Low	8 a (2)	370 a (88)	40 a (10)	419 a	2.9 a
Period 2: 31 December, 1993 - 25 April, 1994						
High		58 a (12)	350 a (73)	75 a (16)	482 a	2.7 a
Low		56 a (11)	351 a (68)	108 b (21)	515 a	2.8 a
	High	90 a (17)	366 a (71)	59 a (11)	515 a	2.7 a
	Low	24 b (5)	334 a (69)	124 b (26)	482 a	2.8 a
Period 3: 25 April - 30 August, 1994						
High		209 a (15)	1118 a (82)	40 a (3)	1367 a	2.6 a
Low		239 a (19)	997 b (80)	-2 b (0)	1234 b	2.3 b
	High	312 a (22)	1111 a (78)	0 a (0)	1422 a	2.8 a
	Low	137 b (12)	1005 b (85)	38 b (3)	1179 b	2.3 b
Period 4: 30 August, 1994 - 28 February, 1995						
High		-11 a (-2)	516 a (86)	97 a (16)	602 a	3.0 a
Low		-35 a (-6)	510 a (87)	112 a (19)	587 a	3.0 a
	High	-53 a (-9)	555 a (97)	68 a (12)	570 a	2.8 a
	Low	7 a (1)	471 b (76)	141 a (23)	618 a	3.3 a

Period 5: 28 February - 3 July, 1995

High		149 a (14)	824 a (78)	79 a (7)	1052 a	2.4 a
Low		132 a (14)	754 a (78)	76 a (8)	961 a	2.2 a
	High	187 a (17)	822 a (75)	84 a (8)	1094 a	2.4 a
	Low	94 a (10)	756 a (82)	70 a (8)	920 b	2.2 a

Period 1 to 5: 31 August, 1993 - 3 July, 1995

High		417 a (11)	3129 a (81)	334 a (9)	3880 a	2.6 a
Low		419 a (11)	2955 a (79)	347 a (9)	3731 a	2.5 a
	High	566 a (14)	3148 a (79)	271 a (7)	3992 a	2.6 a
	Low	270 b (7)	2936 b (81)	410 a (11)	3619 b	2.5 a

- no light interception measurements

* harvest index (HI)

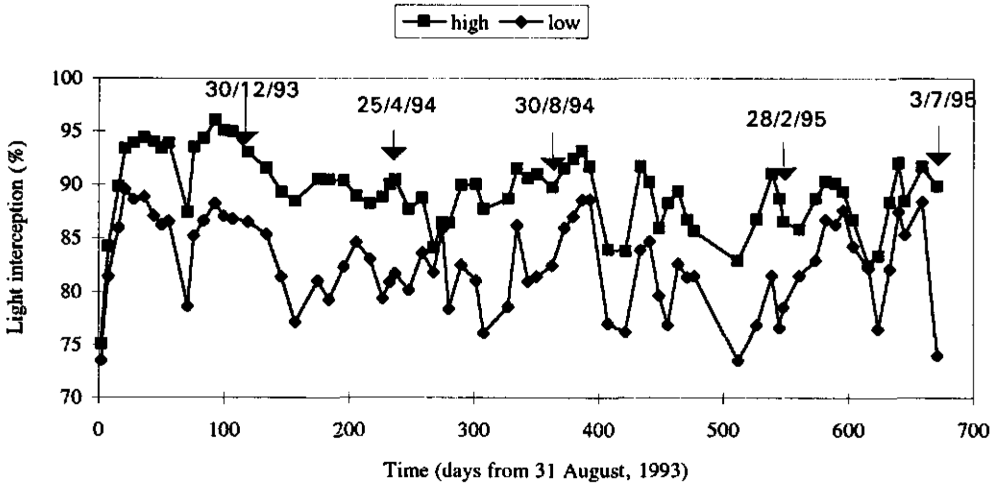


Figure 2. Weekly records of light interception of the canopy for the 'high' or 'low' leaf area treatments. Dates of destructive harvest are indicated by an arrow.

Table 3: Influence of the combined treatments with respect to stem weight (SW) and leaf area (LA) on the number of harvested flowers, total flowering shoot production, shoot weight, number of blind shoots (blind sh.) and weight of discarded prunings (DP) over the whole experimental period (31 August 1993 - 3 July 1995). No statistically significant interaction between stem weight and leaf area was found. Different letters within a column per treatment indicate significant differences ($P < 0.05$).

Treatment		Flower production:		Fresh	Number of	Weight of
		Number	Weight	weight	blind sh.	DP
SW	LA	(no./m²)	(kg/m²)	(g/shoot)	(no./m²)	(kg/m²)
igh		449 a	12.7 a	28.5 a	57 a	1.15 a
Low		421 b	11.7 b	28.0 a	57 a	1.07 a
	High	414 a	12.6 a	30.5 a	26 a	1.33 a
	Low	456 b	11.8 b	26.0 b	87 b	0.89 b

(data not given). There was also a significant difference in the intercepted amount of PAR (Table 1). Stem weight treatment did not affect the amount of intercepted PAR (Table 1). In the initial period of plant building (before 31 August 1993), the high stem weight treatment resulted in higher dry weights of stems and discarded prunings (Table 2) at the expense of the number and weight of flowers harvested (Table 2 and 3), compared to the low stem weight treatment. HI was 20% lower but no significant effect on total dry matter production was found (Table 2).

In the later cropping periods total dry matter production and allocation towards stems and flowering shoots were high during periods of high light intensity (period 3 and 5) and low during periods of low light intensity (period 1, 2 and 4) (Table 2). The pattern was just opposite for the allocation of dry matter towards blind shoots and other discarded prunings. The high stem weight treatment did not affect total dry matter production, except for the third period during summer (Table 2). In that period, allocation towards the harvested flowers was also slightly enhanced by the high stem weight treatment resulting in more flowers for the high stem weight treatment (Table 3). Stem weight had no effect on HI or LCE except in period 3 (Table 2).

The high leaf area treatment positively affected total dry-matter production and allocation towards stems and flowers and reduced the weight of discarded prunings (Table 2). This treatment also reduced the number of flowers harvested (Table 3), especially during summer (data not shown) and the number of harvested blind shoots. As a result, shoot weight was higher. The leaf area treatment showed no clear effects on the average HI and LCE. Regression analysis showed that flower production was more related to number, diameter and cross sectional area (CSA) of first-order laterals than to basal shoots (data not shown). For each period, flower production was often positively related to the cross sectional area (CSA) of first-order laterals and only occasionally to the daily intercepted light as observed per

Table 4. Significance of the linear regression models between several parameters of flower production on the one hand and the cross sectional area of first-order laterals (1oCSA; in mm^2m^{-2}) and daily light interception (DPAR; in MJ $PARm^{-2}$) on the other hand for 5 periods. Models were significant for: * = $P<0.05$; ** = $P < 0.01$; *** = $P < 0.001$; n.s. = not significant.

Period		Flower production (g/m²)	Number of flowers (no./m²)	Flower weight (g)
1	1oCSA	ns	ns	***
	DPAR	**	ns	ns
2	1oCSA	**	ns	ns
	DPAR	ns	ns	***
3	1oCSA	***	**	ns
	DPAR	ns	ns	ns
4	1oCSA	ns	ns	***
	DPAR	ns	ns	ns
5	1oCSA	*	ns	***
	DPAR	ns	ns	ns

period (Table 4). However, as measured when the data for the successive periods of time were taken together, the average crop growth rate, weight and number of harvested flowers were highly positively related to the intercepted PAR (Figure 3A, 3B, 3C). The slope in Figure 3A represents the LCE, i.e. 2.5 g dry matter per MJ intercepted PAR. The individual flower weight was much less closely related to the amount of intercepted PAR (Figure 3D). A very significant relation ($r^2 = 0.99$) was found between total dry weight production per period and the weight of the harvested flower (Figure 4). Only at low values of total dry weight increment, the fraction of dry weight partitioned towards flowers harvested tended to be higher.

Discussion

Plant management

The high stem weight treatment resulted in less but much thicker basal shoots which is in agreement with Kool and Lenssen (Chapter 2.1). Furthermore, for this treatment, harvesting of thicker basal shoots combined with leaving more 5-leaflet leaves on the stem, favoured branching which resulted in more and thicker first-order laterals. Zieslin (1981), Kool and Van de Pol (Chapter 2.2) and Kool (Chapter 3.1) already reported the positive effect of the presence of more 5-leaflet leaves on the mothercane on number of developing lateral shoots due to a higher light interception and hence assimilate production. Thick mothercanes also favour the formation of laterals as observed by Kool and Van de Pol (Chapter 2.2) and Byrne and Doss (1981). The effect of de-shooting for the high stem weight treatment is not directly

