

**Scion-rootstock Relationships
and Root Behaviour
in Glasshouse Roses**

CENTRALE LANDBOUWCATALOGUS



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Scion-rootstock relationships and root behaviour in glasshouse roses

Proefschrift

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Stellingen

1.

Bij roos is de mate waarin bladverwijdering leidt tot wortelsterfte mede afhankelijk van de hoeveelheid beschikbare reserves aan koolhydraten.

Dit proefschrift.

2.

Bij roos komt het effect van een onderstam op de bloemproductie en bloemkwaliteit vooral tot uiting onder ongunstige omstandigheden.

Dit proefschrift.

3.

De beschikbaarheid van koolhydraatreserves en de gevoeligheid voor wortelsterfte dienen selectiekenmerken te zijn bij de keuze van een onderstam voor de jaarrondproductie van kasrozen.

Dit proefschrift.

4.

Bij de jaarrondproductie van kasrozen is de diameter van grondscheuten belangrijker voor productie en kwaliteit dan het aantal.

Dit proefschrift.

5.

Onderstammen voor de kasrozenteelt die in de winter meer groei van de bovengrondse delen induceren, bevatten in de winter minder reserves.

Dit proefschrift.

6.

Bij de bewering dat het blad een remmend effect heeft op het uitlopen van okselknoppen van roos wordt onvoldoende rekening gehouden met onder andere plantbehandeling, plantconditie en seizoen.

Zieslin, N., Halevy, A.H., 1976. Botanical Gazette 137, 4: 291-296.

7.

In het door Lieth en Pasion ontwikkelde simulatiemodel voor groei en ontwikkeling van bloemscheuten in roos wordt ten onrechte geen rekening gehouden met de variatie die binnen de drogestof distributie bestaat gedurende het jaar.

Lieth, J.H., Pasion, C.C., 1991. Scientia Horticulturae 46: 109-128.

8.

Bij kasrozen dienen aparte selectieprogramma's voor ent en onderstam te worden uitgevoerd.

9.

Dat bij vele teeltechnische onderzoeken het traditionele systeem of ras het beste blijkt te zijn, is meer een tekortkoming van het onderzoek dan een verdienste van het traditionele systeem.

10.

Alleen onder voor gewassen niet-stressgevoelige omstandigheden zijn kleine wortelstelsels (hogere scheut-wortelverhouding) geoorloofd.

11.

De redding van de Nederlandse fruitteelt ligt in het centraliseren van bewaring en afzet.

12.

Met de toename van het aantal juristen op het MLNV is het bergafwaarts gegaan met de Nederlandse Landbouw.

13.

De aanduiding 'plat' voor het Limburgse dialect getuigt van weinig realiteitszin: het Limburgs kent meer diepgang en betekenis in woord, toon en uitdrukking dan het ABN.

14.

Het mooie van de zon is dat je in de schaduw kunt zitten.

15.

Het afschaffen van stellingen bij een proefschrift betekent een ernstige verarming van de promotieplechtigheid.

Stellingen behorende bij het proefschrift: *"Scion-rootstock relationships and root behaviour in glasshouse roses"* door H.W.M. Fuchs.

Wageningen, 27 mei 1994.

Voorwoord

Het werken aan een proefschrift doet je beseffen hoe afhankelijk je bent van anderen. Zeer velen hebben een bijdrage geleverd aan het tot stand komen van dit proefschrift. Allen wil ik daarvoor bedanken en een aantal mensen in het bijzonder.

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Ontvangen

25 MEI 1994

UB-CARDEL

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Summary

In the Netherlands, the cultivation of cut roses in the glasshouse is commonly carried out year-round. Most cultivars are grown on a rootstock. The first part of this study investigates various rootstocks for their ability to influence production and quality throughout the year. The mutual influence between scion and root system during normal practical growing management in soil without artificial light was followed and its physiological background studied. In the second part attention was mainly focussed on shoot-root ratio, root carbohydrates and mortality and regeneration of roots.

In Part I, in one long term experiment, the effect of 17 root systems on plant behaviour of the scion cultivar *Rosa* 'Varlon' grown in soil without supplementary lighting was studied for three years under conditions of relatively low greenhouse temperatures. It became clear that the root system influenced the building up of the rose bush, and that this particularly took place during the first year after planting.

Considering only the plants propagated by stenting, the number of bottom-breaks for *R.* 'Varlon' plants varied between 1.5 for *R.* 'Motrea' and 2.3 per plant for *R. indica* 'Major'. About 90% of all the bottom-breaks were formed in the initial months after planting. The quality of these bottom-breaks, e.g. the diameter at the time they were harvested, was 15 percent higher for the best rootstock, *R.* 'Mme Alfred Carrière', compared with the least, *R.* 'Paul's Lemmon Pillar'. The percentage of secondary thickening of bottom-breaks after three years varied somewhat per rootstock and was on average about 20%. Eventually, the difference between rootstocks with respect to bottom-break diameter was about the same as obtained during their harvest.

After three years it became apparent that plants on *R.* 'Moonlight' produced the highest number of branches per bottom-break, i.e. 2.4, whereas the bottom-breaks of *R. zigrii* had only 1.4 laterals. The diameter of these laterals varied from 10.2 mm for plants on *R.* 'Fredica' to 8.6 mm for plants on *R.* 'Paul's Lemmon Pillar'.

The number of shoots at 60 cm above ground level and exceeding 0.5 cm diameter, the so-called structural shoots, was 6.6 per plant for *R.* 'Moonlight', which means that it exceeded the least *R. zigrii* by 60%. This means that the same tendency was found here as was noticed for the number of branches per bottom-break. It became clear that competition existed between the number of structural shoots per plant; the more shoots produced, the more eventually died off. The diameter of the structural shoots reached a maximum when grown on *R.* 'Mme Alfred Carrière' and a minimum when grown on *R.* 'Paul's Lemmon Pillar'. This result is comparable with that found for the diameter of the bottom-breaks.

The method of propagation proved to be an important factor with respect to the building up of the plant; the plants bench grafted on *R. canina* 'Inermis' produced the highest total number of

bottom-breaks but their diameter, secondary thickening and weight remained behind all the other rootstocks including the root-grafted *R. canina* 'Inermis' plants.

In the same *R. 'Varlon'* experiment differences of more than 100% between rootstocks, irrespective of the method of propagation, were found for the period with the lowest production, i.e. winter. The differences between rootstocks in average production per year was less (about 60%). The highest production was found for *R. 'Varlon'* on its own roots and *R. indica* 'Major', the lowest for both *R. canina* types, irrespective of the method of propagation, and *R. zigrii*. Further, it proved that some of the rootstocks exceeded others during the whole year, whereas some diverged only in some periods. The high production of *R. 'Varlon'* might be related to the absence of the graft union.

The number of axillary buds per plant and the number of released buds, but also the readiness to break out and, thereafter, the time required to develop a harvestable flower, are important factors in determining the total amount of flowers produced. In this study it was shown that the differences found in bud break between rootstocks during the year explained, at least partly, the differences found in production between rootstocks and between the seasons of the year. Also, flower stem development after axillary bud break proved to be dependent on rootstock. The importance of the presence of the subtending leaf and the diameter of the parent shoot depends on the chosen rootstock. This in turn depends on the method of carbohydrate supply (from actual photosynthesis or from storage) for the release of the bud and the development of the young shoot.

The effect of rootstock on production (number of flowers) as well as on the quality of the harvested flower (length and weight) was more pronounced in winter than it was in summer. The quality parameters used were well correlated. However, the flower stem length was less influenced by season than flower weight.

Finally, using the data from the long term *R. 'Varlon'* experiment, production and quality were quantified by linear regression models, using the plant development parameters, irrespective of the rootstock, as regressors. Production as well as quality was (partly) explained, for each season, by the transverse sections of the branches of the bottom-breaks. The number of bottom-breaks was less important for production, even less than the number of their laterals; the former parameter is only of importance for production in spring and summer. The importance of the transverse sections is probably due to their role in the storage of reserves and transport capacity. Therefore, easiness of bud break and the time required for flower development is better when emerging from thick parent shoots. This is especially emphasized by the more pronounced role of the transverse section of the shoot for production in winter and for production by older bushes.

It was suggested, when comparing the data concerning bush development parameters at the start and after three years, that the development of the plant in the first six months after planting

was important for the building up of the rose bush and therefore for production and quality throughout its whole life.

In Part II, examination of the plant's root system revealed that root fresh weight for the root systems used as rootstock for *R. 'Varlon'* differed markedly after three years. The root system of *R. 'Mme Alfred Carrière'* had 40% less weight compared with *R. 'Moonlight'*. Further, some evidence was found to suggest that propagation technique may play a role in root characteristics, such as root number and average root length.

In this study, the shoot-root ratio of young rose plants (younger than one year), varied between three and six and proved to depend on growing technique, environmental factors and the combination of rootstock and scion cultivar used. With progressing plant age shoot-root ratio increased to 10 - 15 for three years old plants. It can be stated that the mutual influence of shoot and root, with respect to partitioning of assimilates between shoot and root, depends on the combination and can be influenced by climatic conditions, plant age and growing technique.

For *R. 'Varlon'* grown on different root systems, a close relationship was found to exist between the plant's shoot-root ratio after three years and the ratio between total flower weight produced over three years and final root weight. It was suggested that a fixed share of assimilates of the upper parts is used for flower formation irrespective of the root genotype used.

From several experiments it became clear that disturbance of the balance between shoot and root, either by shoot or root pruning, was followed by a re-establishment of the original shoot-root ratio. This is achieved independently of the scion-rootstock combination used, or the age of the plant. When frequently repeated intervention was carried out by removing upper parts, the shoot-root ratio reached a new stable balance but at a lower level. It was suggested that in this case storage of reserves was taken over by the roots.

In experiments with rooted leaf cuttings it was found that a surplus of assimilates can be reflected in a higher root mass. On the other hand, it was also found that a higher root mass can indicate that the sink activity and/or storage capacity of the root is higher.

The amount of carbohydrates stored in the roots of a rose plant during the year is related to the development of the shoot and root and the photosynthetic activity of the leaves. It was shown that apart from the time of year the combination of scion and rootstock used also had a prominent effect. With respect to the storage of carbohydrates in rose roots, it became clear that rootstocks originating from 'winter active' plants, such as *R. multiflora* 'Multic' and *R. indica* 'Major' showed a less pronounced variation during winter, compared with the originally hardier ones such as the *R. canina* types. Further, aspects such as the difference in storage capacity, sink activity, redistribution and climatic factors may play a role in the storage of carbohydrates in roots.

Root growth was related to the presence of leaves. Consequently the removal of leaves by harvesting flower stems or other methods of shoot pruning, resulted in inhibited root growth within one or two weeks. Additionally, root mortality may occur depending on the severity of pruning. The extent of root mortality proved to be dependent to some degree on the rootstock

used. Their susceptibility to root mortality depended on the amount of carbohydrates stored, internal competition between roots and shoot-root competition.

After root mortality the best root regeneration was observed when more carbohydrates were available. This means that a root system with a higher storage capacity (i.e. mostly thicker roots), plants with more leaves, plants grown under a higher light intensity, or plants treated with supplementary sucrose, showed better root regeneration. Stimulating the root's sink activity by application of auxin improved root regeneration too. The optimal concentration of auxin (IBA) applied for root regeneration was dependent on the temperature used for plant growth. With respect to temperature, root regeneration was optimal around 17 °C.

Root growth of *R. canina* 'Inermis' plants grown in peat was not limited between pH values 4 to 8. Root growth for plants grown on hydroculture was optimal when pH was about 6. Dormant plants only remained inactive at a pH of 3.5 or lower, but young active roots disintegrated within a few hours at this pH value. Bud release was inhibited at pH levels that hampered root growth, probably because production of cytokinin remained behind.

Reduced root growth during a short period or to a relatively low extent was not necessarily damaging for the plant. In fact, shoot growth was enhanced when root mass was decreased temporarily by removing root ends. The emergence after a while of a higher number of root apices, suggested that the improved shoot growth was due to a higher production of cytokinin. A more pronounced reduction of root growth led to less shoot development, more water stress and a higher susceptibility to disease.

In conclusion, it may be said that the whole life of a rose plant and therefore also flower production and quality, is influenced by competition between upper parts and roots. Good development requires not only an adequate assimilating system but also good storage and redistribution capabilities. Storage capacity is of especial importance during unfavourable conditions. For optimal production throughout the year, the roots should be active and after mortality, a quick recovery is required to ensure the correct balance between shoot and root. In this respect the behaviour of the rootstock plays an important role.

Therefore, new scion cultivars should be assessed when growing on rootstocks which have adapted properly to the grower's method of plant management and his growing conditions. Cultivars for year round production for instance should never be tested on *R. canina* selections, due to their poor winter activity.

For the correct balance between shoot and root, plant management should be carried out in dependence of climatic conditions, rooting medium, scion and rootstock combination and plant condition itself.

The requirements for the ideal rootstock as well as for the ideal scion cultivar are tremendous. Therefore, it is more practical to select rootstock and scion cultivars in separate programmes. Finally, the most suitable combination for a certain situation could then be combined by grafting.

1 General introduction

The rose is the most important cut flower grown under glass in the Netherlands. In 1992 the total auction turnover of Dutch produce was 747.5 million Dutch guilders (Anonymous, 1993a). The four most important cultivars were Motrea (Motrea^R), Ruimeva (Madelon^R), Korflapei (Frisco^R) and Sweet Promise (Sonia^R). The total acreage in 1993 was 890 ha (Anonymous, 1993b).

Most of the modern cultivars can produce year round, but in winter even cultivars adapted to year round production and even with a high energy input, produce flowers of an inferior quality and more blind shoots (shoots without flowers). Due to the year round production and the specific climatic needs, the production of roses requires a high energy input and for that reason the rose consumes more energy than any other important crop grown under glass. Since the time that fuel costs started to rise (1970) the technical equipment of the greenhouse has been adapted to conserve energy (smaller pipes in combination with the installation of parts of the piping at canopy height, movable thermal screens, double glazing, acrylic cover and/or sides and, especially in the case of growing on rockwool, heating of the substrate). In addition, the introduction of the computer made it possible to use temperature regimes that were impractical previously (Cockshull, 1985). Furthermore, growing techniques (glasshouse climate) and the grown cultivars (adapted to lower temperature) changed. More recently, the specific need to reduce environmental pollution (CO₂, pesticides, minerals) will also have an impact on the cultivation of roses.

Some of the above mentioned technical solutions (thermal screens, double glazing) reduce the light intensity and therefore flower yield and quality in winter (Halevy, 1986). Changing the growing technique, e.g. by introducing a (longer) rest period may save energy but will result in a loss of market share. A breeding programme for low energy cultivation may be promising but requires a long time, the more so because other aspects (quality, disease resistance) also need attention (Dubois and De Vries, 1979; De Vries *et al.*, 1982). Since in the Netherlands roses are commonly grown on rootstocks (*Rosa canina* selections), a worthwhile alternative may be to look for rootstocks requiring less energy.

Interest in use of rootstocks was in the first place lying in the rapid economic multiplication of desirable scion cultivars that are unable to raise on their own roots (Tubbs, 1973a,b). For instance, for propagation of vine and top fruit grafting scions on rootstocks has been a horticultural practice for over twenty centuries. Nowadays, it is realized that successful production in these crops is intimately related to stock-scion interaction and rootstock environmental adaption is now universally known (Rom and Carlson, 1987). For roses rootstocks are used for several reasons, including economical aspects of propagation, flower production, flower quality, adaptation to different kinds of soil and disease resistance (Edwards, 1955; Krüssmann, 1974; Jurriaanse, 1979; Votruba, 1981).

The physiology of flowering in roses was reviewed by Zieslin and Moe (1985) and Zieslin (1992). The rose is a polycarpic, self-inductive plant, which initiates flowers autonomously on every growing shoot after a certain length is obtained, without needing a specific photoperiod or temperature (Halevy, 1984). To achieve high production, a good bush development and a rapid bud break after removing the previous flower, followed by a good and vigorous development of the emerged young shoot is essential (Halevy, 1986). Therefore, studying the influence of the rootstock on rose production could be worthwhile because it may affect bottom-break production, formation of laterals and bud development.

The production cycle for rose production under glass is on average 6-7 years. This means that selection of rootstocks takes a long time. Furthermore, there is little knowledge about the factors that control bush development, root behaviour and their relation to flower production and quality.

The purpose of this work was to follow bush development and its relationship to production and quality under conditions of a relatively low energy input and standard plant management techniques. Within that scope rootstock effects will occupy a central position in Part I and it will be seen that rootstocks are especially important in winter, when light conditions are poor. Therefore, in Part II attention is focussed on shoot-root relationships and the various aspects of root growing and development, especially under unfavourable conditions of low carbohydrate production, low internal carbohydrate levels and a relatively high carbohydrate demand.

Part I

The effect of rootstock on bush development and production

2 Introduction

A rose rootstock can influence the scion in terms of growth and development in various aspects. Most important are adaptation to certain pH values and drainage conditions of the soil, climatic factors, disease resistance, plant longevity, compatibility, vigour, productivity and flower quality (Edwards, 1955). Later studies added more and more detailed information. Mineral uptake by various rootstocks was studied by Byrne and Furuta (1967), Johansson (1979) and Gammon and McFadden (1979), the influence on plant performance when plants are grown in soils with a high pH by Grueber and Hanan (1980), frost resistance or winter hardiness by Meiss (1985), tolerance for salinity by Singh and Chitkara (1983), (in)compatibility by Hasek (1968), mutual influence of callus growth by both scion and rootstock by Zieslin and Ziv (1986), disease resistance by Buck (1951), Coolen and Hendrickx (1972) and Ohkawa and Saigusa (1981). A number of specific aspects in which the rootstock can influence growth and development of the rose scion are described below.

Bud break

In roses axillary bud break is an important phenomenon with respect to production. The importance of bud break is expressed at four stages of plant development: propagation, bottom-break formation, formation of laterals and axillary bud release after harvest. At each level not only the readiness to break but also the number of released buds is important; both can have positive as well as negative consequences for production and quality.

According to Zieslin *et al.* (1978) axillary buds are never really dormant but just inhibited (quiescent) to sprout. Zieslin *et al.* (1976a) and Zieslin and Halevy (1978) showed a gradient of the ability for bud break along the stem which Zamski *et al.* (1985) ascribed to anatomical and morphological differences. The upper buds were the least inhibited, were fully developed and sprouted more readily after decapitation. Buds in the centre of a shoot were also fully developed, but were kept inhibited by the still growing shoot tip. Finally, the buds in the axils of the lower leaves showed a strong inhibition. Low air humidity and low temperature inhibit bud release in roses (Moe, 1972; Van den Berg, 1987) just as low light intensity and short days do (Moe, 1972). A low ratio of red/far-red light was found to inhibit bud break (Mor and Halevy, 1984). Hardly any data could be found on the effect of rootstocks on bud break (Kool and Van de Pol, 1991b).

Bottom-break formation and bush development

The formation of vigorous shoots on the basal part of the plant, known as bottom-breaks and renewal canes, plays an important role in growing roses. Bottom-breaks are required for high production (Asen and Hamner, 1953; Byrne and Kohl, 1972; Zieslin *et al.*, 1976b; De Vries and Dubois, 1983b). The emergence of bottom-breaks and renewal canes is usually restricted to a few months after planting or, if later, occurs after a certain stress situation (Zieslin and Mor, 1981).

Various climatic factors and growing techniques are involved, such as soil moisture and air humidity (Plaut and Zieslin, 1974), temperature (Hanan, 1979; Zieslin and Mor, 1981; Schrock and Hanan, 1981), light intensity (Carpenter and Rodriguez, 1971a; Carpenter and Anderson, 1972; Kosh-Khui and George, 1977; Zieslin and Mor, 1981), light quality (Mor and Halevy, 1984), pruning and removal of lateral growth (Zieslin and Mor, 1981; Khayat and Zieslin, 1982), shoot bending (Zieslin and Halevy, 1978) and the application of cytokinins (Carpenter and Rodriguez, 1971b; Faber and White, 1977; Ohkawa, 1979; Marczynski *et al.*, 1979) and ethylene releasing substances (Zieslin *et al.*, 1972; Van Montfort, 1978; Marczynski *et al.*, 1979). Broadly speaking one could say that the formation of bottom-breaks occurs when due to some growth retarding stimulus apical dominance decreases (Zieslin and Halevy, 1976) and thereafter favourable conditions prevail (Zieslin *et al.*, 1975; Schrock and Hanan, 1981). The importance of hormones such as auxins and cytokinins and, possibly abscisic acid, in apical dominance has been shown for many plant species including roses (Carpenter and Rodriguez, 1971b; Zieslin *et al.*, 1978). It may be reasoned that due to growth retardation, hormone concentrations shift which is reflected in changes in the source-sink relationship in favour of the basal parts. Since cytokinins are produced by active root tips, rootstocks may have an influence on bottom-break formation, as suggested by Van de Pol *et al.*, 1988a. Furthermore, genetic differences between roots, even within the same species, are reflected in the consumption of different amounts of carbohydrates for above all growth and respiration, as was reviewed by Lambers (1986) for several species, unfortunately excluding roses.

Little is known about the precise influence of rootstock on bush development in roses, but in several rootstock trials differences in bush quality in the nursery were reported (Swarup and Malik, 1974; Singh, 1977; Jurriaanse, 1979; Kloosterhuis, 1979; Grueber and Hanan, 1980; Anonymous, 1983; Ohkawa, 1986). More detailed information was given by Van de Pol and Breukelaar (1982) who found that *R. indica* 'Major' gave more and mostly thicker bottom-breaks than did *R. canina* 'Inermis'. Miller (1986) also reported for both cultivars 'Sweet Promise' and 'Varlon' more bottom-breaks when grafted on *R. indica* 'Major' compared with their own roots. De Vries and Dubois (1983a) and De Vries (1993) found a levelling effect in the number of bottom-breaks when clones of divergent seedlings were bench-grafted on *R. canina* 'Inermis' rootstock.

Flower production and quality

Production of roses depends on cultivar, rootstock and growing conditions. The use of rootstocks can be highly positive compared with their own roots, especially in the open (Vecera, 1967; Goujon, 1974; Lundstad, 1983). However, in several cases the same also appeared to be true under greenhouse conditions (Goujon, 1974; Votruba, 1981; Lundstad, 1983; De Dood *et al.*, 1988). Votruba (1981), growing in the ground, and De Dood *et al.* (1988), growing in rockwool, reported that the necessity of a rootstock depends on the scion; with some genotypes their own roots were preferable but with most genotypes using a rootstock proved to be better. In the latter

case, the best rootstock depended on the scion used (Van de Pol and Breukelaar, 1982; De Dood *et al.*, 1988). Remarkably little is known of the influence of bush development parameters on production. As early as the 1940's research was being carried out on relationships between production and several plant parameters in other woody plants, especially in fruit trees (Wilcox, 1940; Pearce, 1949). Work in roses is limited to the influence of the number of bottom-breaks on production (Kofranek and Fisher, 1949; Asen and Hamner, 1953; Zieslin *et al.*, 1976b; De Vries and Dubois, 1983a,b and 1984). Only Van Rijssel (1982) and Kool and Van de Pol (1992) provided some data with respect to quality (diameter) of the bottom-breaks and production.

Literature concerning flower quality as influenced by rootstock is unfortunately neither clear nor unanimous. Differences in flower quality in general (whatever it means) with respect to rootstocks were reported by Pessala (1977) and Gammon and McFadden (1979). Differences in colour due to rootstocks were found by Van Marsbergen (1952), Hasek (1968), Jurriaanse (1979) and Van Eck and De Vries (1993). Hasek (1968) and Singh (1977) reported the influence of rootstocks on flower size and Meneve *et al.* (1975), Van Marsbergen (1980), Pollock (1983) and Miller (1986) on flower stem length.

Finally, it should be kept in mind that production and quality may have a negative correlation (Van de Pol and Breukelaar, 1982; Van den Berg, 1987; De Dood and Rademaker, 1991; Kromwijk and Van Mourik, 1991).

Objectives

The scope of this part of the study about glasshouse roses was a detailed investigation of the relationship between rootstock on the one hand, and bush development, production and quality on the other hand. In one long term experiment the effect of a number of rootstock types on plant behaviour (scion *Rosa* 'Varlon') was followed for three years. In this experiment plant behaviour was investigated under conditions of relatively low temperatures and otherwise normal greenhouse conditions and plant management. Since the objective was to examine the rootstock potential to produce bottom-breaks under these environmentally less favourable conditions, no (other) distinct stress factor such as drought was used to induce bottom-break formation. Apart from that, these factors usually induce a number of 'renewal shoots' (vigorous shoots not originating from the basal part of the plant; Kohl and Smith, 1969) rather than bottom-breaks (Carpenter and Rodriguez, 1971b).

Finally, on the basis of a number of plant parameters an attempt was made to predict production and quality with the help of linear regression models.

3 Materials and methods

Selection of rootstocks and scion

Since 1977 over one hundred species and cultivars of roses have been collected from all over the world by the Department of Horticulture of the Agricultural University Wageningen. They were selected for vigour and/or ability to form new shoots in winter ('winter activity'), which are important requirements for year round greenhouse production of roses. In 1982, based on previous experiments, twenty species and/or cultivars were selected to test their ability to function as rootstocks. The names of the rootstocks used are listed in Table 1.

Table 1. *Abbreviations, names and propagation technique used of species and cultivars tested for rootstock function.*

abbreviation	name	propagation technique
Var	<i>R. 'Varlon'</i>	rooted cutting
In-b	<i>R. canina 'Inermis'</i>	bench grafted
In-r	<i>R. canina 'Inermis'</i>	root grafted
Br-r	<i>R. canina 'Brögs Stachellose'</i>	root grafted
Bob	<i>R. 'Bobby James'</i>	stented
Maj	<i>R. indica 'Major'</i>	stented
Fre	<i>R. 'Fredica'</i>	stented
Lav	<i>R. 'Lavender Lassie'</i>	stented
Lec	<i>R. lecanstciana</i>	stented
Mac	<i>R. 'Macrophylla Glaucophylla'</i>	stented
Mad	<i>R. 'Madame Alfred Carrière'</i>	stented
Moo	<i>R. 'Moonlight'</i>	stented
Mot	<i>R. 'Motrea'</i>	stented
Kan	<i>R. multiflora 'Kanagawa'</i>	stented
Pau	<i>R. 'Paul's Lemmon Pillar'</i>	stented
Pin	<i>R. 'Pink Cloud'</i>	stented
Vei	<i>R. 'Veilchenblau'</i>	stented
Zig	<i>R. zigrii</i>	stented

As scion cultivar Varlon (Ilona[®]) was chosen for its well-known problems with regard to quality and production, especially in winter. In addition, Varlon was the most important red rose in 1982.

The rootstock shoots were collected in November from the open field or from a low-heated greenhouse and cut into pieces of about 6 cm, each piece having one bud, and stored in plastic bags at about 4 °C until propagation occurred a few days later. The scion shoots were obtained from commercial growers, where they were taken at full bloom. After cutting, the stems were kept in water; they were used within one or two days.

Propagation

Most of the combinations were made by stenting (Van de Pol and Breukelaar, 1982) in November - December 1982. In addition, 'Varlon' cuttings were made for comparison. 'Varlon'

on *Rosa canina* 'Inermis' was propagated by bench-grafting on seedlings in January 1983. For stenting a piece of stem was usually used as rootstock. However, for *Rosa canina* 'Inermis' and *Rosa canina* 'Brögs' a piece of root was taken (Van de Pol, 1986), because stems did not easily form roots.