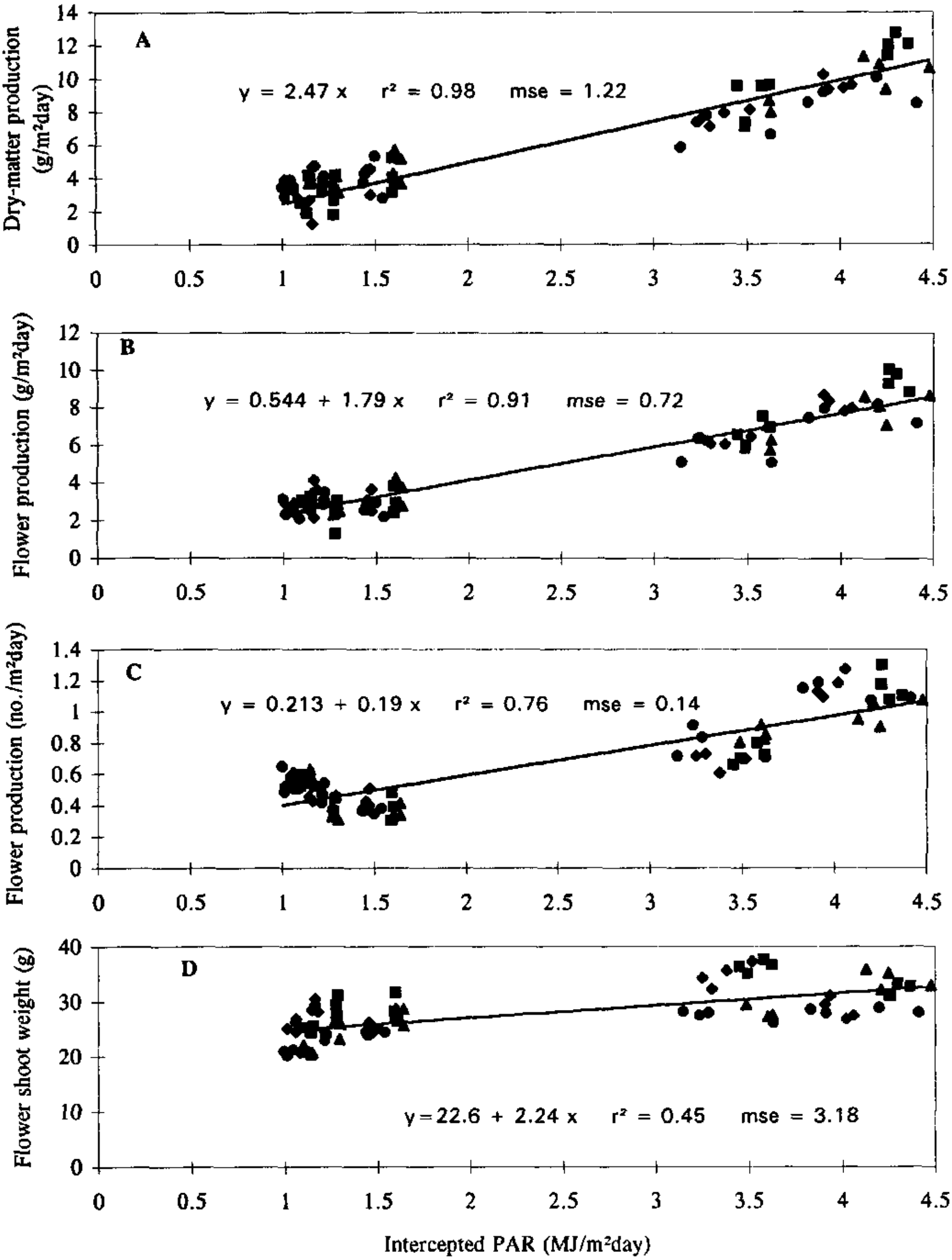


Figure 3. Relationships between intercepted PAR and (A) dry-matter production, (B) flower production, (C) number of flowers produced, and (D) weight of flowering shoots for 4 plant types over 5 different periods. Treatments: ■ - ■ stem weight high, leaf area high; ◆ - ◆ stem weight high, leaf area low; ▲ - ▲ stem weight low, leaf area high; ● - ● stem weight low, leaf area low.

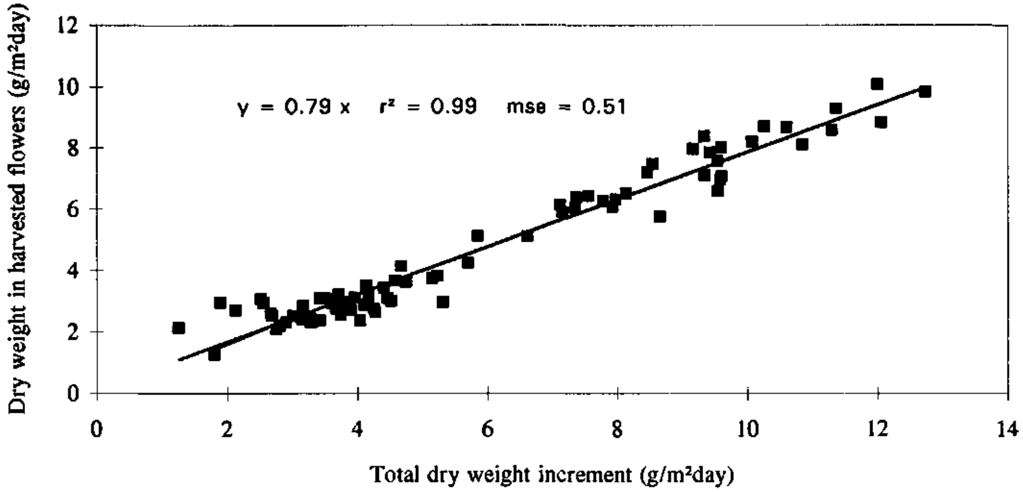


Figure 4. Relation between total dry weight increment and dry weight of harvested flowers over 4 plant types and 5 periods.

shown in the results but this treatment enhanced diameter increase and stimulated branching in a previous study (Chapter 3.1). Apart from an increased light interception, the high leaf area treatment positively affected plant weight. With the tools so far in use it is difficult to create plants with a high leaf area and a low plant weight or plants with a high stem weight and a low leaf area. The first plant type resembles a new way of harvesting roses (Van der Meer, 1994) known in the Netherlands as the knot-rose system and derived from the Japanese arching cultivation system (Anonymous, 1994). In this system, part of the shoots are bent downwards at the base in order to intercept light while other shoots are continuously cut at the base, so no structural laterals are formed. However, this system could not be used in our experimental design since differences in height of the canopy would cause severe shading.

Dry matter production

The high leaf area treatment favoured dry matter production. Crop growth rate was linearly related to the intercepted PAR with a slope (LCE) of 2.5 gMJ^{-1} PAR. The scattering around the regression line (Figure 3A) may partly be due to the fact that the sample mean may deviate from the true population mean. This will affect the growth rate in the period preceding as well as in the period following a destructive measurement. Gijzen (1994) calculated a theoretical crop growth rate of 1.0 gMJ^{-1} global radiation outside the glasshouse, which equals 3.1 gMJ^{-1}PAR incident assuming a glasshouse transmission for diffuse radiation of 0.69 and a ratio of 0.47 between PAR and global radiation (Gijzen, 1992). This value is based on potential crop growth (no limitations in water and nutrition, no pests nor diseases), on a constant LAI of 3 and on a constant carbon dioxide concentration of 340 $\mu mol\ mol^{-1}$. In the present data used (Figure 3A), LAI was mostly between 2 and 3 and carbon dioxide concentration often decreased below 340 $\mu mol\ mol^{-1}$, especially at high light intensity (data not shown). Furthermore in our experiments transmission for diffuse light was 0.62 (Heuvelink *et al.*, 1995). The LCE of 2.5 gMJ^{-1} PAR equals the one calculated for 12 tomato crops by Heuvelink (1995a) in similar glasshouse compartments. However, this author related crop growth rate to incident PAR in the greenhouse since light interception was not measured. This means our value is about 10% lower than the one measured for tomato. Even higher values were found for commercially grown tomato crops by Cockshull *et al.* (1992) and De Koning (1993) probably due to higher carbon dioxide concentrations (Gijzen, 1994). For fruit crops, planted in rows, the rather low value of 1.95 gMJ^{-1} PAR incident was reported (Palmer, 1989) mainly the consequence of the much lower light interception.

LCE was slightly lower for periods of high light intensity compared with periods of low light intensity (Table 2) which may be explained by the lower CO_2-concentration in summer, by supra-optimal temperatures, by low humidity or by lower crop photosynthesis efficiency because of light saturation of part of the leaves. Furthermore a trend was visible towards a lower LCE with age of the crop. This may be explained by a higher percentage of light intercepted by stems. Another explanation is the increased maintenance respiration due to a higher crop mass (Kool and De Koning, 1996).

Flower production

The effect of stem weight on flower production was less pronounced than the effect of leaf area. The positive effect of the high stem weight treatment on number and weight of harvested flowers could be explained in view of the transport and storage function of the stem (Fuchs, 1994). This author observed high correlations between number and weight of flowers on the one hand and the CSA of basal stem parts for each season separately on the other hand in a long-term experiment on the effect of 17 root systems on behaviour of rose cv Varlon. Similar relations were found by Moore (1978) for apple.

Weights of harvested flowers and discarded prunings were higher at the higher leaf area which is logical in view of the well-known positive relationship between growth and intercepted irradiance (Cannell *et al.*, 1987; Robinson and Lakso, 1991; Heuvelink, 1996). Besides the effect on growth, the high leaf area treatment reduced the number of flowering shoots, especially in summer. This may be related to self-shading which suppresses lateral bud growth and branching in rose (Mor and Halevy, 1984). Several workers have demonstrated that mutual shading effects are reflected in a reduction of the red/far-red ratio in the transmitted light through the canopy which may strengthen apical dominance (Cline, 1991). Furthermore, bending of blind and small flowering shoots into the canopy for maintaining a high leaf area reduced the number of sprouting buds as compared to the situation in which those shoots were cut.

An increased assimilate supply in rose shortened the growth period from bud break until harvest and had a positive effect on shoot weight (Marcelis-van Acker, 1994a). Latter result was also found in the present study where a higher assimilate supply in the high leaf area treatment in combination with a lower number of sprouting buds resulted in a remarkable increase in weight of harvested shoots (Table 3). Especially during winter flowering stems from the low leaf area treatment were unsaleable due to poor quality (low weight, low firmness).

A continuous low leaf area resulted in dying of the lower positioned structural shoots. Continuous removal of leaves may deplete carbohydrates in shoots and roots and may lead to dying as observed for roots by Fuchs (1994). Dying of lower orientated shoots may cause serious problems in maintaining a minimum number of shoots necessary for further high flower production as emphasized by Van Rijssel (1982), Kool and Van de Pol (Chapter 2.2), Fuchs (1994) and Kool (Chapter 3.1).

Dry-matter distribution

The seasonal differences in HI are directly related to harvesting method. During winter the underhook cutting procedure was applied in order to reduce crop height which increased HI. The low leaf area treatment forms a clear exception to this due to the formation of numerous blind shoots as a direct result of the high number of developing shoots and the low assimilate supply. During spring and summer flowering shoots were cut on the first- or second 5-leaflet leaf. Thus, part of the newly grown shoots remained on the plant which reduced (HI) and clearly increased the percentage of assimilates directed towards stem parts (Table 2). However, apart from these fluctuations in dry-matter distribution, due to harvesting method, in the long run a linear relationship was observed between total dry weight increase and dry weight increase in harvested flowers (Figure 4). Such a linear relationship was also reported by Challa and Heuvelink (1993) for several crops. In addition to harvesting method, plant management affected the fraction of dry matter distributed to the flowers harvested. In this study the high leaf area treatment reduced HI which was most pronounced during summer. This probably resulted from bending small shoots inside the canopy and of cutting flowers on the second- instead of the first 5-leaflet leaf. During winter (period 4), this treatment increased the HI because blind shoots were bent into the canopy instead of cut off. Furthermore, a high leaf area reduced the number of sprouting buds which reduced the formation of blind shoots due to a less severe competition for assimilates.

Conclusion

Rose crop management should be primarily directed to a high light interception by the canopy since (1) crop growth rate was linearly related to intercepted PAR by the canopy with a slope (LCE) of almost 2.5 g dry matter MJ^{-1} intercepted PAR and (2) the HI, which averaged 79% in the long run, was linearly related to crop growth rate. Management tools such as bending shoots and height of flower cutting are needed to maintain a balance between light interception (= total dry matter production) and number of developing shoots in order to harvest flowers of a desirable weight. Number, diameter and spacing of basal-, first- and second-order laterals must guarantee an optimal light interception as well as an optimal physiological functioning with respect to transport of water and nutrients and storage of assimilates.

5. General discussion

Goals for optimal rose crop production

A complex system of factors affects rose crop production as summarized in Chapter 1. In Figure 1 (Chapter 1), these factors were divided into 2 groups: factors which are directly related to the plant and factors related to the environment and technical equipment. A grower must combine these factors to maximize the difference between the financial input and output. In physiological terms rose growing is aimed at:

1) maximizing dry matter production given the environmental conditions,
2) increasing the share of assimilates distributed towards harvestable flowers, without interfering with the
3) cut-flower quality with respect to stem length, weight and diameter.

Dry-matter production

Light interception

Most of the observed variation in dry-matter production could be explained by differences in light interception (Chapter 4.3). Generally, the dry-matter production rate of a uniform stand of vegetation is closely related to the interception of radiant energy by the foliage (Russell *et al.* 1989; Robinson and Lakso, 1991). Since light interception is primarily determined by leaf area (Chapter 4), a high leaf area should be maintained. Theoretically, at a LAI of around 3 for a closed canopy, almost 89% of the photosynthetically active radiation is intercepted which is optimal for the growth of greenhouse crops (Gijzen, 1992). The positive effect of a higher light interception at a higher LAI does not compensate for the loss of assimilates through increased maintenance respiration (Gijzen, 1992). With respect to seasonal crop growth, a high light intensity during summer is accompanied by a high optimal LAI (De Koning, 1996), as opposed to a much lower optimum LAI during winter.

For many crops, e.g. fruit vegetables, a favourable balance can be maintained between vegetative (future productivity) and generative growth (short-term productivity) (Heuvelink, 1996). In most of these crops a strict distinction can be made between leaves as source for assimilates and the fruits as sinks (Marcelis, 1994; Heuvelink, 1996). However, in rose, the harvestable shoot contains the flower head, stem and leaves and, consequently, is source and sink at the same time. From bud break until harvest, the growing shoot gradually changes from a sink into a source (Mor and Halevy, 1979). However, the uppermost leaves with the highest photosynthetic capacity are continuously removed by harvesting and, therefore, maintenance of an optimal balance between source and sink is rather complicated.

To maintain a balanced LAI, i.e. light interception, a continuous harvesting system has to be applied (Chapter 3.4 and 4.1). Harvesting all shoots in a short period of time, as in flush harvesting, leads to a sharp reduction of light interception immediately after harvest which greatly reduces dry-matter production. Moreover, just before harvesting the flush, a dense canopy exists. Since dry matter gain is not only dependent on carbon gain during the day but also on carbon loss during the night (Dutton *et al.*, 1988), the extra gain of carbon due to the increased amount of intercepted radiation might not compensate for the extra loss of carbon due to the greater overall crop weight. The negative effect of root dying as a direct result of removing too many leaves at once in the case of flush harvesting, as observed by Fuchs (1986), was not found in this study (Chapter 3.4).

A more balanced LAI may also be achieved by the method of harvesting. The foliage density may determine the height of cutting at harvest. As described in Chapter 2.2, leaving more 5-leaflets leaves on the mother shoot generally enhanced bud break and shoot growth due to an increased interception of light. Furthermore, the present leaf area determines whether blind shoots should be bent or removed. A low leaf area justifies bending whereas blind shoots should be removed in case of a dense leaf foliage. Flowering shoots can be bent also inside the canopy but such a treatment should be prevented since each flower which is not harvested directly reduced the harvest index (Chapter 4.3). Moreover, shoot bending might influence leaf photosynthesis. Kool *et al.* (1996) found for rose a reduction in leaf photosynthesis of 15% 1-3 weeks after bending as compared to the vertical control shoot but later a complete recovery occurred. Moreover, in grape bending of shoots more than 90° significantly limited leaf photosynthesis (Schuber, 1995). For apple, the CO_2-uptake was reduced in trees placed horizontally (Myers, 1983).

The positive effect of bending shoots into the canopy on light interception is only temporary. Eventually, leaves drop and new shoots will have to be bent. Furthermore, leaf photosynthesis declines since it is highest between 20-40 days after bud outgrowth and declines thereafter (Lieth and Pasian, 1990).

Leaf spacing may also play a role with respect to dry matter production. In the case of rose crops, regularly shoots are bent down into the path between the rows, especially in the new knot-rose system (Van der Meer, 1994). Such a dense foliage may intercept a considerable amount of light but its net assimilation will be reduced by high maintenance respiration. A negative effect of a dense downward-bent leaf package especially occurred in winter (unpublished results).

Spacing

By relating yield to inter-row and intra-row spacing, Berry (1967) calculated that the highest light interception and yields should be achieved by a square planting pattern (uniform spatial distribution of 1:1) which has been confirmed for various crops (Stützel and Aufhammer, 1991; Wagenmakers, 1995). For fruit trees, such a distribution and a low degree of leaf clustering favour dry matter production (Wagenmakers, 1995). For path widths <30% of the row height, simulation results showed that light absorption and crop photosynthesis under diffuse light are not much lower than in a closed canopy (Gijzen and Goudriaan, 1989).

Plant architecture

According to a review by Waring and Schlesinger (1985) in many woody plants relatively stable relationships are maintained between leaf area, stem diameter, sapwood cross-sectional area (CSA) and root biomass due to the internal control exerted by water, carbohydrates, nitrogen supply and hormone levels. In the present study, such biometrical relations were reported between the CSA of basal and upper stem parts (Chapter 2.2; Chapter 3.1), between stem weight and flower production (Chapter 3.1), between stem CSA and flower production (Chapter 3.1; Chapter 3.2; Chapter 4.3) and between stem CSA and biomass accumulation (Chapter 4.3). After 8 months of growth, number and diameter of second-order laterals could already explain more than 70% of the variation in flower production for the next two cropping years (Chapter 3.1). This positive correlation is probably strongly related to the effect of plant architecture on light interception through its effect on canopy structure and leaf area (Chapter 4.3). Number and diameter of second-order laterals are probably closely related to the number and diameter of higher-order stems, including those that will supply the flowers. Number and growth of new shoots strongly determine light interception, i.e. photosynthetic capacity.

There seems to be an optimal level in the development of the basal parts of a rose bush. In Chapter 3.3 it was reported that flower production declined at extremely high CSA values i.e. at a high stem biomass. As recently discussed by Kool and De Koning (1996), in that situation more assimilates are needed for maintenance respiration, resulting in a reduced net biomass production. The annual decrease of rose production of 4-8% from the second year onwards (Chapter 3.2; Chapter 3.3), which is in the range of values reported by Rupprecht (1963), Obiol and Cardus (1972) and Pessala (1977), may be related to the observed increase in stem biomass as reflected in the CSA (Chapter 3.2). In Chapter 3.3, therefore, it was proposed to cut out older stems as soon as their photosynthesis approaches the compensation point, a practice also suggested by Kozlowski *et al.* (1991) and often applied in fruit growing.

To summarize, a high CSA in the form of an optimal number of uniformly spaced, thick laterals should be balanced by a limited stem biomass. Spacing of laterals is directly related to plant spacing whereas biomass is closely related to plant height. Therefore, plant density should not be too low.

Carbohydrates

Stored carbohydrates play an essential role in woody plants (Loescher *et al.*, 1990) but that role is probably restricted to the initial stages of development (Chapter 4.2). A relatively constant level of sucrose was found in the lower plant parts whereas an extra amount of carbohydrates was usually stored as starch (Chapter 4.1 and 4.2). Storage of a minimum amount of carbohydrates may be essential since continuous removal of flowering and blind shoots depletes the lower-positioned shoots and engenders death of shoots, as found in Chapter 4.3. Shoot die-back opens up the canopy and reduces light interception and assimilate production.