For each combination about 70 plants were made. After cutting, the scion and rootstock were combined by using tape of glued paper (Van de Pol and Breukelaar, 1982). The stentlings were subsequently dipped in a solution of indole-3-butyric acid (IBA, 1500 mg/l) and put in a plastic frame for a few minutes to absorb the adhering solution. Finally the stentlings were planted in small pots (9*9*9 cm, 0.7 l) containing a one to one mixture of peat and riversand (by volume). The pH of the rooting medium was 5.5. Rooting occurred in a heated greenhouse at about 25 °C. In order to obtain an air humidity of almost 100 percent the plants were covered with a transparent plastic sheet. To prevent premature bud release of the scion and to stimulate root growth, natural daylight was extended to 18 hours using HPLR 400 W Philips lamps (minimum irradiance 3 W/m² at plant level). When necessary, mist was applied twice a day. The plastic sheet was covered with cheese cloth if the light intensity was too high. After five weeks about 35 plants of each combination were selected for uniformity and hardened off for one week by gradually lowering the air humidity to normal greenhouse level.

In the meantime the soil in the greenhouse (a sandy clay) at the Department of Horticulture of the Agricultural University Wageningen was prepared, including manuring with stable dung and steam sterilisation. At the beginning of March 1983 the young plants were planted in a two row system at a plant density of 16.5*50 cm.

As the percentage of dead plants during the experiment was extremely high for *R. multiflora* 'Kanagawa' (62.5%), this rootstock was further left out. For the other rootstocks the percentage of dead plants was on average about 5% (Appendix I).

Experimental lay-out

The experimental lay-out was a randomized block design of eighteen treatments (=rootstocks) with six replications of four plants per plot. Each plot was guarded on both sides by two *Rosa* 'Sweet Promise' plants bench-grafted on *Rosa canina* 'Inermis' to nullify border effects. Further, in order to favour the greenhouse climate rose bushes (*Rosa* 'Varlon') of the same age were planted around the experimental plot.

Growing technique

Roots of the scion cultivar ('own roots'), which appeared incidentally nearby the graft-union, were removed shortly after occurrence. With respect to watering, fertilization and disease protection the plants were cultivated as usual in practical growing. The temperature in the greenhouse in summer (March - October) was at least 20 °C during the day and 17 °C at night. In winter, day and night set-points were 18 °C and 15 °C, respectively. No supplementary

artificial light was used. The flowers formed by the primary shoot and their laterals were not harvested, but bent to promote bottom-break formation.

Three times a week, flowers that had reached the normal auction stage were harvested (cut back). During the summer (mid July - mid August) of 1984 and 1985 flowers were not harvested as is usual in practice. Bottom-breaks are defined as the vigorous shoots originating from the very basis of the primary shoot and renewal canes defined as the (also vigorous) shoots that originate from the primary shoot at some distance from the basis (up to 20 cm height) were cut back just above the second five-foliate leaf from shoot basis. The flowers that were formed by the laterals of the bottom-breaks and the renewal canes were cut just above the first (in the beginning) or the third five-foliate leaf (from July 1983). From October - November the bushes were undercut (i.e. each flower cut under the place of insertion) but after the winter, in February - March, each shoot was cut back on the first five-foliate leaf. From July on the stems were cut again on the third five-foliate leaf.

Observations

All the bottom-breaks and renewal canes were counted and at harvest their diameter about 5 cm above the point of origin was recorded as well as the length of the stem from point of origin to the flower bud (=length 1). After harvest, the length (=length 2) and weight of the harvested flower stem were recorded. Number, length 2 and weight of all the other flowers (formed by the laterals of the bottom-breaks and the renewal canes) were also measured.

Further details will be described where needed.

Statistics and models

All the data was analyzed for variance using the statistical package GENSTAT, SYSTAT or SPSS. Where necessary, further analysis was made by using Tukey's range test with a critical level (P-value) of 5%. In the various Tables, values within a column (or sometimes within a row) that significantly differ are followed by different letters. Correlation tests were carried out by using appropriate tests like Spearman's or Friedman's test (Snedecor and Cochran, 1967) with a P-value of 5%.

The linear regression models, described in Chapter 5, were calculated in accordance with the general formula for such a linear model:

$$Y = a + bX_1 + cX_2 + \dots + E,$$

where Y is a vector of the dependent variable, X_1, X_2, \dots are vectors of independent variables (regressors), E is a vector of the random errors, a is the intercept and b, c, ... are the estimated regression coefficients of the independent variables. For the selection of the regressors for the best fitting model the procedure of backward elimination was followed (Montgomery and Peck, 1982). Regressors were removed from the model until the absolute value of the t-statistics for any parameter exceeded 2 ($=p < 0.05$). The squared multiple correlation coefficient (R^2) was used as an indication for the fit of the regression model.

4 Results

4.1 Plant behaviour

4.1.1 Bush development

Because of interaction between rootstock and time all data concerning bush development was analyzed per period (season).

As Table 2 shows usually more bottom-breaks became ready for cutting in summer 1983 (June, July and August) than in spring (March, April and May). In the rest of the experimental period production of bottom-breaks was low (in average 0.2 per plant). The variation between rootstocks was considerable. For example, *R. canina* 'Inermis' (bench graft) formed 2.9 bottom-breaks against *R. 'Motrea'* only 1.5 per plant. Noticeable is the high summer activity for the rootstock *R. canina* 'Inermis' (root graft and bench graft).

Table 2. Numbers of bottom-breaks (per plant) harvested in the spring and the summer of 1983, and in the rest of the experimental period of three years for *R. 'Varlon'* as influenced by rootstock.

rootstock	number per period			
	spring	summer	rest	total
Var	1.0 a	1.0 b	0.5 ab	2.4 ab
In-b	0.7 ab	2.1 a	0.2 abc	2.9 a
In-r	0.5 ab	1.4 ab	0.0 c	2.0 bc
Br-r	0.8 ab	1.1 b	0.3 abc	2.1 abc
Bob	0.9 a	0.9 b	0.3 abc	2.2 abc
Maj	0.9 a	1.0 b	0.3 abc	2.3 abc
Fre	0.6 ab	1.2 b	0.2 abc	1.9 bc
Lav	1.1 a	0.6 b	0.1 bc	1.8 bc
Lec	0.7 ab	0.9 b	0.2 abc	1.8 bc
Mac	0.2 b	1.1 b	0.6 a	2.0 bc
Mad	0.8 ab	1.1 b	0.3 abc	2.1 abc
Moo	0.9 a	1.0 b	0.3 abc	2.1 abc
Mot	0.5 ab	0.7 b	0.2 abc	1.5 c
Pau	0.9 a	0.8 b	0.2 abc	1.8 bc
Pin	0.8 a	1.0 b	0.0 c	1.9 bc
Vei	0.9 a	1.0 b	0.1 bc	2.1 abc
Zig	0.6 ab	1.2 b	0.2 abc	1.9 bc
average	0.8	1.0	0.2	2.0

Broadly speaking, bottom-breaks formed in summer were thicker than those formed in spring (Table 3). Differences up to 39 and 21 percent were found in spring and summer respectively. Relatively thick bottom-breaks were formed on *R. 'Mme Alfred Carrière'* and *R. 'Fredica'*, whereas *R. canina* 'Inermis' (bench and root grafted) and 'Brögs' lagged behind. After three years, the average increase due to secondary thickening was 23 percent. With respect to

differences in diameter between rootstocks after secondary thickening, about the same tendency was found as in the first year with differences up to 26 percent. However, percentage of secondary thickening was more than 25 percent for *R. 'Mme Alfred Carrière'* and *R. 'Paul's Lemmon Pillar'*. For others, e.g. *R. canina 'Inermis'* (root grafted) and *R. 'Pink Cloud'* it was less than 20 percent.

Table 3. *Diameter per bottom-break (mm) at harvest in the spring and summer of 1983 and the weighed average for the total experimental period for R. 'Varlon' as influenced by rootstock. In addition the diameter (mm) after three years is also given.*

rootstock	diameter			
	per period		weighed total	after three years
	spring	summer		
Var	9.2 abcd	9.5 ab	9.3 abc	11.2 abcd
In-b	7.0 e	8.4 b	8.2 c	9.9 d
In-r	7.8 cde	8.8 ab	8.6 abc	10.2 cd
Br-r	7.8 cde	8.8 ab	8.4 bc	10.6 bcd
Bob	9.4 abc	9.3 ab	9.4 abc	11.9 ab
Maj	9.3 abc	9.4 ab	9.4 abc	11.4 abc
Fred	9.7 a	9.4 ab	9.6 ab	11.8 ab
Lav	8.1 bcde	9.4 ab	8.6 abc	10.7 bcd
Lec	8.7 abcd	9.7 ab	9.1 abc	11.0 bcd
Mac	9.5 ab	9.8 ab	9.5 abc	11.7 abc
Mad	9.7 a	10.2 a	9.8 a	12.5 a
Moo	9.2 abcd	9.5 ab	9.3 abc	11.4 abcd
Mot	8.8 abcd	9.5 ab	9.2 abc	11.3 abcd
Pau	8.2 abcde	9.2 ab	8.5 bc	10.8 bcd
Pin	9.4 abc	9.3 ab	9.3 abc	11.0 bcd
Vei	9.5 ab	9.5 ab	9.5 ab	11.9 ab
Zig	7.7 de	8.9 ab	8.8 abc	11.1 abcd
average	8.7	9.3	9.1	11.2

With respect to the total bottom-break length (length 1) and the length of the harvested bottom-breaks (length 2), differences between seasons were small and therefore only the weighed averages over the total experimental period are given in Table 4. Differences in length between rootstocks were maximal 20 percent. *Rosa 'Paul's Lemmon Pillar'* produced short bottom-breaks and *R. 'Varlon'* (own roots) long bottom-breaks. In Table 4 the weights of the harvested bottom-breaks are also given. Differences in weight up to 33 percent were found. *Rosa 'Veilchenblau'* formed the heaviest and *R. canina 'Inermis'* (root and bench grafted) the lightest bottom-breaks. Dividing weight by length at harvest gives the specific weight of the bottom-breaks, which may be considered as a measure for firmness of the shoots. Differences up to 26 percent were found with respect to this parameter.

Table 4. Total length (cm) and length (cm) of the harvested bottom-breaks per bottom-break for *R. 'Varlon'* as influenced by rootstock. In addition the individual weight (g) and the specific weight (g/cm) of the harvested bottom-breaks is given.

rootstock	length		weight	specific weight
	total	at harvest		
Var	108.8 a	85.8 a	58.1 abc	0.68 abc
In-b	97.4 abc	73.2 cd	46.5 c	0.64 bcd
In-r	95.9 abc	76.9 abcd	46.7 c	0.61 d
Br-r	100.9 abc	78.3 abcd	49.4 abc	0.63 cd
Bob	106.6 ab	85.1 ab	60.5 abc	0.71 abcd
Maj	104.9 ab	79.5 abcd	58.0 abc	0.73 abc
Fre	104.9 ab	84.0 abcd	59.9 abc	0.71 abcd
Lav	95.2 bc	75.9 abcd	53.2 abc	0.70 abcd
Lec	96.3 abc	73.5 bcd	54.1 abc	0.74 ab
Mac	106.6 ab	80.4 abcd	57.5 abc	0.72 abc
Mad	104.7 ab	84.4 abc	61.3 ab	0.73 abc
Moo	100.0 abc	78.2 abcd	60.2 abc	0.77 a
Mot	104.2 ab	80.8 abcd	56.7 abc	0.70 abcd
Pau	89.0 c	72.3 d	47.4 bc	0.66 bcd
Pin	99.0 abc	82.5 abcd	58.0 abc	0.70 abcd
Vei	105.6 ab	85.7 a	61.8 a	0.72 abc
Zig	96.5 abc	75.3 abcd	52.0 abc	0.69 abcd
average	100.8	79.4	55.4	0.70

Table 5 shows that just as was found for bottom-breaks, most of the renewal canes were produced in the summer of the first year. After the first summer hardly any renewal shoots were formed. Differences between rootstocks were not very large. It should be noted that in contrast to what was found for bottom-breaks *R. canina* 'Inermis' (bench grafted) produced less renewal shoots whereas *R. 'Varlon'* on its own roots produced by far the most.

Table 6 indicates that the renewal shoots formed in the summer were thicker than those formed in the spring. The variation with respect to diameter between rootstocks showed differences up to 40 and 22 percent in spring and summer, respectively. Differences up to 19 percent were found with respect to total length of the renewal shoots, whereas these differences exceeded 50 percent for weight. Specific shoot weight between rootstocks differed a maximum of 26 percent. Comparison with the data for bottom-breaks (Tables 3 and 4) shows that renewal canes were about 20 percent lower with respect to diameter, length and specific weight, whereas the absolute weight of the shoots was 34 percent lower.

Information about linear correlation coefficients between bush development parameters is given in Appendix II.