Potential dry-matter production

Important tools for achieving optimal crop growth are summarized in Chapter 1 (Figure 1). However, to analyze the actual level of production, comparison with potential production is needed. To calculate the potential dry-matter production, the use of simulation models seems appropriate, as these models have shown to be successful tools predicting and explaining the behaviour of such a complex, dynamic system as a growing crop (De Wit and Arnold, 1977; Loomis and Rabbinge, 1979; Heuvelink, 1996). Simulation models for greenhouse crops have been reviewed by Heuvelink (1996). For rose only statistical (regression or black-box) models have been developed (Lieth and Pasian, 1991; Jiao *et al.*, 1991; Hopper *et al.*, 1994). A comprehensive and explanatory (physiological) general model for the simulation of photosynthesis and dry matter production of greenhouse crops (SUKAM) was developed by Gijzen (1992). The potential growth of a crop, i.e. its dry-matter production under ample supply of water and nutrients and in a pest-, disease- and weed-free environment, is simulated under the prevailing greenhouse conditions. Based on SUKAM, Gijzen (1994) calculated a theoretical crop growth of 1.0 g/MJ global radiation, equalling 3.1 g/MJ PAR incident, at a constant LAI of 3 and a constant carbon dioxide level of 340 μl/l. This value exceeds the 2.47 g/MJ intercepted PAR, calculated over a 2-year period, in the experiment described in Chapter 4.3. However, in that experiment the environmental conditions probably did not allow potential crop growth.

The potential growth of a rose crop can be simulated by ALSIM(1.0) (De Koning, 1996) which is based on the model of Gijzen (1992) adjusted with a module for artificial lighting. The model was validated by Kool and De Koning (1996) who analyzed the actual crop production of two commercial rose crops differing in cultivar use and in growing conditions. In general, the model greatly over-estimated dry matter production but during winter the production was under-estimated which may be due to incorrect calculation of maintenance respiration. Furthermore it has been suggested that specific maintenance coefficients are not only temperature-dependent as in the model but also depend on the general metabolic activity of the crop (Amthor, 1989; Heuvelink, 1995a) and, therefore, may be higher in summer than in winter. In addition, the low actual dry-matter production for both cultivars in summer could also be due to sub-optimal environmental conditions and to a lower leaf photosynthesis as compared to greenhouse vegetable crops as recently found by De Koning and Spaargaren (unpublished results).

Actual levels of dry-matter production achieved under the existing climate and crop conditions can be analyzed by comparison with potential dry-matter production simulated with the crop growth model ALSIM(1.0). This may become an important tool for improving long-term crop management with respect to optimizing the temperature, irradiance and CO_2-control and for early detection of major growth disorders.

Dry-matter distribution

Environmental conditions

The allocation of assimilates to the flowering shoots is equally important as maximal dry-matter production. For several crops, including rose, a linear relationship has been found between the cumulative dry-matter production and the percentage distributed towards the harvestable parts (Challa and Heuvelink, 1993). Each shoot is genetically programmed to initiate a flower bud but unfavourable environmental conditions may cause early abortion of flower buds (Moe, 1971; Zieslin and Halevy, 1975). Therefore, the overall harvest index probably directly reflects the environmental conditions with respect to blind shoot formation. Under controlled environmental conditions no blind shoots were produced and a harvest index (HI) of 88% was reported (Chapter 3.4). For glasshouse conditions with and without supplementary lighting and carbon-dioxide enrichment the HI averaged 84% and 82%, respectively (Chapter 4.3; Kool and De Koning, 1996).

Management treatments

Apart from the environmental conditions, various growing techniques minimize blind shoot formation. Blind shoot formation is aggravated by a reduction of assimilate supply, either caused by a decreased light intensity (Moe en Kristofferson, 1969; Moe, 1971; Carpenter and Rodriquez, 1971; Carpenter and Anderson, 1972; Cockshull, 1975; Zieslin and Halevy, 1975; Nel and Rasmussen, 1979) or by too large a number of developing shoots as in the case of flush harvesting (Chapter 4.1). The number of shoots can be regulated by taking shoot diameter as criterion for the height of cutting the flowering shoot (Chapter 2.2); by doing so blind-shoot formation will be greatly reduced. However, cutting close to the basis of the shoot generally promoted bud break (unpublished results) and hence increased the risk of flower abortion.

The method of harvesting also directly influences the harvest index. Harvesting methods vary per season in order to retain enough leaves during summer and to reduce plant height in winter. Generally, during summer and autumn, shoots are harvested with an upward cut, i.e. some leaves of the shoot are left behind on the plant. During winter and spring, shoots are harvested with a downward cut, i.e. the complete shoot is harvested by an underhook cut (Zieslin, 1981). Leaving more 5-leaflets on the cane at harvest will directly decrease both flower shoot weight and harvest index. The overall harvest index varied from 65% in summer to 99% in winter (Chapter 4.3).

Carbohydrates

Depending on the treatments applied, carbohydrates are distributed to lower plant parts (Chapter 4.2). These parts may serve as a reservoir for the normal development of flowering shoots, especially under conditions of insufficient light. However, the amount of stored carbohydrates was only of minor importance in relation to continuous flower production (Chapter 4.2).

Flower stem quality

Apart from directing a high percentage of dry matter towards harvestable flowers, a minimum flower quality with respect to weight, length and diameter, should be maintained in line with the consumer's wishes. Since shoot growth is to a major extent dependent on assimilate supply during growth (Marcelis-van Acker, 1994c) a balance should be kept between dry-matter production, as a direct result of light intensity and light interception, and number and development rate of new shoots. The daily dry-matter production can be predicted from the expected amount of intercepted light (Chapter 4.3; Kool and De Koning, 1996), and shoot weight from the number of developing shoots and the period of time from cutting until harvesting. Length of shoots depends in particular on relative humidity and temperature (Van den Berg, 1987). Taking a certain average shoot weight, the grower has to control number and growth rate of shoots; latter aspect can be controlled by the average daily temperature (Van den Berg, 1987). Number of developing shoots also depends on method of harvesting. Leaving more 5-leaflet leaves on the parent shoot generally resulted in an increased number of emerging shoots (Chapter 3.2). Furthermore, flush harvesting promoted bud break and thus shoot number (Chapter 3.4) but bending blind shoots into the canopy reduced overall bud break (Chapter 4.3). An extreme variant of the latter treatment is the so-called knot-rose system (Van der Meer, 1994). In that system the number of developing shoots is strongly reduced whereas average shoot weight is markedly increased (Kool *et al.*, 1996).

Plant architecture

The number and diameter of second-order laterals as present after 8 months could explain more than 70% of the variation in number of flowers harvested during the next 2 cropping years (Chapter 4.1). These laterals are probably closely related to number and diameter of laterals which supply the flowering shoots. The number of shoots at this height may be an indication of the potential flower yield because new shoots originate from the most distal axillary buds after harvesting a flowering shoot. So number of shoots harvested directly influences the number of subsequently developing shoots which is very important during periods of high light intensity (Fuchs, 1994) but less important during periods of low light intensity due to an increased risk of shoots becoming 'blind'. Shoot diameter is important since thick shoots bear heavier buds (Marcelis-Van Acker, 1994a) and produce thicker and heavier lateral shoots (Chapter 2.2 and 3.1). Moreover, when thick shoots are cut, buds break more readily and the period of time required for flower development is shorter.

Carbohydrates

Apart from the daily assimilate production, flower development was also influenced by stored carbohydrates (Chapter 4.2). A highly significant increase in weight of flowers harvested was achieved as a direct result of supply from stored carbohydrates. However, it is doubtful whether treatments encouraging the redistribution of carbohydrates to improve rose crop management will pay (Chapter 4.2).

Practical consequences

Early plant development

In the foregoing study light interception proved to be the major determinant for rose crop growth (Chapter 4.3). Therefore, after planting a high leaf area index should be achieved as soon as possible by decapitating visible flower buds and keeping the primary shoot upright (Chapter 2.1). Both treatments will enhance the breaking of distal axillary buds and limit the outgrowth of basal buds. The latter aspect is important because early basal-shoot formation results in thin basal shoots with affects plant architecture negatively (Chapter 2.1).
Just after reaching a leaf area index of approximately 3.0 the primary shoots should be bent in order to stimulate the outgrowth of basal buds. Competing side shoots near the base of the horizontal primary shoot should be removed (Chapter 2.1). Rootstocks may also influence crop development and growth rate (Kool and Van de Pol, 1992; De Vries, 1993; Fuchs, 1994). However, it seems that treatments such as manipulating basal-shoot formation

(Chapter 2.1 and 4.1), de-shooting (3.1 and 4.3), shoot bending (4.3) and plant spacing (3.1) had considerably more impact on plant architecture than rootstocks did. Nevertheless, having a good rootstock may further improve plant development and crop growth. According to De Vries (1993) the vigour of rootstocks is only optimally expressed in quantity and quality of the shoots harvested if the plants have sufficient space.