Table 5. Numbers of renewal canes (per plant) harvested in the spring and summer of 1983, and in the rest of the experimental period of three years for *R. 'Varlon'* as influenced by rootstock.

rootstock	number per period			
	spring	summer	rest	total
Var	0.8 a	1.6 a	0.1 NS	2.5 a
In-b	0.1 b	0.5 b	0.0	0.5 c
In-r	0.1 b	0.7 ab	0.5	1.2 bc
Br-r	0.2 ab	0.8 ab	0.2	1.2 bc
Bob	0.1 b	0.8 ab	0.0	1.0 bc
Maj	0.5 ab	0.7 ab	0.0	1.2 bc
Fre	0.5 ab	0.9 ab	0.0	1.4 abc
Lav	0.3 ab	0.6 b	0.0	0.9 bc
Lec	0.6 ab	0.8 ab	0.0	1.4 bc
Mac	0.5 ab	0.6 b	0.1	1.3 bc
Mad	0.6 ab	0.8 ab	0.0	1.4 bc
Moo	0.4 ab	1.3 ab	0.1	1.8 ab
Mot	0.5 ab	0.7 ab	0.1	1.2 bc
Pau	0.5 ab	1.1 ab	0.0	1.6 ab
Pin	0.6 a	0.8 ab	0.0	1.5 abc
Vei	0.4 ab	0.9 ab	0.2	1.5 abc
Zig	0.4 ab	1.0 ab	0.0	1.3 bc
average	0.4	0.9	0.1	1.3

Table 6. Diameter (mm), total length (cm), weight (g) and specific weight (g/cm) per renewal shoot at harvest for *R. 'Varlon'* as influenced by rootstock.

rootstock	diameter		weighed total	total length	weight	specific weight
	period					
	spring	summer				
Var	7.1 ab	7.7 NS	7.5 NS	82.3 NS	41.0 ab	0.59 abc
In-b	5.3 c	7.5	7.5	79.3	31.6 b	0.50 c
In-r	5.7 bc	7.1	7.5	73.9	33.1 b	0.50 c
Br-r	7.1 abc	6.4	6.7	78.2	32.8 b	0.52 bc
Bob	7.2 ab	8.2	8.1	84.6	46.1 a	0.63 a
Maj	6.6 abc	7.2	6.9	77.1	39.7 ab	0.58 abc
Fre	6.1 abc	7.8	7.1	77.4	35.9 ab	0.59 abc
Lav	5.6 bc	7.3	6.8	73.5	33.8 ab	0.55 abc
Lec	6.4 abc	7.2	6.8	76.1	40.0 ab	0.62 a
Mac	7.2 ab	6.9	7.5	85.5	41.5 ab	0.61 ab
Mad	6.2 abc	7.2	6.5	71.8	34.6 ab	0.55 abc
Moo	6.0 abc	7.5	7.2	78.1	35.1 ab	0.57 abc
Mot	6.5 abc	7.4	7.2	83.6	38.8 ab	0.60 ab
Pau	5.8 abc	6.8	6.8	73.9	38.1 ab	0.62 a
Pin	6.4 abc	6.6	6.6	80.7	29.6 b	0.50 c
Vei	6.3 abc	6.8	6.9	81.3	33.5 b	0.52 bc
Zig	7.4 a	7.3	7.7	81.0	39.6 ab	0.58 abc
average	6.4	7.2	7.1	78.4	36.5	0.57

At the end of the experiment the number and diameter of all living branches per bottom-break and the 'structural shoots' (i.e. shoots exceeding 5 mm diameter that can be regarded as the frame of the bush) per plant at 60 cm above ground level were recorded (Table 7). It shows that the number of branches per bottom-break was rather high for *R.* 'Moonlight' and their diameter was high for *R.* 'Fredica' and *R.* 'Bobby James'. The good correlation between this diameter and that of the bottom-breaks ($r=0.744$) is worth mentioning. With regard to the total number of branches at 60 cm above ground level *R.* 'Moonlight' again exceeded the others. Differences in diameter were insignificant. The linear correlation coefficient for the relationship between number of branches of the bottom-breaks and number of branches remaining at 60 cm height was significant ($r=0.859$), as can be expected. Furthermore, for their diameters it was 0.726. The linear correlation coefficient for the relationship between the diameter of bottom-breaks and the diameter of branches at 60 cm height was 0.644.

Table 7. *Number (per bottom-break) and diameter (mm) of bottom-break branches and total number and diameter (mm) of structural shoots per plant (at 60 cm above ground level), three years after planting for R. 'Varlon' as influenced by rootstock.*

rootstock	branches on bottom-breaks		branches on 60 cm height	
	number	diameter	number (per plant)	diameter
Var	2.1 ab	9.4 abc	5.9 ab	7.7 NS
In-b	1.5 b	8.8 bc	3.8 b	7.6
In-r	1.6 ab	8.9 abc	3.9 b	7.5
Br-r	1.6 ab	8.8 bc	4.9 ab	7.3
Bob	1.6 ab	10.1 ab	5.2 ab	7.9
Maj	2.0 ab	9.5 abc	5.9 ab	7.7
Fre	1.6 ab	10.2 a	5.1 ab	8.0
Lav	1.5 ab	9.3 abc	4.5 ab	7.6
Lec	1.7 ab	9.5 abc	4.8 ab	7.9
Mac	1.5 b	9.4 abc	4.6 ab	7.7
Mad	1.7 ab	9.7 abc	4.2 b	8.2
Moo	2.4 a	9.2 abc	6.6 a	7.4
Mot	1.8 ab	9.5 abc	5.0 ab	7.3
Pau	1.9 ab	8.6 c	5.9 ab	7.3
Pin	1.5 ab	9.5 abc	4.7 ab	7.7
Vei	2.0 ab	9.5 abc	5.9 ab	7.8
Zig	1.4 b	9.5 abc	4.1 b	7.8
average	1.7	9.3	5.0	7.7

4.1.2 Production

Due to interaction between rootstock and time all data was analyzed per period of harvest. To give an impression of the production per season the averages over three years are given, as well as the average production per year (Table 8).

The highest production was realized in autumn (September, October and November), the lowest in winter (December, January and February). The relatively low summer production has no physiological basis but is due to not harvesting in (a part) of that period (cf. Materials and Methods, p. 23). Differences in yield up to 100 percent between rootstocks were found in winter, whereas differences up to 60 percent were found for the average production per year. The highest total production was found for *R.* 'Varlon' on its own roots and the lowest for both *R. canina* types (irrespective of the method of propagation). Some rootstocks exceeded the average throughout the experimental period (*R.* 'Varlon', *R.* 'Bobby James', *R. indica* 'Major', *R.* 'Mme Alfred Carrière' and *R.* 'Veilchenblau').

Table 8. *Average number of flowers produced per plant in each season and per year, averaged over three years for R. 'Varlon' as influenced by rootstock.*

rootstock	number of flowers in				average per year
	spring	summer	autumn	winter	
Var	3.7 a	4.6 a	6.4 a	1.5 abc	16.3 a
In-b	2.6 def	3.3 bc	4.3 cde	1.3 abcde	11.4 ghij
In-r	2.4 f	2.9 c	3.8 e	0.8 f	9.9 j
Br-r	2.4 f	3.3 bc	4.0 e	0.9 ef	10.5 ij
Bob	3.4 abc	3.9 abc	5.6 abc	1.6 ab	14.4 bc
Maj	3.6 ab	4.1 ab	5.6 abc	1.5 abc	14.7 ab
Fre	3.3 abcd	3.5 bc	5.0 bcde	1.2 abcdef	13.0 cdefgh
Lav	2.9 abcdef	3.2 bc	5.2 abcde	1.4 abcd	12.7 defgh
Lec	3.2 abcdef	3.6 bc	5.3 abcd	1.3 abcde	13.4 bcde
Mac	2.8 bcdef	3.4 bc	5.0 bcde	0.9 def	12.0 efghi
Mad	3.5 ab	4.1 ab	5.8 ab	1.2 abcdef	14.5 bc
Moo	3.0 abcdef	4.0 abc	5.2 abcde	1.2 abcdef	13.4 bcde
Mot	2.8 bcdef	3.6 bc	5.4 abc	1.3 abcde	13.1 cdef
Pau	2.6 cdef	3.5 bc	4.4 bcde	1.1 cdef	11.6 fghi
Pin	3.1 abcdef	3.6 bc	5.0 bcde	1.3 abcde	13.0 cdefg
Vei	3.3 abcde	3.8 abc	5.7 abc	1.7 a	14.3 bcd
Zig	2.5 ef	3.1 bc	4.5 bcde	1.3 abcde	11.4 ghij
average	3.0	3.6	5.0	1.2	12.9

4.1.3 Quality

Quality is defined as flower stem length and flower stem weight at harvest. For reasons of interaction the data for quality was analyzed per period. Tables 9 and 10 summarize the quality aspects of flower stems per season and per rootstock over the three years.

The differences in length between seasons are not relevant due to the cutting procedure followed (cf. Materials and Methods, p. 23). Differences between rootstocks varied from a maximum of 11 percent in summer to 38 percent in winter. Usually, *R.* 'Pink Cloud', *R.* 'Fredica' and *R. indica* 'Major' produced long flower stems, whereas flowers of *R.* 'Paul's Lemmon Pillar' and *R.* 'Motrea' were relatively short.

Table 9. Length (cm) per flower stem per season (mean of three years) for *R. 'Varlon'* as influenced by rootstock.

rootstock	average length of flowers in			
	spring	summer	autumn	winter
Var	72.0 abc	67.1 abc	66.8 ab	73.1 NS
In-b	69.8 abc	68.6 a	67.8 ab	69.1
In-r	71.0 abc	68.2 ab	66.9 ab	61.5
Br-r	71.4 abc	67.7 ab	69.4 ab	60.1
Bob	76.2 a	68.2 ab	69.4 ab	68.7
Maj	73.8 ab	67.4 ab	69.0 ab	72.5
Fre	73.1 abc	68.6 ab	67.9 ab	77.2
Lav	69.8 abc	67.1 abc	66.9 ab	74.1
Lec	72.6 abc	67.2 abc	67.0 ab	69.0
Mac	72.8 abc	67.6 ab	68.8 ab	75.1
Mad	73.8 ab	67.0 abc	66.0 ab	70.9
Moo	72.8 abc	66.5 abc	66.4 ab	69.3
Mot	70.7 abc	64.3 abc	64.8 ab	68.4
Pau	66.3 c	62.0 c	62.4 ab	69.9
Pin	72.9 abc	68.7 a	70.1 a	73.8
Vei	73.0 abc	68.5 ab	66.9 ab	67.9
Zig	71.2 abc	66.2 abc	66.9 ab	72.6
average	72.0	67.1	67.3	70.2

Compared with shoot length the differences in shoot weight between different periods were more pronounced. In all cases the highest shoot weights occurred in spring and the lowest in winter (Table 10). Differences between rootstocks varied from a maximum of 23 percent in summer to 44 percent in winter. *Rosa 'Varlon'* on its own roots, *R. 'Fredica'* and *R. lecanstiana* produced relatively heavy flower stems. Light shoots were found for *R. 'Paul's Lemmon Pillar'* and *R. canina 'Inermis'* (bench grafted). Finally, Table 10 shows the total shoot weight produced (number times weight) over three years, indicating that *R. 'Varlon'*, *R. indica 'Major'*, *R. 'Bobby James'*, *R. 'Mme Alfred Carrière'* and *R. 'Veilchenblau'* produced far more and the *R. canina* types and *R. 'Paul's Lemmon Pillar'* clearly less than the average.

Information about linear correlation coefficients between quality parameters per period is given in Appendix III.

Table 10. Weight (g) per flower per season (mean of three years) and total produced fresh flower weight (g) in three years for *R. 'Varlon'* as influenced by rootstock.

rootstock	weight				
	mean per flower per season				total in 3 years
	spring	summer	autumn	winter	
Var	38.0 abc	35.0 ab	27.3 a	19.5 NS	1517
In-b	31.2 c	33.1 ab	25.6 abc	17.7	970
In-r	32.5 bc	34.3 ab	25.9 abc	16.1	866
Br-r	35.7 abc	32.8 ab	26.9 a	18.0	953
Bob	39.5 ab	37.1 a	26.5 ab	18.4	1370
Maj	39.8 a	33.9 ab	26.9 a	19.7	1387
Fre	37.9 abc	35.0 ab	26.0 abc	20.5	1207
Lav	33.9 abc	34.3 ab	24.8 abc	19.8	1094
Lec	37.6 abc	35.8 ab	27.6 a	19.0	1260
Mac	35.5 abc	34.1 ab	26.3 abc	19.8	1094
Mad	38.1 abc	34.5 ab	25.8 abc	18.9	1341
Moo	38.8 ab	33.4 ab	24.9 abc	19.2	1208
Mot	36.5 abc	33.5 ab	26.5 ab	18.3	1169
Pau	30.8 c	30.1 b	22.8 bc	18.4	918
Pin	35.6 abc	35.2 ab	28.1 a	20.7	1213
Vei	38.8 ab	36.7 a	26.4 ab	18.2	1341
Zig	36.5 abc	33.9 ab	26.2 abc	20.0	1021
average	36.3	34.3	26.0	18.9	1172

4.2 Bud release and shoot growth

From September 1983 to April 1984 observations were made on (axillary) bud release and shoot growth. It should be remarked that on the plants involved in these records, in contrast with the normal cutting procedure (cf. Materials and Methods, p. 23), each harvestable flower shoot was cut back on the first five-foliate leaf until February and that thereafter they were undercut (cut underneath). In this way, because age influences axillary bud break (Zieslin, 1981), the age of the buds during the most unfavourable period could be kept more or less equal. Further, only flowers with a stem diameter of at least 5 mm were taken into account.

After cutting back, records were made of the diameter (diameter 1) of the stem just below the remaining uppermost bud and of its ranking order. With regard to ranking order the bottom-break itself has ranking order 0, its laterals ranking order 1, and so on. When the next generation of flowers was harvested the time they needed for development (days), their diameter (mm) (diameter 2), their length (cm) and their weight (g) were recorded.

Appendix IV (Figure 1a, b) shows that the average of most of the above mentioned parameters changed somewhat with time, as expected from Tables 9 and 10. With regard to the time between two successive harvests, further examination indicated that the differences between rootstocks as to this parameter, were generally not significant. The most widely used rootstocks for practical growing, *R. canina* 'Inermis' (root and bench grafted) and *R. indica* 'Major', as well as the plants propagated by cutting, were examined in more detail (Appendix IV (Figure 2)). In most cases,

where the time of flower stem development is concerned, the other rootstocks took an intermediate position between these four rootstocks. With regard to this parameter, differences between rootstocks proved to be significant throughout the time of observation. Due to interaction between rootstock and observation period, rootstock effects had to be analyzed for each observation period separately. Table 11 shows for the above mentioned rootstocks the results from September to January. The pattern appeared to be the same in this period. Noteworthy was the slow development in *R. canina* (irrespective of their way of propagation) compared with plants on their own roots and plants on *R. indica* 'Major'.

Table 11. Time (days) between two successive harvests for *R. 'Varlon'* as influenced by rootstock and time of year.

rootstock	previous harvest date			
	28 September	26 October	12 December	16 January
Var	106.7 b	109.0 NS	93.5 ab	71.9 c
In-b	146.4 a	111.4	102.4 a	84.7 a
In-r	169.6 a	129.1	104.0 a	73.6 bc
Ma j	98.4 b	110.1	89.9 b	79.2 ab

Further examination revealed that for these four rootstocks over the whole observation period the time from harvest to harvest decreased with the diameter of the parent stem (data not given).

Since roses drop their leaves easily in winter, even in greenhouses, it may be interesting to study the effect of the presence of leaves and their interaction with rootstock on axillary bud break and shoot development. In February 1986 all flower stems were cut back (undercut) to a well-developed axillary bud, of which the attending leaf was or was not removed. All the axillary buds of the selected stems were labelled and parameters of possible interest, such as diameter of the stem (between 4 to 10 mm), were determined. The rootstocks were selected for the known differences in their 'winter activity' or their commercial importance. At 9, 16 and 23 days after cut back, the length of all the developing shoots (broken buds) was measured. Buds longer than 1 cm and still growing were considered as 'broken'. Finally the percentage of flowering shoots was determined.

As expected, the effect of the presence of the uppermost leaf was shown to be highly important and the best axillary bud break, growth vigour and flowering was obtained from stems with subtending leaf (Table 12). With respect to rootstock differences varied from about 100 percent for buds with subtending leaf as well as for buds without subtending leaf. In both cases *R. 'Pink Cloud'* induced the best growth, whereas for *R. 'Veilchenblau'* the worse growth occurred.

Furthermore, growth vigour and the ability to form flowers was positively correlated with height above ground level and the diameter of the parent stem; this was especially clear for buds with leaves.

Table 12. *Time course of average length (cm) of the shoots ultimately developing a flower, and flowering percentage of all the developing shoots for R. 'Varlon' as influenced by rootstock.*

rootstock	length at day			flower (%)
	9	16	23	
with leaf:				
Var	1.5 a	5.8 a	16.1 ab	70 NS
In-r	0.7 b	2.9 bc	12.3 bc	70
Maj	1.2 ab	4.0 abc	14.3 bc	80
Fre	1.1 ab	4.0 abc	15.1 b	80
Mac	1.1 ab	3.2 bc	13.0 bc	80
Mad	1.3 ab	4.0 abc	14.8 b	70
Pau	1.4 a	3.4 bc	12.2 bc	65
Pin	1.2 ab	4.9 ab	19.8 a	80
Vei	1.3 ab	2.4 c	10.0 c	70
mean	1.2	3.9	14.4	75
without leaf:				
Var	1.1 NS	3.4 ab	11.2 abcd	65 ab
In-r	1.2	2.7 bc	12.5 ab	65 ab
Maj	0.9	2.9 abc	9.7 bcde	70 ab
Fre	1.0	2.9 abc	11.9 abc	60 ab
Mac	1.1	2.3 bc	8.8 cde	60 ab
Mad	1.4	3.3 ab	11.6 abcd	65 ab
Pau	1.0	2.7 bc	9.1 bcde	50 b
Pin	1.2	3.9 a	14.1 a	85 a
Vei	0.9	2.3 c	6.1 e	60 ab
mean	1.1	2.9	10.3	65

5 Influence of bush development on production and quality; quantification by linear regression models

5.1 Production

It is self-evident that production of roses depends on bush development. The relative importance may be estimated by calculating the linear correlation coefficient of bush development parameters with production (Table 13). As a parameter for the transport capacity of the various shoots, their transverse sections were calculated $((\text{diameter}/2)^2 \cdot \pi)$. Table 13 shows that for production in spring and autumn (number of flower shoots) the quality parameters (transverse section, length, weight) of the various structural shoots (excluding the renewal canes) were generally more important than the number of these shoots, whereas for summer the number of structural shoots was more important.

Table 13. Correlation coefficients between (i) production per year and per season and (ii) bush development parameters ($n=18$).

bush development parameter	number of flowers in				
	spring	summer	autumn	winter	year
Bottom-breaks:					
Number/plant	0.200	0.275	0.063	0.217	0.180
transverse section	0.759**	0.636**	0.731**	0.337	0.846**
Length 1	0.660**	0.620**	0.675**	0.357	0.766**
Weight	0.754**	0.681**	0.776**	0.504*	0.762**
Renewal canes:					
Number/plant	0.444*	0.686**	0.517*	0.180	0.469*
transverse section	-0.016	-0.047	0.040	0.157	0.027
Length 1	0.166	0.187	0.315	0.305	0.304
Weight	0.377	0.352	0.456*	0.317	0.423*
Branches bottom-breaks:					
Number	0.295	0.633**	0.344	0.199	0.397
transverse section	0.699**	0.355	0.633**	0.508*	0.645**
Branches on 60 cm:					
Number	0.437*	0.652**	0.458*	0.363	0.512*
transverse section	0.620**	0.295	0.475*	0.362	0.577**

(r is significant at $p < 0.05$ (indicated by *) or at $p < 0.01$ (indicated by **).)

Using all these parameters as regressors, an attempt was made to fit them into a linear regression model with production (per season and per year) as the dependent variable. The regressors were selected by the method of backward elimination (cf. Material and Methods, p. 23). The best fitting models for the production (number of flower stems) per plant per season (average of three years) are listed in Table 14 and for production per plant in the first year (P1), the first plus the second year (P2) and the total production in three years (P3) in Table 15. Table

14 shows that for each season the transverse sections of the branches of the bottom-breaks (BBBD2) were of importance. For summer production especially, the number of the structural shoots (BBB, BBN and RCN) was important, whereas for production in winter only the transverse section of the bottom-break branches showed a describing value. In addition, Table 14 shows that the fit of the model (R^2) was quite low for winter production and satisfactory for the other seasons.

Table 14. *Best linear models selected by a backward elimination procedure for production (number) of flowers per plant per season. Independent regressors used are the bush development parameters. The key to abbreviations is given at the end of this Chapter, p. 39.*

selected models	R^2	S.E.
P-spring = $-2.27+0.19*BBBD2+0.61*BBB+0.55*BBN-0.08RCD2$	83.0	0.20
P-summer = $-1.09+0.09*BBBD2+0.67*BBB+0.50*BBN+0.41RCN$	82.5	0.20
P-autumn = $-2.43+0.24*BBBD2+1.23*BBB$	63.0	0.45
P-winter = $0.02+0.06*BBBD2$	25.8	0.21

Table 15 shows that the importance of the quality parameters of the bush increased with age, indicated by the higher ratio between the estimated regression coefficients of number of laterals per bottom-break (BBB) and that of their transverse sections (BBBD2); i.e. 17 ($=3.77/0.22$), 8 ($8.05/0.96$) and 6 ($10.00/1.71$), respectively.

Table 15. *Best linear models selected by a backward elimination procedure for the cumulative production (number of flowers) in the first years. Independent regressors used are the bush development parameters. The key to abbreviations is given at the end of this Chapter, p. 39.*

selected models	R^2	S.E.
P1 = $0.33+3.77*BBB+0.22*BBBD2$	63.8	0.84
P2 = $-8.52+8.05*BBB+0.96*BBBD2$	66.5	2.02
P3 = $-16.26+10.00*BBB+1.71*BBBD2$	66.6	3.05

5.2 Quality

The relative importance of the various bush development parameters for the quality of the flower stems may be estimated by calculating their linear correlation coefficients with flower stem quality (stem length and stem weight) (Tables 16 and 17, respectively). In these Tables annual averages are not considered as they are of no practical importance. Generally speaking, the correlations between bush development parameters and quality were less pronounced than for quantity (Table 13). Table 16 shows that the quality parameters were higher correlated with the length of the harvested flowers than with the number of the structural shoots.

Table 16. Correlation coefficients between stem length (cm) per season and the bush development parameters (n=18).

bush development parameter	stem length in			
	spring	summer	autumn	winter
Bottom-breaks:				
Number/plant	0.195	0.465*	0.348	0.014
transverse section	0.698**	0.216	0.173	0.409*
Length 1	0.736**	0.449*	0.433*	0.263
Weight	0.676**	0.205	0.161	0.341
Renewal canes:				
Number/plant	0.040	-0.263	-0.236	0.168
transverse section	0.301	0.250	0.287	0.166
Length 1	0.434*	0.290	0.469*	0.308
Weight	0.370	-0.111	0.102	0.320
Branches bottom-breaks:				
Number	-0.077	-0.389	-0.460*	-0.248
transverse section	0.796**	0.468*	0.467*	0.607**
Branches on 60 cm:				
Number	0.101	-0.257	-0.156	0.079
transverse section	0.604**	0.450*	0.266	0.409*

(r is significant at $p < 0.05$ (indicated by *) or at $p < 0.01$ (indicated by **).)

Table 17 shows again that the quality parameters of bush development were higher correlated with the weight of the harvested flower stems than with the number of the various shoots. As was also seen in Table 16, the quality of the harvested flower stem in spring and summer was higher correlated with bush development parameters than were flower stems harvested in autumn and winter.

The best linear regression models for stem length and stem weight were selected using the independent regressors listed in Tables 16 and 17 respectively, in accordance with the backward elimination procedure (Tables 18 and 19).

Table 18 shows that the transverse section of the bottom-break branches (BBBD2) proved to be the most important parameter; the describing value was low for winter. Table 19 shows that the transverse section of the bottom-break branches again proved to be the most important parameter. Here, the fit of the linear regression models was poor for winter and autumn.

Table 17. *Correlation coefficients between stem weight (g) per season and bush development parameters, whether or not modified (n=18).*

bush development parameter	stem weight in			
	spring	summer	autumn	winter
Bottom-breaks:				
Number/plant	-0.026	0.075	0.135	-0.062
transverse section	0.792**	0.567**	0.315	0.369
Length 1	0.732**	0.581**	0.517*	0.258
Weight	0.854**	0.616**	0.253	0.339
Renewal canes:				
Number/plant	0.410*	0.028	0.045	0.228
transverse section	0.059	0.256	0.187	0.054
Length 1	0.311	0.359	0.524*	0.339
Weight	0.415*	0.216	0.190	0.262
Branches bottom-break:				
Number	0.364	-0.120	-0.317	-0.256
transverse section	0.714**	0.715**	0.521*	0.592**
Branches on 60 cm:				
Number	0.471*	-0.041	-0.111	0.144
transverse section	0.498*	0.658**	0.305	0.315

(r is significant at $p < 0.05$ (indicated by *) or at $p < 0.01$ (indicated by **).)

Table 18. *Best linear models selected by a backward elimination procedure for stem length (cm) per flower per season. Independent regressors used are the bush development parameters. The key to abbreviations is given at the end of this Chapter, p. 39.*

selected models	R ²	S.E.
L-spring = $46.99 + 0.92 \cdot \text{BBBD2} + 2.30 \cdot \text{BBN}$	72.1	1.29
L-summer = $52.23 + 0.66 \cdot \text{BBBD2} + 3.35 \cdot \text{BBN} - 0.18 \cdot \text{RCW}$	62.7	1.28
L-autumn = $55.39 + 0.49 \cdot \text{BBBD2} + 3.26 \cdot \text{BBN} - 3.30 \cdot \text{BBB}$	53.6	1.72
L-winter = $34.80 + 1.58 \cdot \text{BBBD2}$	36.9	4.44

Table 19. *Best linear models selected by a backward elimination procedure for the stem weight (g) per flower per season. Independent regressors used are the bush development parameters. The key to abbreviations is given at the end of this Chapter, p. 39.*

selected models	R ²	S.E.
G-spring = $4.02 + 1.06 \cdot \text{BBBD2}$	77.5	1.37
G-summer = $6.92 + 1.09 \cdot \text{RBD2} + 0.14 \cdot \text{RCL1}$	58.0	1.07
G-autumn = $17.86 + 0.37 \cdot \text{BBBD2}$	27.2	1.30
G-winter = $9.09 + 0.44 \cdot \text{BBBD2}$	35.0	1.29

Key to abbreviations

G-spring:	the mean flower stem weight (g) in spring (March - May)
G-summer:	the mean flower stem weight (g) in summer (June - August)
G-autumn:	the mean flower stem weight (g) in autumn (September - November)
G-winter:	the mean flower stem weight (g) in winter (December - February)
L-spring:	the mean flower stem length (cm) in spring (March - May)
L-summer:	the mean flower stem length (cm) in summer (June - August)
L-autumn:	the mean flower stem length (cm) in autumn (September - November)
L-winter:	the mean flower stem length (cm) in winter (December - February)
P-year :	the mean production (number) per plant per year
P-spring:	the mean production (number) per plant in spring (March - May)
P-summer:	the mean production (number) in summer (June - August)
P-autumn:	the mean production (number) in autumn (September - November)
P-winter:	the mean production (number) in winter (December - February)
r :	linear correlation coefficient
R ² :	the squared multiple correlation coefficient times 100 (%); summarising the fit of a regression model
S.E. :	Standard Error
BBB :	the mean number of branches per bottom-break
BBBD :	the mean diameter (mm) of the branches of the bottom-breaks.
BBBD2 :	$(BBBD/2)^2 * \pi$ (mm ²)
BBD :	the mean diameter (mm) of the bottom-breaks
BBD2 :	$(BBD/2)^2 * \pi$ (mm ²)
BBL1 :	the mean length (cm) of the bottom-breaks at harvest
BBN :	the mean number of bottom-breaks per rootstock
BBW :	the mean weight (g) of the harvested part of the bottom-breaks
RB :	the remaining branches (number) per plant on 60 cm above ground level
RBD :	the diameter (mm) of the remaining branches
RBD2 :	$(RBD/2)^2 * \pi$ (mm ²)
RCD :	the mean diameter (mm) of the renewal canes
RCD2 :	$(RCD/2)^2 * \pi$ (mm ²)
RCL1 :	the mean length (cm) of the renewal canes at harvest
RCN :	the mean number of renewal canes per rootstock
RCW :	the mean weight (g) of the harvested part of the renewal canes

6 Discussion

Preliminary remarks

Three preliminary remarks should be made. Firstly, it should be kept in mind that in the present experiment plant management and greenhouse conditions were applied that were appropriate for cut rose production on *R. canina* rootstocks. Hence, the results might have been different, if climatic conditions had been applied that were more suitable for one or more of the other rootstocks. This is illustrated by the fact that different growing areas, use different rootstocks. For example, the most widely used rootstock in the United States is *R. 'Manetti'*, in eastern Asia *R. multiflora* types and in the Mediterranean *R. indica* 'Major', whereas in North-West Europe *R. canina* types are favourite. This indicates that several aspects (cultivar, climate, growing technique) may interfere with the rootstock. However, Dubois *et al.* (1990) reviewed over twenty rootstock experiments in the greenhouse and found that relative yield of various rose cultivars grafted on 12 different rootstocks were more or less the same.