Crop growth and development

It is complicated to measure light interception, but the CSA of stems, especially of the first- or second-order laterals, proved to be an excellent parameter to estimate light interception and to define plant architecture with respect to flower production. It could be calculated from the experiments described in Chapter 4.1, 4.2, 4.3 and from commercial rose growing experiments (data not published) that the CSA of first- or second-order laterals must approach 2000 mm^2/m^2 in order to guarantee a high flower production. For example, for cv Madelon, a long-stemmed rose cultivar, at a plant density of 10 plants per m^2, and consisting of 3 basal shoots with 5 first-order laterals of 7 mm diameter each, the CSA will amount to 1923 mm^2/m^2. For cv Frisco at the same plant density and a plant type formed by 3 basal shoots, 5 first-order laterals and 7 second-order laterals of 6 mm each, the CSA will amount to 1978 mm^2/m^2. Such plant architectures can be achieved by varying the height of cutting (Chapter 2.2), de-shooting (3.1) and bending (4.3). Because crop growth is negatively affected by maintenance respiration, determined by temperature and crop dry weight, and because carbohydrate reserves are of minor importance (Chapter 4.2), total crop weight should be limited (Chapter 3.3). This can be achieved by reducing crop height. To that end, flowering shoots should be harvested as low as possible from the second-order stems, but a balance should be kept between dry matter production and number of developing shoots in order to ensure a minimum flower stem quality. This balance could be better regulated in a continuous harvesting system than in the case of flush harvesting (Chapter 3.4). In order to avoid ageing or dying back of basal shoots and laterals, replacement pruning should be applied as soon as the CSA of stems exceeds 2000 mm^2/m^2 by far (Chapter 3.3, 4.3).

In order to analyze the actual level of production it should be compared with the potential dry-matter production (Kool and De Koning, 1996). A further improvement of the crop growth model ALSIM(1.0) will make it possible to predict the periodical potential flower production for each individual crop. The potential daily dry-matter production can be predicted from daily global radiation outside the greenhouse, greenhouse temperature and CO_2-concentration, LAI and crop weight, factors which the grower will take into account in managing actual flower production. Moreover, this opens the possibility to objectively compare growing systems that differ widely with respect to cultivar, supplementary lighting and other technical equipment. Finally, major growth disorders can be detected early by comparison with growth predictions by the model.

Conclusion

Rose crop growth and development primarily depend on the amount of intercepted photosynthetic active radiation which is closely related to plant architecture. These factors can be controlled by both specific plant treatments and methods of harvesting. In as far as this study contributes to a better understanding of the physiological background of growth and development of the rose crop the findings can be applied in the design and optimization of new growing systems.

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Summary

In the Netherlands the rose is the most important glasshouse cut flower having a production area of 919 ha and an auction turnover of 785 million Dutch guilders. Rose is a perennial woody shrub. Plants are built on vigorous shoots, the so-called basal shoots or bottom breaks, which are originating from the basal part of the plant during early development. Throughout the year, glasshouse roses continuously form new shoots. Each shoot is programmed to initiate a terminal flower bud which will develop into a harvestable flower under favourable conditions.

It should be stated that the greater productivity as achieved during the last decennia has been mainly realized through the progress in control of the environmental conditions and optimization of the technical equipment. These improvements required great investments which highly increased the production costs per m^2. However, little attention has been paid to other factors to control the growth of the plant. For other woody plants, especially fruit trees, the significance of plant structure and plant management on growth and productivity has been long recognized. For rose, the dependency between plant structure and flowering shoots has been hardly revealed. Research has been mainly focused on the enhancement of the number of basal shoots and their branching capacity. However, up to the early nineties, within a rose crop an undesirable large variation in shoot number and size still exists which affects flower yield. Great differences in productivity between individual growers are found. Moreover, comparison of crop vigour is difficult due to different environmental conditions and technical equipment. A suitable parameter for expressing crop vigour has to be developed.

In the present study is was investigated which plant factors can be used to manipulate the growth and development of young rose plants. Moreover, it was explored to which extent plant architecture can affect crop growth and flower performance. Furthermore, an attempt was made to clarify the physiological control of the influence of plant architecture on flower production. A better understanding of the physiological background of rose crop performance enables the development and optimization of new growing systems. Finally, an effort has been made to express crop growth in more general usable parameters such as dry-matter production and crop efficiency (CE).

In Chapter 2.1, attention was focused on the effect of specific plant treatments and plant density on basal-shoot formation in young rose plants. After bending the primary shoot a clear preference existed for the outgrowth of the 2 most basal buds which are already present as secondary buds in the axils of the scales of the axillary bud when used as a cutting for propagation. Delayed bending increased the development rate, diameter, weight and cross sectional area (CSA) of basal shoots per plant. Outgrowth of axillary buds positioned higher on the stem strongly inhibited the outgrowth of basal shoots. Removal of competitive lateral

growth increased the number and CSA of basal shoots per plant. Reducing the number of developing basal shoots strongly increased the diameter and weight of the remaining ones but hardly affected plant growth rate. With increasing plant density, number and CSA of basal shoots per square meter were highly positively influenced whereas the individual shoots were slightly thinner.

A general concept on ways to improve plant building of young rose plants, with respect to basal-shoot formation, is discussed. Number, diameter and CSA of basal shoots, expressed per plant or per square meter, could be highly controlled using plant related factors such as time of bending of the primary shoot, removal of lateral and basal buds and by plant density.

Apart from basal-shoot manipulation, plant development was highly affected by managing the pruning height of basal shoots and subsequent laterals and by controlling the number of outgrowing laterals on the remaining stem after harvesting; both treatments were performed as dependent on the diameter of the harvested shoots (Chapter 2.2). As a result an increase in the stem diameter of second-order flowers and a decrease in the percentage of blind shoots, from 19% to 4%, could be achieved. Moreover, 9 months after planting, the CSA of laterals at a height of 60 cm above soil level, was improved by more than 50 %.

The close relation between the diameter of basal shoots and the CSA of laterals on a height of 60 cm, 9 months after planting, together with the observed differences on plant development between 'smaller' and 'bigger' plants, stressed the importance of uniform plant material and an optimal control on the process of basal-shoot formation.

The effect of plant architecture on flower production was evaluated in Chapter 3. In Chapter 3.1., the relationships between plant architecture and flower production of rose were studied for a cropping period of 2.5 year. Four different types of plants, varying in number of basal shoots and in architecture were combined with 3 plant densities (7.7, 11.6 and 17.4 plants/m^2).

Treatments that invest in stem mass significantly reduced the number and weight of flowers for the first 8 months. This was due to a delay in time of basal-shoot growth, restriction of number of outgrowing shoots and disbudding of shoots. However, this initial financial loss amply paid itself in the next 2 cropping years. Regression analysis showed that number and diameter of second-order laterals as formed during the first 8 months, could explain more than 70% of the variation in number and weight of flowers harvested in well over 2 cropping years. Flower production was much less related to number and diameter of basal shoots than to number and diameter of second-order laterals. The importance of plant structure with respect to assimilate storage and transport capacity is discussed in relation to flower production. Increasing plant density led to a higher biomass- and flower production but to a reduced individual plant weight. Furthermore, weight and firmness of harvested flowers was reduced. The harvest index was neither affected by the applied treatments nor by plant density.

The effect of planting system and rootstock clone on plant development and flower production of *R. hybrida* 'Motrea' was followed for more than 4 years (Chapter 3.2).

Initially rootstock 'Ludiek' gave the highest number of flowers as compared to 'Multic' and 'Moonlight'. However, the decline in flower production for 'Ludiek' after 2 years of culture was more severe than for the other rootstocks. Plants on 'Moonlight' out-yielded those on the other rootstocks during the third and fourth year of culture, probably due to their high renewal cane production. Death of basal shoots during 4 years of culture was mainly due to competition between numerous shoots.

Comparison of basal-shoot growth during the early period of plant development in single-stemmed plants at double plant density with two-stemmed planting system at normal plant density showed that intra-plant competition between basal shoots was stronger than inter-plant competition. During subsequent years of production no differences in basal-shoot competition between or within plants occurred, as reflected in equal total flower fresh weight production, number of new basal-shoot formation and number of dead basal stems. However, the higher plant density increased the number of harvested flowers and decreased individual shoot weight.

In Chapter 3.3, the importance of new basal-shoot formation for plant development and flower production of *Rosa hybrida* 'Motrea' was described on the bases of data of a long-term experiment. After 1 year, new basal-shoot formation was either restricted or unaffected. In both treatments, fresh weight production decreased after the second year which is discussed in relation to an increase in respiration as a result of an increase in stem biomass. Limiting the number of new basal shoots increased flower weight and slightly enhanced flower production during the second year as compared to leaving all renewal canes on the plant. In the latter case, the number of basal stems was almost twice as high after 3 years. New basal shoots may compete with existing ones as indicated by the limited diameter increase and the higher mortality rate for old basal shoots in comparison with the treatment in which basal-shoot formation was restricted. Furthermore, the weight of flowering shoots harvested from new basal shoots was clearly higher than from older shoots. However, restricted basal-shoot growth had hardly any significant effect on total number of harvested flowers and average shoot weight as compared to the undisturbed situation. In the fourth year a slightly decreased flower production in the case of restricted basal-shoot formation was observed. It may be concluded that there is no clear relation between the number of basal shoots and flower production over a series of years.

Plant architecture and flower production could be also manipulated by method of harvesting and shoot density as shown in Chapter 3.4.. Continuous harvesting as compared to flush harvesting, reduced the number of developing shoots but it increased the amount of intercepted photosynthetic active radiation (PAR) and production weight. Both continuous harvesting and the lower shoot density had a positive effect on flower shoot performance. Furthermore, the time from cutting until harvesting a flower was shortened by these treatments due to an increased assimilate supply. Distribution of dry matter towards flowers harvested was not influenced by method of harvesting or shoot density. All treatments seem equally efficient in converting PAR into dry weight.

The physiological background of rose flower production was discussed in more detail in Chapter 4. The effect of harvesting method ('flush' versus 'continuous') and plant type ('control' versus 'one-stemmed') on flower production as related to plant architecture and carbohydrate content was followed over 18 months of cultivation. For a full-productive year, flush harvesting generally promoted bud break as compared to continuous harvesting but at the same time, also due to a lower light interception, blind shoot formation was enhanced and the individual flower weight reduced. Flower production was more sensitive to the number and diameter of branches at the height of cutting the flowers than to the number and diameter of basal shoots.