Secondly, for *R. canina* we used a seedling chosen at random, which was cloned by root grafting; for the bench-grafted plants similar seedlings were used. Recent results showed that there is a marked genetic variation in *R. canina* (Van de Pol, 1986; De Vries and Dubois, 1987; De Dood and Rademaker, 1990; Kool *et al.*, 1991; De Vries, 1993).

Thirdly, *R. 'Varlon'* grafted on *R. 'Varlon'* was not tested in the present experiment (because this combination did not survive). Instead *R. 'Varlon'* cuttings were used. It is unknown to what degree the graft union affected the behaviour of the combination. The graft union can reduce production, however, as was shown for *R. 'Ruimeva'* by Kool and Van de Pol (1991a).

Bush development

Bottom-breaks and renewal canes are important elements in the structure of the rose bush. Their formation is controlled by a varying degree of correlative inhibition. The present results, recently confirmed by Kool and Van de Pol (1991b) and De Vries (1993), show that rootstocks affect bottom-break formation (Tables 2, 3 and 4) and formation of other structural shoots (Tables 5, 6 and 7). Since rootstocks influence bush development it is put forward here that the effect of rootstocks on formation and quality of bottom-breaks and renewal canes (Tables 2 to 6) occurs via its influence on correlative inhibition. Growing conditions (such as climate, growing technique or utilized plant material) may be an important interfering factor. For example, unlike our present data (Table 2) Miller (1986) reported more bottom-breaks for *R. 'Varlon'* when grafted on *R. indica* 'Major' than growing on its own roots. Miller worked with plants made in late summer, that started flowering from the beginning of October and producing bottom-breaks next spring, whereas in the present experiment the plants were made in winter (cf. Materials and Methods, p. 21) and produced both their first flowers and bottom-breaks in spring.

The present results (Table 2 and 5) confirm that the formation of bottom-breaks and renewal canes occurred almost exclusively in the first year (Kofranek and Fisher, 1949; Byrne and Kohl, 1972; Plaut and Zieslin, 1974). This confirms that screening rootstocks with regard to their ability to produce bottom-breaks can be done within one year. The reason for restricted bottom-break formation in time is, probably, the inhibiting effect of the increasing number of leaves and active growing points higher on the plant as time proceeds (Zieslin *et al.*, 1976a; Khayat and Zieslin, 1982).

The better quality of the bottom-breaks and renewal canes produced in summer, reflected in their greater diameter (Table 3 and 6), is probably due to the high light intensity and the (probably) high leaf area index occurring in that time of year. It is known that various aspects in roses respond positively to light intensity (Cockshull, 1975; Zieslin and Halevy, 1975). In our experiment with *R. 'Varlon'* no correlation occurred between rapidity of bottom-break formation (Table 2) and average secondary thickening after three years (Table 3) as has recently been proved for individual shoots after one year for *R. 'Motrea'* on *R. canina 'Inermis'* by Kool and Van de Pol (1991b). Further, no correlation was found between diameter at harvest (and after 3 years) on the one hand and total number of bottom-breaks (Table 2 and 3) or renewal canes (Tables 5 and 6) on the other hand (Appendix II). However, between the quality parameters (diameter, length, weight) of these shoots significant correlations were found (Appendix II). This means probably that competition between bottom-breaks was present but relatively small.

The percentage of dead plants was exceptionally high in *R. multiflora 'Kanagawa'* (Appendix I), especially in winter. This was probably due to graft-incompatibility. In roses graft-incompatibility in varying degrees is reported in several studies; it may vary with combination, time of the year, virus contamination, grafting technique, growing conditions and propagation technique as reviewed by Edwards (1955) and was shown more recently by Hasek (1968), Swarup and Malik (1974), Singh (1977) and Ohkawa (1986). The process of starvation due to incompatibility described by Hasek (1968) for *R. 'Golden Wave'* on *R. 'Manetti'* was about the same as we observed for *R. 'Varlon'* on *R. multiflora 'Kanagawa'*: a gradual decline in vigour which eventually lead to loss of plants. Both *R. 'Varlon'* on its own roots and *R. canina 'Inermis'* (bench grafted) showed a relatively high loss of bottom-breaks (54 and 38% respectively) and branches (17 and 16% respectively) (Appendix I) which could be due to competition (Marcelis-Van Acker, 1993; Marcelis-Van Acker *et al.*, 1993) in view of their initially high number (Tables 2 and 7). It can be concluded here that for selection of rootstocks with respect to longevity of structural shoots it is necessary to follow the plant for several years.

The effect of the rootstock on the number and diameter of branches formed higher in the plant was little pronounced (Table 7); the good branching capacity of *R. 'Moonlight'* was confirmed recently (Kool and Van de Pol, 1992). According to De Vries (1993) this is probably the main reason of good production in several trials for plants on *R. 'Moonlight'* (De Dood and Rademaker, 1990). De Vries and Dubois (1984) and De Vries (1993) found that plant vigour (expressed as number of bottom-breaks) of different clones of glasshouse roses grafted on

seedlings of *R. canina* was mainly determined by the scion itself and to a lesser degree by the rootstock. Vecera (1967) came to a similar conclusion for roses grown in the open but he attributed an important additional influence to the rootstock. The situation is opposite to that in fruit trees such as apple where rootstocks may influence vigour considerably (Vyvyan, 1955; Moore, 1975). Recently, the influence of rootstocks on vigour (and production) was reported for *Protea* species (Ben-Jaacov *et al.*, 1991).

The bench grafted *R. canina* 'Inermis' rootstock showed some striking results for several aspects. For instance, it produced the highest total numbers of bottom-breaks (Table 2) but their diameter, secondary thickening (Table 3) and weight (Table 4) remained behind. The above did not apply to the root grafted *R. canina* plants which may be due to the grafting technique as was found for other woody plants by Skene *et al.* (1983) or to the greater amount of starting material as showed for roses in the open by Nikolova (1974) and for greenhouse roses by De Vries and Dubois (1984) and De Vries (1993). The clue may be the greater amount of (stored) carbohydrates (Zieslin *et al.*, 1975; Schrock and Hanan, 1981) at the start. Further, because bench grafted plants neglect their new root growth (Van de Pol *et al.*, 1988b) the quality of the formed shoots may lag behind.

Production and quality

Potential flower production is determined by the number of buds per plant but, in addition, their readiness and number to break and time required to develop a flower, as well as the percentage of blind shoots, are equally important (Carpenter and Anderson, 1972; Halevy, 1986). In the present experiment the longest time between two successive harvests was recorded following the harvest of end September (Table 11). It should be taken into account, that this time is determined by the number of days until bud break as well as by the rate of shoot growth. However, Van den Berg (1987) found that the rate of growth, for the same cultivar under equal greenhouse conditions, is faster in autumn than in spring. As a consequence, in the present experiment axillary bud break must be delayed in autumn. This is supported by results from Van den Berg (1987) which show that in autumn axillary bud break for *R. 'Varlon'* could be delayed up to 20 weeks. A longer time needed for bud break in roses with decreasing day length and light intensity is reported by Moe (1972) and in a number of other higher plants. It is attractive to take two factors into consideration: the ratio red/far-red light and light intensity. Both factors influence bud break, as was reported for roses by Mor and Halevy (1984) and in other crops by Kaspenbauer (1971) and Nederhoff (1984). The ratio red/far-red light declines in autumn and therefore bud release will be slower. The importance of the ratio red/far-red for bud release in roses is supported by our results that buds (with subtending leaves) in the top of the plant (a relatively high red/far-red ratio) showed the best bud release (Section 4.2). In general sink activity is stimulated when buds, or young shoots, receive more light (Mor and Halevy, 1979, 1980 and 1984; Mor *et al.*, 1980; Van Staden *et al.*, 1981b; Halevy, 1984 and 1986). For that reason, the newly formed flowers showed the smallest diameter when they emerged from shoots cut back at

the end of October and then the diameter slowly increased, probably dependent on the amount of light received from release until harvest (Appendix IV (Figure 1a)). Roughly speaking, the data of Van den Berg (1987) was in line with this reasoning.

Our results showed that there are differences between rootstocks in respect of time between successive harvests (Table 11, Appendix IV (Figure 2)), especially in autumn and winter. Later in winter these differences disappeared. An important factor is probably the variation in winter activity of the rootstocks as will be discussed later on. It may be argued that differences in winter and spring production between rootstocks (Table 8) are, at least partly, due to differences in time required to form flowers after harvest. Because rootstock affects the diameter of shoots (Tables 3, 6 and 7) and diameter affects bud release, as was also reported by Byrne and Doss (1981), the effect of rootstocks can be due to variation in shoot quality.

Any inhibition of bud release by its subtending leaf, as reported by Zieslin and Halevy (1976), was not found in the present experiment (Table 12). A possible explanation is that two antagonistic effects are involved; a stimulating photosynthetic effect and a delaying effect caused by inhibitory substances. According to Zieslin *et al.* (1978) and Zieslin and Khayat (1983) it is likely that ABA is one of the inhibitory substances formed by the attending leaf in roses. Since in many cases the amount of ABA is at a maximum during short days and decreases thereafter (Addicott and Lyon, 1969) it is stated here that the relative importance of the inhibiting and stimulating effect of the subtending leaf may be determined by the time of the year, light intensity, cultivar used or growing conditions. In line with the results of Zieslin and Halevy (1976) the growth of the emerged shoot was usually better if the subtending leaf was present as a source of assimilates. Otherwise, the shoot is dependent on resources from the older parts of the plant until it becomes self-supporting, which only occurs at the time that the flower bud appears (Mor and Halevy, 1979). Moreover, flowering percentage of the released buds depends on flower bud abortion, which in turn is mainly caused by shortage of carbohydrates (Mor and Halevy, 1979) and therefore by low light intensity (Moe, 1971; Zieslin and Halevy, 1975). It was shown that the advantage of the subtending leaf depends on the rootstock (Table 12). It may be suggested that at least in winter the less active plants (rootstocks) possess a higher amount of stored assimilates. This will be discussed in more detail in Part II.

When all tested root systems are considered, the difference in mean production per year between the highest ('Varlon' on its own roots) and the lowest (*R. canina* 'Inermis', root grafted) was 65% (Table 8). Comparing only the stentlings, the best (*R. indica* 'Major') was 30% ahead of the worst (*R. zigrii*). This is in line with data of Miller (1986) that 'Varlon' on its own roots produced more flowers than grafted on *R. indica* 'Major' and far more than grafted on *R. canina* 'Inermis'. In agreement with English findings (Anonymous, 1973; Pollock, 1983; Miller, 1986) the difference between the various rootstocks was most pronounced in winter (more than 100%) and less in spring and summer (maximum 60%). Pollock (1983) suggested that the rootstocks of sub-tropical origin such as *R. indica* 'Major' were superior to the more winter-hardy rootstocks as *R. canina*, which originate from temperate zones. It may be stated that this better winter-hardiness

is reflected in inhibiting growth in winter even at higher temperatures in the greenhouse or in combination with a non winter-hardy scion cultivar. In the literature there is some evidence that winter-hardiness of the rootstock in roses may be transferred to the scion (Webster, 1952; Buck, 1977) and consequently inhibits the growth of the scion in winter (Webster, 1952; De Vogel, 1953). Rose rootstocks of sub-tropical origin are more active in winter and therefore produce more stems than do more winter-hardy rootstocks.

The linear correlation coefficient between the diameter of the various kinds of shoots (Tables 3, 6 and 7) was for the most part significant and, as expected, there was also a significant positive correlation between stem length (Table 9) and stem weight (Table 10) (Appendix III). However, for weight the variation over the year was greater than for length, resulting in more firm flowers (expressed as specific weight) in summer than in winter (0.51 and 0.27 g/cm, respectively) as can be calculated from Tables 9 and 10. In the present experiment *R. indica* 'Major' gave a higher quality flower (stem length and weight) throughout the year compared with *R. 'Varlon'* on their own roots (Tables 9 and 10). The latter, in their turn, produced more firm flowers than all the *R. canina* rootstocks. The good quality of flowers from plants grafted on *R. indica* 'Major' was also reported by Pessala (1977) and Gammon and McFadden (1979).

Model

The effect of the environment on the growth and development of rose crops has been the focus of several studies. It has been found that temperature, light and CO₂ each also play a major role in determining the level of production (Moe, 1972; Zieslin *et al.* 1986; Van den Berg, 1987). Recently Lieth and Pasian (1991) considered several variables simultaneously and developed a simulation model for the growth and development of individual rose shoots. For this purpose several assumptions had to be made about physiological processes like partitioning and translocation of dry matter, sink strengths and so on, although it could be assumed that such relations will depend on environment as well as plant performance (Kramer and Kozlowski, 1979). In the present study the situation was reversed. A model to predict production and quality from available bush development parameters was proposed. The advantage here is that the plant's potential production will become better known, after which the best plant performance for optimal production and quality may be achieved by means of climatic factors and cutting procedure (Kool and Van de Pol, 1993). Because the influence of rootstock on various bush development parameters, production and quality was restricted, the data of the different rootstocks was taken together. These combined data formed the basis of linear regression models for the prediction of production and quality.

The mean production per season could largely be explained by the mean area of the transverse section per lateral of the bottom-breaks (Table 14). This relationship is not illogical in view of the physiological meaning of the stem in its transport and storage function. A similar relationship was found by Moore (1978) for apple. Due to the importance of the area of the transverse section and the differences observed between rootstocks with respect to secondary thickening (Table 3), it

should be kept in mind that rootstocks with an initially higher diameter can be overyielded after some time by a rootstock with a lower one due to a relative higher secondary thickening. In literature about roses little attention is paid to the importance of diameter of the 'basic' shoots; their number is reported to be most important (Kofranek and Fisher, 1949; Asen and Hamner, 1953; Zieslin *et al.*, 1976b; Van Rijssel, 1982 and De Vries and Dubois, 1983a,b and 1984). However, Van Rijssel (1982) and Kool and Van de Pol (1992) also indicated the importance of their diameter. However, De Vries (1993) reported that the diameter has only an indirect effect and that the better branching capacity of the thicker shoots is of major importance for production. In the present study the number of bottom-breaks mostly proved to be an important parameter, but the diameter of laterals of the bottom-breaks proved to be even more important. The absence of the shoot number in the model for production in winter obviously indicates that in that season shoot quality (diameter) is the predominant factor. Thicker shoots having a higher storage potential have a better competition capacity and show a more rapid bud release, which as previously reported and discussed (cf. p. 44) is especially important in winter. Heterogeneity (expressed as relative standard error and percentage of fit) of the model was relatively lower in spring, summer and autumn than in winter (Table 14). This is partly due to the reduced number of observations in winter but may also be influenced by the more complicated situation in winter due to other factors such as interaction between temperature, light and rootstock. For the models predicting the quality of the harvested flowers (Tables 18 and 19) roughly the same aspects were found as mentioned for production. The models describing the cumulative production in the first year, the first plus the second year and the total production after three years, showed that the importance of the number of laterals decreases with time and, conversely, the importance of their transverse section increases (Table 15). This is as expected, because the older the canopy, the higher the bushes. Additionally, branches with a thinner diameter will occur, as a result of which their quality will lessen thereby causing more problems to arise with bud release, shoot development and so on. The 'diluted' transport capacity of more shoots higher on the plant, compared with fewer but thicker shoots at the base, can be illustrated by comparing the total surface of all basic shoots with the total surface of all shoots at 60 cm height. Multiplication of the number of bottom-breaks (Table 2) and renewal canes (Table 5) by their transverse section (πr^2) (Tables 3 and 6, respectively) on the one hand, and the multiplication of the number of branches per plant at 60 cm height (Table 7) by their transverse section on the other, gives about the same value (249 vs. 233 mm²).

In conclusion, it may be said that for production and quality the number, and in addition especially the diameter of bottom-breaks and their laterals, is of primary importance. Hence, in practice, many thick branches should be an aim, especially for production in winter and for older crops with higher branched bushes. As a consequence management of bottom-breaks (cutting procedure) should be dependent on their diameter (Kool and Van de Pol, 1993). In this respect it should be borne in mind that the choice of the rootstock influences the diameter of the bottom-breaks (Table 3).

Concluding remark

Differences in bush development, production and quality caused by rootstock have been shown and are mostly pronounced in winter. The potential practical possibilities have not yet been exhausted and by means of adaption of growing technique to the chosen rootstock the results may improve. Since rootstock influences are often clearer for roses in the open (i.a. Vecera, 1967) the question remains how far a good control of growth circumstances as obtained from culture under glass can nullify the effect of a rootstock. If control of environmental factors is inadequate then the rootstock influence will come to the fore.

In this section it has become clear that at least part of the differences found to exist between rootstocks were mainly due to their behaviour in winter. Nevertheless, more winter active cultivars used as rootstock like *R. 'Motrea'* can also give unsatisfactory results with regard to production and quality. Therefore, in the following section more attention will be focussed on behaviour of roots, especially during less favourable conditions, so that a better understanding of shoot-root relationships may be achieved.

Part II

Root development; various aspects of shoot-root relationships

7 Introduction

In the first part of this study it was demonstrated that, particularly in winter, rootstocks could affect the production and quality of glasshouse roses. With respect to these parameters it was concluded that root performance was important as it influences bush development and bud release including growth rate of the flower stem. Therefore, in this second part the relationship between root behaviour and rose production and quality will be clarified, especially under unfavourable growing conditions. In this context attention will be mainly focussed on the factors shoot-root ratio, root carbohydrates and on mortality and regeneration of roots.

Shoot-root ratio

It is generally accepted that root and shoot are interdependent with respect to supply of water, mineral nutrients and carbohydrates. This statement has led to the concept that at constant environmental conditions, the ratio of shoot to root mass remains constant for a specific plant during a certain stage of its ontogeny (Turner, 1922; Crist and Stout, 1929; Brouwer, 1962a,b; Kramer and Kozlowski, 1979). As a consequence, disturbance of the prevailing conditions is reflected in a shift of the shoot-root ratio to a new stable value attuned to the new situation (Troughton, 1977). Many investigators would agree that the relationship observed between shoot and root results from a functional equilibrium between these two parts of the plant, although there is little agreement on the mechanisms involved (Lambers, 1983). Many investigators consider that the CO₂ uptake of leaves and the water and mineral uptake of roots must be balanced against one another (Brouwer, 1983). Others suppose that the numbers of growing meristems determine the relative sink strengths of these two plant sections. For example, in bean seedlings excision of either the root or the shoot increased the translocation rate of sucrose to the intact organ, but either auxin or cytokinin could restore the severed organ in its influence on sucrose movement (Gersani *et al.*, 1980). This indicates that biochemical signals, likely hormones, may be involved in the maintenance of shoot-root ratios (De Wit and Penning de Vries, 1983).

Data on shoot-root ratios for roses is rather scanty. In a few reports on the effect of soil temperature and aeration on root development, ratios between 4 and 20 were found (Boicourt and Allen, 1941; Shanks and Laurie, 1949a, b and 1950). Zieslin *et al.* (1976c) reported ratios between 6 and 20 for a number of cultivars of roses at varying ages and exposed to a few shoot growth affecting treatments.

Since in the economic sense roots are waste products in rose culture, the interesting question arises whether part of the root mass may be discarded without giving reduced production, more so because in the modern technique of growing plants on rockwool root volume is lowered dramatically, as was reported by Sonneveld (1981) for tomato. For a few annual crops (maize, beans, ryegrass) Brouwer (1981) found that under favourable conditions removing half of the root mass did not affect shoot growth and development. However, for young plants of some woody

perennials as yellow poplar (Sterling and Lane, 1975) and tulip tree (Kelly and Moser, 1983) regrowth and re-establishment after transplanting was only optimal when the original shoot-root ratio remained unaffected.

Carbohydrates

Zieslin *et al.* (1975) argued that the most important factor influencing plant development in year round production of roses is the level of (stored) carbohydrates and that in that respect roots occupy a prominent position. The amount of stored carbohydrates in roses varies throughout the year (Brandon, 1939) and, in addition, is determined by the physiological activity of the plant (Blanc *et al.*, 1976; Van de Pol *et al.*, 1986). Furthermore, genetic differences between roots, even within the same species, are reflected in the use of different amounts of carbohydrates, especially for growth and respiration, as was reviewed by Lambers (1986) for a number of other plant species.

Root mortality and regeneration of roots

Normal cultural measures such as harvesting flowers, removing blind shoots and cutting back in spring after a rest period, have a pronounced effect on root behaviour in terms of periodical mortality and regeneration (Fuchs, 1986b). In that respect, competition between plant parts for water and minerals on the one hand and carbohydrates on the other, must be an important factor. Thus for a few glasshouse crops Van der Post (1968) and De Stigter (1969) found that reproductive organs and roots compete for assimilates, resulting in lesser root growth. In addition, for apple (Head, 1966 and 1967), tea (Visser, 1969), perennial ryegrass (Ennik, 1966; Kleinendorst and Brouwer, 1969) and citrus (Eissenstat and Duncan, 1992) defoliation resulted in reduced root development.

For regrowth of roots the term root regenerating potential (RRP) is mostly used. It is defined as the capacity of roots to elongate, or initiate and elongate, new lateral roots (Stone *et al.*, 1962). For a number of perennial species the RRP has been found to vary depending on species (Struve *et al.*, 1984) and the developmental stage of their shoot system (Stone and Schubert, 1959; Lathrop and Mecklenburg, 1971; Farmer, 1975; Lee and Hackett, 1976). Likewise, for roses the shoot growth activity (Zieslin *et al.*, 1976c) and the scion cultivar used (Lee and Zieslin, 1978) appeared to be important factors. Auxin treatment of roots may stimulate the RRP in various plant species (Looney and McIntosh, 1968; Lee and Hackett, 1976; Kelly and Moser, 1983; Struve and Moser, 1984; Struve *et al.*, 1984) including roses (Fuchs, 1986a; Starbuck, 1987). For more detailed information refer to the review of Struve *et al.*, 1984).

Objectives

In a number of experiments, various aspects of the shoot-root ratio for glasshouse roses were examined. Attention was paid to genetic, cultural and environmental factors, or to a combination of these, in their effect on root weight, morphology, number, diameter and carbohydrate content.

To that aim a method to examine root growth without the disturbing influence of the continuous changing shoot development had also to be developed. Specifically, the following subjects were studied:

- differences in storage of reserves in roots of several scion and rootstock combinations under various climatic conditions, as well as their effect on plant growth and development;
- the phenomenon of root mortality in roses as influenced by various cutting treatments in different developmental stages and under various environmental conditions in combination with genetic differences in scion and rootstock used;
- the effect of different types of auxin, method of application and concentrations on root behaviour;
- the effect of various environmental factors (temperature, day length, pH) and genetic differences on root regeneration and growth;
- the relationship between root regeneration and shoot behaviour.

8 General materials and methods

Plant material

Rootstocks and scions were obtained from stock plants grown at the Department of Horticulture, Wageningen. Unless stated otherwise, plants were propagated by stenting (Van de Pol and Breukelaar, 1982) or, for *R. canina* rootstock types, by root grafting (Van de Pol, 1986). Further details will be given where relevant.

Growing system

In order to allow non-destructive observation of shoot and root development, in several experiments plants were grown in hydroculture as described by Steiner (1965). In 15 separate units of 50 l each (Figure 1) nutrient solution kept at 22-26 °C circulated continuously to provide sufficient aeration. The nutrient solution had the following composition (Van den Berg, 1980): 935 mg/l Nutriflora-T (Windmill Holland BV, containing all major and minor nutrients except Ca), 1000 mg/l $\text{Ca}(\text{NO}_3)_2$ and 20 mg/l EDTA. The pH was adjusted to 5.5-6.0 and the EC (Electric Conductivity) was kept at about 2.0 mS. Using rubber corks, the plants were fastened in pvc sheets (10*10 cm), which were placed at about 1 cm above the solution level.



Figure 1. An overview of the used hydroculture system.

In the first few weeks after transfer of the plants (unrooted cuttings or soil-rooted plants) to the hydroculture system, water was used instead of nutrient solution. Drought injury was prevented by shielding and frequent misting. After new roots had been formed and buds released, the water was gradually replaced by nutrient solution until the normal strength was reached.

Supplementary light was provided by SON-T lamps (Philips MGR 102, 400 W). Day length was 16 h; light intensity at plant level was at least 4.5 Watt/m².

Weight estimation

In most cases root and shoot fresh weights were determined by the method of De Stigter (1980) and De Stigter and Broekhuysen (1986). This method is based on the weight difference between plants of which the roots are either immersed in water or not. Data obtained by this non-destructive method does not deviate more than 1 % from that of cut off roots and shoots (data not given).

Leaf area

Leaf area was determined after removing the leaves from the plants by the leaf area meter LI 3100 (LI-COR Inc.).

Carbohydrates

Starch was estimated visually (Figure 2) according to the methods of Brandon (1939) and Van de Pol *et al.* (1986) using the scale given in Table 20. For that purpose thin transverse root slices were stained with KJ-iodine and mounted in glycerine.

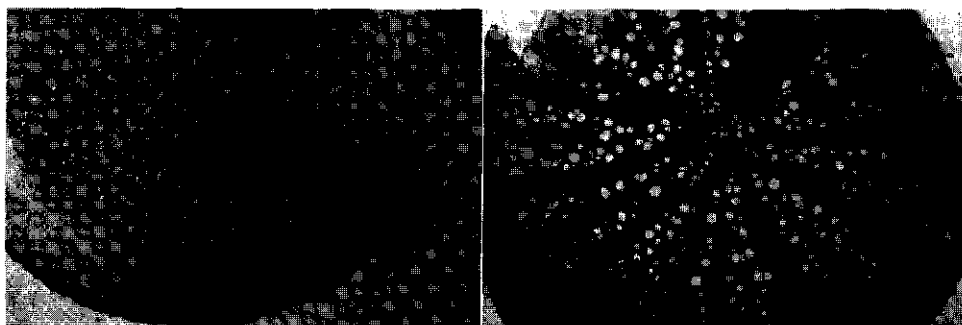


Figure 2. Starch in transverse slices of roots. Left score 0 - 1 and right score of 5 - 6 (cf. Table 20).

The analytical determination of carbohydrates was carried out according to Hassid and Neufeld (1964), using test kits of Böhrringer (Böhrringer Biochemica 1984, Böhrringer Mannheim GMBH). In a preliminary investigation (data not given) a significant correlation between the data of the visual and the chemical method was found ($p < 0.005$).

Table 20. Scale used for estimation of starch in roots.

score ratings	description
0	no starch at all
1	occasionally in medullary rays
2	1/4 of medullary rays filled
3	1/2 of medullary rays filled
4	3/4 of medullary rays filled and occasionally in phloem
5	in medullary rays abundant and phloem filled by half
6	medullary rays packed and phloem completely filled

Sticking of bark

Sticking of bark is well correlated with the activity of the cambium i.e. physiological activity of the plant (Hartmann *et al.*, 1990). To estimate physiological activity of the roots, expressed as bark sticking, two vertical cuts through the bark were made (about 4 mm apart) in root sections of a length of 2 cm. The ease of separation of the bark strip in between from the wood was judged using the score ratings of Table 21.

Table 21. Scale used for estimation of sticking of bark.

score ratings	description
1	bark loosens very easily
2	bark loosens easily but some parts remain initially
3	bark does not loosen easily and parts remain initially
4	bark loosens with difficulty and parts remain even after several attempts
5	bark loosens with great difficulty or not at all

Root growth activity

To estimate root growth activity without damaging the roots, plants were lifted from their containers. The degree in which white unsuberized roots were present was estimated by measuring light reflection of the under surface of the root clod. To that aim an instrument was constructed as drawn in Figure 3. It consisted of three photo cells about 10 cm apart, mounted in a triangle and screened from the upper side. Above this triangle a circular fluorescent lamp (DAKS, 22 Watt, coolwhite) was fixed. Both parts were built into a non-reflecting pvc pipe 25 cm high and 25 cm wide. At the bottom a hole 15 cm wide was made. The reflection, expressed as the percentage of light reflected by the root clod, proved to be a good measure for the presence of young, white roots at the lower part of the clod (Figure 14).