The applied treatments did not affect carbohydrate allocation. Total carbohydrate storage is much too low for ascribing a clear role to carbohydrates reserves for new growth. Maximum starch level was found in the beginning of summer and gradually dropped to a minimum in December whereafter it increased again to a maximum in spring. A cold treatment did increase the total non-structural carbohydrate (TNC) level but no positive influence on new basal-shoot formation was observed. No starch gradient was found in basal stem parts.

The importance and use of carbohydrate reserves in above ground stem parts was discussed in more detail in Chapter 4.2. The effect of de-shooting of flowering stems of rose cv Motrea as compared to a normal harvesting procedure was studied with respect to carbohydrate storage and subsequent flower production after downward pruning of shoots. Growth analysis and analyses of soluble sugars and starch in stem samples taken at different height in the plant were carried out.

In general, starch concentrations increased and sugar concentrations decreased from upper to lower stem parts. De-shooting resulted in an increase in total non-structural carbohydrates, mainly starch. The stored carbohydrates were used during a subsequent flowering cycle. Total extra carbohydrate reserves due to de-shooting could explain the resulting increase in fresh weight production. De-shooting did not reduce biomass production but greatly reduced flower production and enhanced weight of discarded pruning. It is concluded that treatments primarily directed on redistribution of carbohydrates probably are of little use for rose crop management.

In Chapter 4.3, the separate effects of the woody stem parts and leaf area on rose crop performance of rose cv Madelon were unravelled. Four plant types were created, combining 2 levels of stem weight and 2 levels of leaf area. In a 2-year experiment, crop growth rate and dry-matter partitioning between stems, flowers harvested and discarded pruning, including blind shoots, were analyzed over 5 successive periods.

A high leaf area enhanced weight of harvested flowers and discarded pruning as a result of a higher light interception but the number of harvested flowers was less resulting in an markedly increase in weight of flowering shoots. The positive effect of a high stem weight on flower production stresses the physiological importance of the stem in its transport and storage function.

A linear relationship between intercepted photosynthetically active radiation (PAR) by the canopy and crop dry weight increase was observed. Average light conversion efficiency (LCE) was 2.5 g/MJ PAR. LCE was slightly higher in winter than in summer and decreased with crop age. The percentage of dry matter distributed to harvested flowers (harvest index; HI) was on average 79%. Values were somewhat higher in winter than in summer which could be explained by the way of harvesting. Bending shoots into the canopy to increase light interception reduced HI.

In Chapter 5, the optimal rose crop production is defined as:

1) dry-matter production should be maximized given the environmental conditions
2) the share of assimilates distributed towards harvestable flowers should be increased without interfering with the
3) flower stem quality with respect to length, weight and diameter.

Maximizing dry matter production is ensured by a high light interception and a low maintenance respiration which can be achieved by creating a plant structure with an optimal number of uniformly spaced, thick laterals and a low stem biomass. To obtain a balanced LAI, a continuous harvesting system has to be applied while special attention should be given towards the height of cutting at harvest and the handling of blind shoots.

Actual levels of dry-matter production achieved under the existing climate and crop conditions can be analyzed by comparison with potential dry-matter production simulated with the crop growth model ALSIM(1.0). This might be an important tool for improving crop management on the long-term with respect to optimizing the temperature, irradiance and CO_2-control and early detection of major growth disorders.

Increasing the share of assimilates distributed towards harvestable parts, is probably directly reflected by the environmental conditions with respect to blind shoot formation, since blind shoots directly reduced the HI. Management treatments such as the height of cutting at harvest, flush versus continuous harvesting, or an 'upward' or 'downward' cut at harvest also influence HI.

The flower stem quality, being the third aspect, highly depends on the balance between daily dry-matter production, as a direct result of light intensity and light interception, and number and development rate of new shoots. Plant architecture as reflected in number and diameter of stems at a certain height also determines the flower performance. Finally some practical consequences of the results obtained are discussed.

Samenvatting

In Nederland is de kasroos de belangrijkste snijbloem met een produktieareaal van 919 ha en een veilingomzet van 785 miljoen gulden (1995). De roos is een meerjarig houtig gewas. Een rozenstruik is opgebouwd uit een aantal groeikrachtige scheuten, grondscheuten genaamd, welke in een vroeg ontwikkelingsstadium ontstaan aan de basis van de struik. Kasrozen vormen gedurende het gehele jaar nieuwe zijscheuten. Elke scheut vormt in principe een bloemknop en groeit onder gunstige omstandigheden tot een oogstbare bloemtak uit.

Er kan worden gesteld dat de toegenomen produktiviteit in de afgelopen decennia voornamelijk is gerealiseerd door een verbeterde beheersing van het kasklimaat en een verdere optimalisatie van de technische uitrusting. Deze verbeteringen vereisen hoge investeringen welke tot een aanzienlijke toename van de produktiekosten per vierkante meter hebben geleid. Andere faktoren die ook de groei van de rozenstruik bepalen hebben relatief weinig aandacht gekregen. Dit in tegenstelling tot bijvoorbeeld veel andere houtige gewassen, in het bijzonder fruitbomen, waar het belang van plantopbouw en gewasbehandeling voor de groei en produktiviteit van het gewas al veel eerder is onderkend. De relatie tussen plantopbouw en bloemproduktie is bij de roos nauwelijks onderzocht. Het onderzoek heeft zich voornamelijk geconcentreerd op het stimuleren van de grondscheutenvorming. Tot op heden bestaat er echter nog steeds een ongewenst grote variatie in aantal en diameter van scheuten in de struik hetgeen de bloemproduktie zeker zal beïnvloeden. Ook worden er grote verschillen in produktie tussen rozentelers gevonden. Het is moeilijk de produktie onderling te vergelijken omdat er grote verschillen in klimaatomstandigheden en technische uitrusting bestaan. Er moet een meer uniforme parameter worden ontwikkeld om de gewasgroei in uit te drukken.

In dit onderzoek zijn in de eerste plaats de mogelijkheden, om met behulp van een aantal plantbehandelingen de struikopbouw van een jong gewas te sturen, bestudeerd. Vervolgens is onderzocht in hoeverre de struikopbouw van invloed is op de groei en bloemkwaliteit. Getracht is de fysiologische achtergronden van deze relatie tussen enerzijds bloemproduktie en anderzijds struikopbouw te ontrafelen. Meer inzicht in de fysiologische processen die hierbij een rol spelen, kan leiden tot de ontwikkeling en verbetering van nieuwe teeltsystemen. Ten slotte is ook getracht de groei van een gewas uit te drukken in een meer algemeen bruikbare maat zoals drogestof produktie of lichtbenuttingsefficiëntie (LBE) van een gewas.

In hoofdstuk 2.1 is de aandacht gevestigd op het effect van een aantal plantbehandelingen en plantdichtheden op de vroege grondscheutvorming. Na het buigen van de primaire scheut bestaat er een duidelijke voorkeur voor het uitlopen van de twee meest basale knoppen die al als secundaire knoppen aanwezig zijn in de gebruikte knop voor de vermeerdering.

Wanneer de primaire scheut later werd ingebogen nam de initiële gewasgroei toe en werden er zwaardere grondscheuten gevormd met een groter cumulatief oppervlak van hun dwarsdoorsneden per plant. De uitloop van axillaire knoppen op de horizontaal ingebogen griffel remde de uitloop van grondscheuten. Het verwijderen van deze concurrerende, uitlopende knoppen verhoogde het aantal en de cumulatieve dwarsdoorsnede van de grondscheuten. Beperking van het aantal grondscheuten per plant had een sterk positief effect op de diameter en het gewicht van de overblijvende grondscheuten en beïnvloedde nauwelijks de groeisnelheid. Een toenemende plantdichtheid had een positief effect op het aantal en de cumulatieve dwarsdoorsnede van grondscheuten per m^2. De individuele grondscheutdiameter nam wel iets af.

Een algemeen concept om de opbouw van jonge rozenplanten te verbeteren wordt bediscussiëerd. Het aantal, de diameter en de cumulatieve dwarsdoorsnede van grondscheuten, uitgedrukt per plant of per m^2, kon goed worden gemanipuleerd door het tijdstip van buigen van de primaire scheut, het verwijderen van zijscheuten of een teveel aan grondscheuten en door de plantdichtheid.

Naast de beïnvloeding van de grondscheutvorming kon de struikopbouw ook worden beïnvloed door de hoogte van snoei van de grondscheuten en zijscheuten en door regulatie van het aantal uitlopende zijknoppen na snoei. Toepassing van beide behandelingen, rekening houdend met de dikte van de geoogste scheuten, leidde tot een toename van de diameter van de tweede-orde scheuten en een afname van het percentage loze scheuten van 19 naar 4%. Negen maanden na planten kon zelfs een verbetering van 50% in de cumulatieve dwarsdoorsnede van de scheuten op een hoogte van 60 cm boven de grond worden gerealiseerd.

Het belang van uniform plantmateriaal en een optimale sturing van de grondscheutvorming werd onderstreept door de nauwe relatie tussen enerzijds de initiële diameter van grondscheuten en de initiële plantomvang en anderzijds de na 9 maanden gerealiseerde cumulatieve dwarsdoorsneden van scheuten op een hoogte van 60 cm.

De relaties tussen plantopbouw en bloemproduktie zijn onderzocht in hoofdstuk 3. In hoofdstuk 3.1 is de invloed van een viertal planttypen, variërend in aantal, diameter- en vertakkingsgraad van grondscheuten, gecombineerd met 3 plantdichtheden (7.7, 11.6 en 17.4 planten per m^2), op de bloemproduktie gedurende 2,5 jaar beschreven. Een investering in gewasopbouw ging vrijwel altijd samen met een lagere bloemproduktie gedurende de eerste 8 maanden. Dit werd ondermeer veroorzaakt door een uitstel in grondscheutvorming, een beperking van het aantal grondscheuten en het toppen van scheuten. Deze initiële opbrengstderving werd echter ruimschoots goedgemaakt in de daaropvolgende 2 volproduktieve jaren. Regressie-analyse toonde aan dat meer dan 70% van de variatie in aantal en gewicht van oogstbare bloemen in 2 volproduktieve jaren kon worden verklaard door het aantal en de diameter van de tweede-orde vertakkingen zoals aanwezig 8 maanden na aanplant. De bloemproduktie was duidelijk minder gerelateerd aan het aantal en de diameter van grondscheuten dan aan het aantal en de diameter van tweede-orde vertakkingen.

Het belang van de plantopbouw voor de bloemproduktie is bediscussiëerd in relatie tot assimilaten-opslag en transportcapaciteit van stengeldelen. Een toenemende plantdichtheid leidde tot een hogere biomassa- en bloemproduktie maar het individuele plantgewicht nam af. Het gemiddelde takgewicht nam ook af bij toenemende plantdichtheid. De uitgevoerde behandelingen en plantdichtheden hadden geen invloed op de oogstindex (gedefinieerd als het percentage van de totale drogestofproduktie dat ten goede komt aan het oogstbare produkt).

In een meer dan 4 jaar durend onderzoek met de cultivar Motrea is het effect van plantsysteem en onderstam op de struikopbouw en bloemproduktie onderzocht. Aanvankelijk gaf onderstam 'Ludiek' meer oogstbare bloemenscheuten dan de onderstammen 'Multic' en 'Moonlight'. De produktiviteit op onderstam 'Ludiek' nam na 2 jaar echter sterker af dan die op de andere onderstammen. De bloemproduktie op onderstam 'Moonlight' lag gedurende het derde en vierde groeiseizoen duidelijk hoger dan die op de andere onderstammen hetgeen nauw gerelateerd leek aan de sterke mate van nieuwe grondscheutvorming. Het afsterven van grondscheuten gedurende 4 produktiejaren kon voornamelijk worden toegeschreven aan de competitie tussen grondscheuten.

De vergelijking tussen enerzijds planten met 1 grondscheut bij een dubbele plantdichtheid en anderzijds planten met 2 grondscheuten bij een normale plantdichtheid in groei van de grondscheuten gedurende de initiële fase van plantopbouw liet zien dat de competitie tussen grondscheuten aan één en dezelfde plant groter was dan tussen afzonderlijke planten. Dit verschil in competitie kwam in latere jaren niet tot uiting in totale produktiegewicht, in het aantal nieuwgevormde grondscheuten of in het aantal afgestorven grondscheuten. Een hogere plantdichtheid leidde wel tot een groter aantal bloemscheuten maar het gemiddelde gewicht lag lager.

Het belang van nieuwe grondscheuten met betrekking tot de plantontwikkeling en bloemproduktie gedurende een viertal produktiejaren is beschreven in hoofdstuk 3.3. Na 1 jaar van normale gewasontwikkeling werd de grondscheutvorming voor de helft van het aantal beschikbare planten consequent verhinderd. Onafhankelijk van de grondscheutbehandeling nam de totale versgewichtproduktie vanaf het tweede jaar af hetgeen wordt bediscussiëerd in relatie tot een toenemende onderhoudsademhaling als gevolg van een toename in gewasmassa. Het verwijderen van nieuwe grondscheuten gedurende het tweede groeiseizoen had een licht positief effect op zowel de totale versgewichtproduktie alswel het gemiddelde takgewicht. De normale gewasontwikkeling gaf een verdubbeling van het aantal grondscheuten te zien na 3 jaar ten opzichte van de behandeling waarin grondscheuten consequent werden verwijderd. Nieuwe grondscheuten beconcurreerden de oudere hetgeen zichtbaar was in een verminderde diametertoename en een verhoogd sterftepercentage van oude grondscheuten. Verder was het gemiddeld takgewicht van scheuten afkomstig van nieuwe grondscheuten hoger dan van scheuten afkomstig van oude grondscheuten. Verwijdering van nieuwe grondscheuten had echter nauwelijks enig effect op het totale aantal en het gemiddelde takgewicht van oogstbare bloemscheuten in vergelijking tot de normale grondscheutontwikkeling. Pas in het vierde groeiseizoen kon een lichte vermindering van de bloemproduktie worden geconstateerd bij het continu verwijderen van nieuwe grondscheuten. Er kan worden geconcludeerd dat er een aantal jaren geen duidelijke relatie aanwezig is tussen het aantal grondscheuten en de bloemproduktie.

De plantopbouw en bloemproduktie kunnen ook worden beïnvloed door oogstmethode en scheutdichtheid zoals aangetoond in hoofdstuk 3.4. Een continue oogstmethode, in vergelijking tot het oogsten 'op snee', verminderde het aantal uitlopende scheuten maar verhoogde de versgewichtproduktie door een hogere onderschepping van bruikbaar licht. De continue oogstmethode had evenals het handhaven van een lagerd scheutdichtheid een positief effect op het gemiddelde takgewicht. Bij deze behandeling nam door een toenemend assimilatenaanbod per zich ontwikkelende scheut ook de tijd tussen snoei en oogst af. Het percentage aan droge stof dat aan het oogstbaar produkt ten goede komt werd niet beïnvloed door oogstmethode of scheutdichtheid. Alle behandelingen waren even efficiënt in de omzetting van onderschepte hoeveelheid licht in droge stof ten behoeve van oogstbare bloemen.

In Hoofdstuk 4 is voornamelijk gekeken naar de fysiologische achtergronden van de bloemproduktie. Het belang van struikopbouw en koolhydraatopslag in stengeldelen is onderzocht tijdens een 18 maanden durende produktieproef waarbij de effecten van oogstmethode (continu of 'op snee') en planttype (normale plantopbouw of plant met slechts 1 grondscheut) op de bloemproduktie zijn bepaald. Gedurende een periode van een jaar terwijl het gewas in volle produktie was stimuleerde het telen 'op snee' de knopuitloop ten opzichte van de continue oogstmethode maar door de lagere lichtonderschepping van eerstgenoemde teeltmethode werd de loosvorming sterk gestimuleerd en lag het oogstbare takgewicht duidelijk lager. De bloemproduktie was duidelijk meer gerelateerd aan het aantal en de diameter van scheuten op oogsthoogte dan aan het aantal en de diameter van grondscheuten.

De uitgevoerde behandelingen hadden geen effekt op de verdeling van koolhydraten. De totale opslag van koolhydraten bleek dusdanig laag dat geen belangrijke rol voor hernieuwde scheutvorming kon worden vastgesteld. Zetmeel opslag was het hoogst aan het begin van de zomer, daalde daarna geleidelijk tot een minimum in december en steeg vervolgens weer tot een maximum in het voorjaar. Er werd geen zetmeelgradiënt waargenomen in de houtige stengeldelen. Een periode van lage temperatuur veroorzaakte een vergroting van de totale opslag aan niet-structurele koolhydraten. Deze extra opslag leidde niet tot een duidelijk zichtbaar effekt op de grondscheutvorming.

Het belang van koolhydraatreserves in houtige stengeldelen van de roos is in meer detail bediscussiëerd in hoofdstuk 4.2. In dit hoofdstuk is het effekt beschreven van het gedurende een bepaalde periode toppen van bloemscheuten op de opslag van koolhydraten in vergelijking met de normale oogstprocedure. De totale biomassaproduktie en de opslag van koolhydraten op verschillende niveaus in de plant werden gevolgd.

Van hogere naar lagere stengeldelen werd een stijgende concentratie aan zetmeel en een dalende concentratie aan suikers gevonden. Het toppen van bloemscheuten leidde tot een toename van de reserves aan niet-structurele koolhydraten en wel voornamelijk zetmeel. Deze opgeslagen koolhydraten werden gedurende een volgende bloemcyclus verbruikt. De extra hoeveelheid koolhydraten ten gevolge van het toppen kon het positieve effekt op de na snoei gerealiseerde versgewichtproduktie grotendeels verklaren. Het toppen van bloemscheuten leidde niet tot een lagere biomassaproduktie maar de bloemproduktie werd drastisch verlaagd ten gunste van het gewicht aan snoeiafval en loze scheuten. De conclusie is getrokken dat de invloed van plantbehandelingen op de koolhydraatopslag nauwelijks van waarde is voor sturing van de bloemproduktie.

In hoofdstuk 4.3 is getracht het effect van struikopbouw op de bloemproduktie te scheiden van het effect van het aanwezige bladpakket. Daartoe zijn 4 behandelingen uitgevoerd waarbij 2 niveau's van stengelmassa werden gecombineerd met 2 niveau's van bladpakket. Het effect van deze behandelingen op de totale drogestofproduktie en de verdeling over stengeldelen, oogstbare bloemen en snoeiafval werd bepaald voor 5 opeenvolgende periodes gedurende 2 volproduktieve jaren.

Een dikker bladpakket resulteerde dankzij de hogere lichtonderschepping in een groter produktie- en afvalgewicht. Het aantal oogstbare scheuten lag echter lager hetgeen tot een duidelijk zwaarder takgewicht leidde. Een zwaardere stengelmassa door vooral dikkere grondscheuten en vertakkingen stimuleerde de bloemproduktie hetgeen het belang van de transport en opslagfunctie van stengeldelen onderstreept.

Er werd een lineaire relatie tussen gewasgroei en onderschepte hoeveelheid fotosynthetisch bruikbare straling (PAR) gevonden. De gemiddelde lichtbenuttingsefficiëntie (LBE) was 2.5 g/MJ PAR. De LBE lag in de winter hoger dan in de zomer en nam iets af met de leeftijd van het gewas. Het percentage drogestof dat aan het oogstbare produkt ten goede kwam (oogstindex) lag gemiddeld op 82%. De oogstindex lag 's winters hoger dan in de zomer hetgeen verklaard kan worden door de methode van oogsten. Het buigen van loze scheuten en bloemscheuten in het gewas verhoogde de lichtonderschepping maar verlaagde de oogstindex.

Een optimale gewasproduktie is in hoofdstuk 5 gedefiniëerd als:
Een maximale drogestofproduktie gegeven de omgevingsfaktoren (1) een zo groot mogelijk deel van deze drogestof moet ten goede komen aan de bloemproduktie (2) zonder nadelige gevolgen voor de gewenste bloemkwaliteit (lengte, scheutdiameter en takgewicht) (3).

Een maximale drogestofproduktie is verzekerd door een hoge lichtonderschepping van het gewas gecombineerd met een lage onderhoudsademhaling. Dit kan worden gerealiseerd door een plantopbouw te creëren bestaande uit een optimaal aantal, uniform verdeelde, dikke stengels gecombineerd met een zo laag mogelijk struikgewicht. Om een evenwichtig bladpakket te handhaven zal een continue oogstmethode moeten worden toegepast waarbij speciale aandacht wordt gegeven aan de hoogte van snoei van bloemscheuten en het al dan niet inbuigen van loze scheuten.

De gerealiseerde drogestofproduktie onder de gegeven omgevingsfaktoren en de condities van het gewas kunnen worden beoordeeld door vergelijking met de potentiële drogestof produktie zoals berekend met het simulatiemodel ALSIM(1.0). Dit kan een belangrijk hulpmiddel vormen voor het optimaliseren van de gewasgroei op de langere termijn en het tijdig ontdekken van groeistoornissen.

Het aandeel van de drogestof dat ten goede komt aan de oogstbare delen is nauw gerelateerd aan de omgevingsfaktoren omdat deze laatsten een grote invloed hebben op de vorming van loze scheuten. De oogstindex blijkt verder af te hangen van de hoogte van snoei van de bloemscheuten en de gehanteerde oogstmethode.

De bloemkwaliteit (3) is afhankelijk van enerzijds het aantal en de ontwikkelingssnelheid van de bloemscheuten, en anderzijds van de dagelijks beschikbare hoeveelheid assimilaten. De plantopbouw zoals gereflecteerd in het aantal, de diameter en verdeling van stengels op een bepaalde gewashoogte bepaalt ook de uiteindelijke bloemkwaliteit.

Tot slot worden er enige praktische toepassingen besproken die uit de resultaten naar voren komen.

Nawoord

Aan het einde van het schrijven van dit proefschrift komt onafwendbaar een moment van bezinning. Zonder al te veel filosofische overpeinzingen wil ik deze ruimte graag benutten om een aantal mensen te bedanken die een bijdrage hebben geleverd aan de totstandkoming van mijn proefschrift.

Voor het bewaken van de wetenschappelijke diepgang ben ik mijn promotor Prof.dr. J. Tromp zeer erkentelijk. Alhoewel uw inbreng de lengte van mijn artikelen niet ten goede kwam, werd de leesbaarheid er enorm door vergroot. Het begrip 'concise' schrijven behoort nu tot mijn vaste 'engelse' vocabulaire.

Een bijzonder woord van dank gaat uit naar co-promotor Dr.ir. P.A. van de Pol, wiens ongeëvenaarde enthousiasme voor rozen en geur zeer aanstekelijk werkt. Peter, jij hebt mij de kans geboden om, in een oriënterend onderzoek naar de wortelkwaliteit van rozenonderstammen, onderzoekservaring op te doen. Mede dankzij jouw hulp voor het verkrijgen van de noodzakelijke subsidies van PVS en NOVEM kon dit onderzoek worden uitgevoerd. Jouw veelzijdige contacten met de praktijk zorgden er bovendien voor dat het projekt ook buiten de vakgroep voldoende aandacht kreeg.

Zonder de medewerking van Lianne Haest-Rou en Jan Vos, die als assistenten aan het onderzoek hebben deelgenomen, zouden veel arbeidsintensieve proeven niet zijn uitgevoerd. Lianne, bedankt voor je nauwkeurige en zelfstandige uitvoering van alle koolhydraatbepalingen. Jan, bedankt voor het 'slopen' van veel rozenstruiken en het geduldig verwerken van de vele tienduizenden getallen. De hulp van kasmedewerkers Dick Voogd en Cees Vos was onmisbaar bij de uitvoering van de proeven. Alleen al voor de vier jaar durende 'Motrea' proef hebben jullie ruim 100000 rozen geteld en gewogen. Voor de verzorging van gewas en kasklimaat dank ik ook Maarten Baan Hofman en de overige medewerkers van het kassencomplex. Theo Damen ben ik veel dank verschuldigd voor de technische ondersteuning, vooral bij het opzetten van de substraatteelt op roltafels. Nog voor wij, als onderzoekers, iets hadden bedacht, had jij het al gemaakt!

Veel studenten en stagiaires hebben een bijdrage geleverd aan mijn onderzoek: Marcel Barten, Jack Beerkens, Mark Breugem, Theo Groen, Johan Hummel, Louis Kester, Edward Lenssen, Ageeth Manschot, Jan-Willem Spaargaren, Peter Stoop en Erick Westerman, bedankt voor jullie enthousiaste inbreng.

Veel 'praktijk' mensen hebben bewust of onbewust een bijdrage geleverd. De firma's Steenks, Zuurbier en de Gebr. Van Erkel dank ik voor het beschikbaar stellen van kasruimte en plantmateriaal voor het uitvoeren van enkele 'praktijkproeven'. Jullie praktijk-kennis heeft vaak tot een bijsturing van experimenten geleid. Vooral Bill Steenks wil ik in het bijzonder noemen: jouw enthousiasme en visie zijn goud waard voor de Nederlandse rozenteelt al is je dat niet altijd in dank afgenomen. Met plezier heb ik deelgenomen aan de rozenprojectgroep die als doel heeft de rozenteelt op een hoger niveau te brengen. Daarnaast hebben er altijd goede contacten bestaan met het onderzoeksbureau ETKO, de PBGN-lokaties Aalsmeer en Naaldwijk en het CPRO-DLO en AB-DLO in Wageningen. De daaruit voortvloeiende discussies met Walter Berentzen, Joop de Hoog, Rein de Graaf, Dick de Vries, Lidwien Dubois, Daan Kuiper, Anja Dieleman en Francel Verstappen, heb ik altijd zeer op prijs gesteld.

Naast de twee leden van de Internationale 'roosmaffia' Peter van de Pol en Dick de Vries bedank ik ook de overige leden van de begeleidingscommissie, Guus Van den Berg, Monique Mentjox, Frans Verbeek en Constan Custers voor hun belangstelling en meedenken over mijn onderzoek.

De collega's van de vakgroep Tuinbouwplantenteelt wil ik bedanken voor de plezierige werksfeer in het algemeen en het cabaret, de feestavonden, de vele PV-activiteiten en ons jaarlijkse uitstapje in het bijzonder. Enkele (ex)-collega's wil ik met name noemen: kamerbuurman Jeroen de Koning, voor zijn bijdrage aan het in een model stoppen van de gewasgroei van rozen: dat een tomatengewas eenvoudiger te modelleren valt dan een rozengewas begint ons zo langzamerhand duidelijk te worden, Ep Heuvelink, voor zijn nimmer aflatend enthousiasme, de vele nuttige statistische adviezen en zijn mede-bezorgdheid omtrent allerlei vakgroepbesoignes, Menno Bakker, onze mega-systeembeheerder, voor alle interrupties i.v.m. de nodige computerondersteuning, Harry Scholten en Marga Joziasse, voor de uitdaging om met ons drieën de redactie van het Labjournaal te vormen en daarmee de voorafgaande HEMA-produkties vrijwel te doen vergeten, en Christianne Marcelis-Van Acker voor de goede samenwerking en het zetten van de laatste puntjes (nou ja, puntjes?) in de drukversie.

Tenslotte bedank ik Irma. Zonder jouw begrip, liefde en steun zouden de laatste loodjes nog zwaarder zijn geworden.

Het is mooi geweest.

Michaël Kool

Curriculum vitae

Michaël Theodorus Nicolaas Kool werd geboren op 2 februari 1963 in Schalkwijk. In 1982 behaalde hij het Atheneum B diploma aan het St. Bonifacius college te Utrecht. In datzelfde jaar werd de gewaskundige Tuinbouwstudie aan de toenmalige Landbouwhogeschool (thans Landbouwuniversiteit) gestart. In 1987 slaagde hij voor het doctoraalexamen met als afstudeervakken Bloementeelt, Plantenfysiologie, Plantenveredeling en In vitro cultuur van hogere planten. Na het afstuderen heeft hij gedurende een half jaar stage gelopen op het Department of Ornamental Horticulture van de Hebrew University of Jerusalem, in Rehovot. In 1988 werd hij als toegevoegd onderzoeker aangesteld bij de vakgroep Tuinbouwplantenteelt ten behoeve van een oriënterend onderzoek naar het functioneren van rozenonderstammen. Gedurende de periode februari 1992 tot april 1996 verrichtte hij het onderzoek dat beschreven is in dit proefschrift.