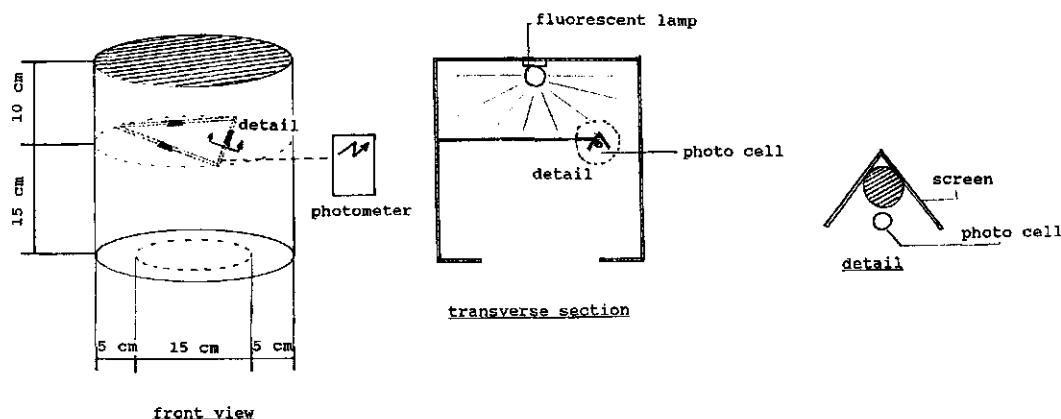


Figure 3. *Sketch of apparatus used for estimation of root growth activity by light reflection of plants grown in containers.*

Root regeneration

The use of root segments instead of intact plants for determination of RRP has been reported to be a convenient measure of the inherent capacity of roots to initiate lateral roots in *Pistacia* (Lee and Hackett, 1976) and in rose (Lee and Zieslin, 1978). This method was modified as follows. Root segments (length 7.5 cm, diameter 1-2 mm) were soaked in sodium hypochlorite (0.5%) for 10 minutes and then washed thoroughly in tap water. The segments were placed polarly in plastic cups (15 ml) containing moistened (20% v/v) perlite. The cups were put into polyethylene bags and kept in the dark at 21 °C. After 21 days the number of new roots (> 1 mm) and their length were recorded.

Experimental lay-out and statistics

The experimental lay-out mostly was a randomized block design. Details are given where appropriate. All data was analyzed for variance by using the statistical package GENSTAT, SYSTAT or SPSS-PC. In Experiment 9.2.1 and 9.3.1 univariate analysis of variance (ANOVA) as well as multivariate analysis of variance (MANOVA) was used (in order to determine the growth curve per treatment). In that case, according to Keuls and Garretsen (1982) the combination of the level (m), the slope (l) and the curvature (q), in this particular natural hierarchy, were taken into account. Where necessary, further analysis was carried out by using

Tukey's range test. In each Table significant differences within a column (or sometimes within a row) are indicated by using different letters after the data. Correlation tests were done by using appropriate tests like Spearman's or Friedman's test (Snedecor and Cochran, 1967). If not mentioned explicitly, the level of significance was 5%.

In order to enhance ease of reading, not all figures are given in the text and more detailed statistical analysis is given in the Appendix.

9 Experiments and results

9.1 Shoot-root ratio

Experiment 9.1.1 Root weight and shoot-root ratio of *R. 'Varlon'* as influenced by various rootstocks

In Part I a description was given of the development of the above ground parts during a year round production cycle of *R. 'Varlon'* plants grafted on various rootstocks developed for three years and grown in soil. For experimental details refer to Chapter 3. At the end of the three year period, the plants were lifted and the root fresh weight, the number of roots and the root length were determined.

Table 22 shows that *R. 'Varlon'* on its own roots and on *R. 'Moonlight'*, showed the highest, and the *R. canina* types the lowest root weights after three years. It can further be calculated that the number of roots is positively correlated with fresh weight, whereas the correlation between number of roots and individual root length is negative.

Table 22. Root parameters, expressed as units per plant, of *R. 'Varlon'* grown for three years on various rootstocks (Experiment 9.1.1).

rootstock	root fresh weight (g)	number of roots	average length of roots (cm)
Var	100.0 a	9.0 ef	38.8 abcd
In-b	65.2 cdefg	9.9 cdef	33.1 fghi
In-r	51.4 g	6.4 g	41.2 ab
Br-r	56.1 fg	8.6 fg	42.8 a
Bob	66.2 cdefg	9.8 cdef	39.5 abc
Maj	69.9 cdefg	13.2 b	29.9 i
Fre	76.8 bcde	9.8 def	37.3 bcdef
Lav	87.9 ab	13.2 ab	34.6 defghi
Lec	63.4 defg	11.0 bcdef	37.9 bcde
Mac	71.0 cdef	12.1 abcd	34.8 defgh
Mad	62.2 efg	10.3 cdef	40.2 abc
Moo	100.1 a	11.8 abcd	36.0 cdefgh
Mot	93.3 ab	12.3 abc	33.9 efghi
Pau	78.4 bcd	10.9 bcdef	31.5 hi
Pin	91.5 ab	14.1 a	36.0 cdefgh
Vei	80.0 bc	13.8 a	34.7 defgh
Zig	64.4 cdefg	10.1 cdef	32.6 ghi
average	75.2	11.0	36.5

From the root weight data of Table 22 and the total produced fresh flower weight (Table 10), the flower shoot to root ratio (ratio between produced flower fresh weight during three years and the root fresh weight after three years) can be calculated (Figure 4). In this Figure the actual

shoot-root ratio of the plants at the end of the three year period is also given. The linear correlation coefficient between both ratios is highly significant ($p < 0.001$). However, there is no clear relationship between total produced flower weight (or actual shoot weight) and fresh root weight at the end of the three year period.

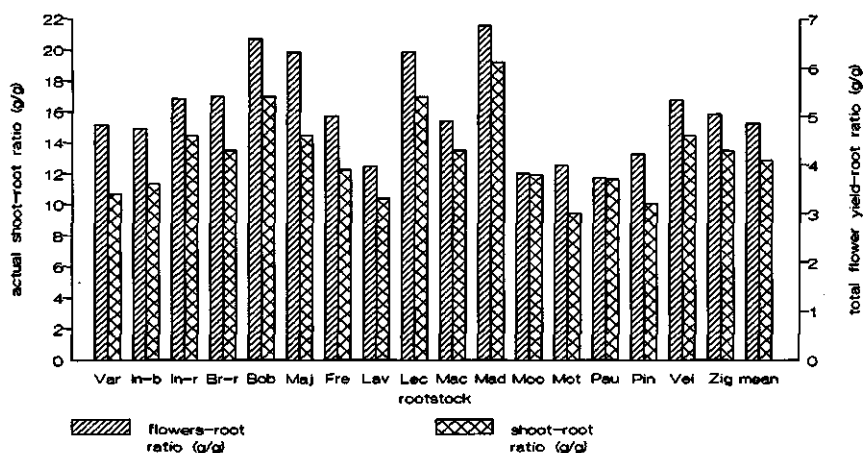


Figure 4. The actual shoot-root ratio (g/g fresh weight) after three years and the ratio between produced flower weight during three years and root weight (g/g fresh weight) after three years of *R. 'Varlon'* as influenced by various rootstocks (Experiment 9.1.1).

Furthermore, quantification of production by linear regression models, using the root parameters listed in Table 22, showed that the number of flowers produced and total flower weight, was for the greater part explained by number of roots. Root weight was the most important regressor for the summer period only (data not given).

Experiment 9.1.2

Leaf-root ratio as influenced by root temperature and day length

In a preliminary experiment it was found that rooted leaf cuttings of *R. 'Sweet Promise'* remain in good condition for a considerable time (data not given). Such simplified plants cannot show any shoot growth and consequently are highly suitable for the study of root development in the absence of shoot development. In the present experiment using leaf cuttings the effect of temperature and day length on plant behaviour of three rose cultivars was studied.

The cultivars chosen on the basis of known differences in 'winter activity' (cf. Materials and Methods, Part I, p. 21) were *R. 'Sweet Promise'* and *R. 'Golden Wave'* (Dr. A.J. Verhage^B) and, in addition, a cultivar highly sensitive to bud abortion, *R. 'Tekla'*. To root leaves, the basal ends of the petiole were dipped in 0.4% IBA (in talcum powder) and were kept for rooting in a humid

controlled greenhouse at 26 °C for four weeks. Subsequently, the rooted cuttings were transferred to small containers (0.7 l) with soil for potting plants and after another week at the same conditions exposed in a phytotron to five temperatures (9, 13, 17, 21 and 25 °C: soil as well as air temperature) and two day lengths (16 and 8 hours). The light intensity was about 35 W/m² at plant level. Three weeks later the plants were lifted and leaf area and fresh and dry weight of the roots were recorded. The experiment was carried out in the period August - September 1983. The experimental lay-out was a split-plot design with temperature as main factor and cultivar as side factor. There were four replications of four plants each.

Figure 5 shows that especially under long day conditions root weight per leaf area is highest for *R. 'Sweet Promise'* and lowest for *R. 'Dr.A.J.Verhage'*. At 16 h day length more roots, reflected in a higher root weight, were produced than at the short day conditions. Root weight decreased somewhat with increasing temperature. A similar, but slighter decrease occurred for percentage dry matter (Table 23). The roots were thicker and their number (not recorded) decreased somewhat at lower temperatures (Figure 6).

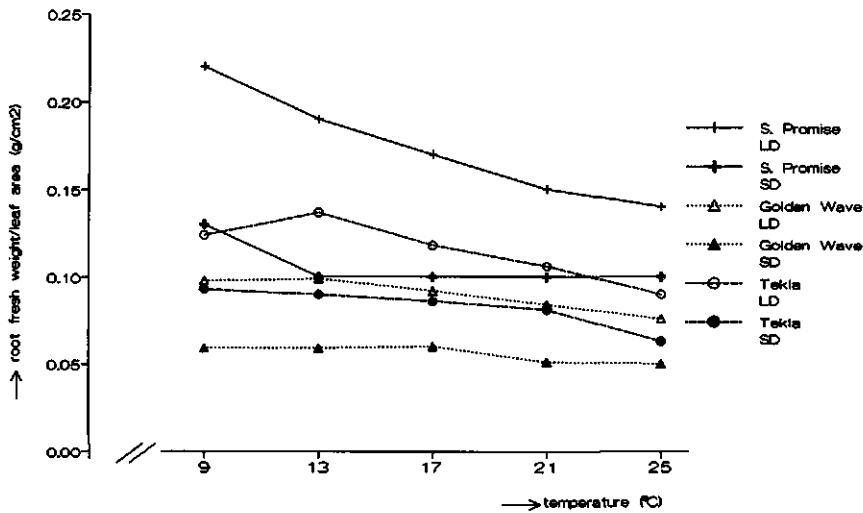


Figure 5. Root weight per leaf area (g fresh weight/cm²) of leaf cuttings grown under long days (16 h.) or short days (8 h.) as influenced by (soil and air) temperature (Experiment 9.1.2).

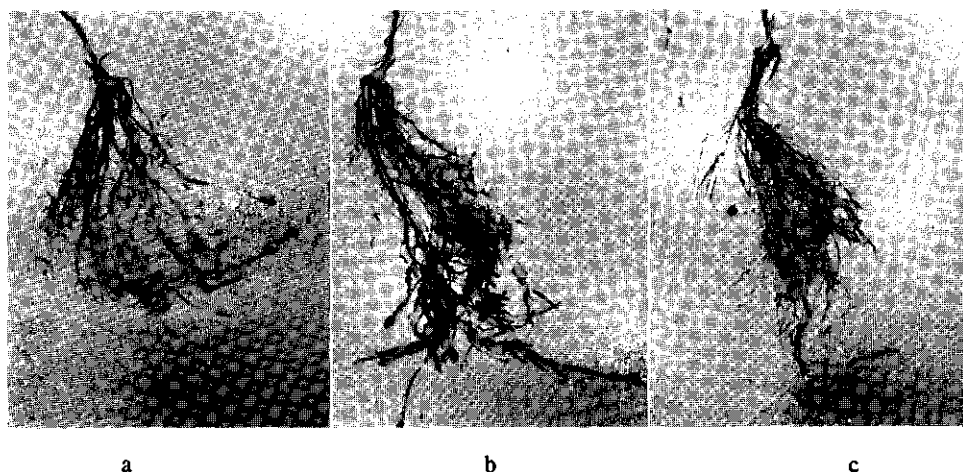


Figure 6. The root system of *R. 'Tekla'* at (a) short days and 9 °C, (b) long days and 9 °C, and (c) long days and 25 °C (Experiment 9.1.2).

Table 23. Percentage root dry weight as influenced by (soil and air) temperature and day length. Values are means of three cultivars (Experiment 9.1.2).

temperature (°C)	dry matter percentage	
	16 hours	8 hours
9	10.4	10.4
13	9.6	9.8
17	9.4	9.0
21	9.2	9.1
25	9.3	8.8

Experiment 9.1.3 Shoot-root ratio as influenced by root genotype and root pruning

In the foregoing experiment the leaf and the roots were of the same genotype. For these plants, the difference found in root reaction between genotypes can be originated either by shoot or root behaviour. Therefore, in the present experiment the same scion cultivar was combined with a number of different rootstock genotypes. Furthermore, it was evaluated whether, when root mass was reduced by pruning, the original shoot-root ratio was restored as was predicted by the simulation model of Brouwer and De Wit (1968).

Plants of *R.* 'Sweet Promise' stented (st) or root grafted (rg) on four rootstock genotypes, viz. *R. multiflora* 'Adenocheata' (st), *R.* 'Motrea' (st), *R.* 'Veilchenblau' (st) and *R. canina* 'Inermis' (rg) were grown in soil at about 21 °C for six weeks. Subsequently the plants were lifted and, after washing the roots free of soil, transferred to the hydroculture system. Starting early in November, supplementary light (Philips, HPL 400 Watt, 3 Watt/m² at plant level) was given from 6.00 - 22.00 h each day. Two months later, at the beginning of January (1984) the actual experiment lasting six weeks began. At the start of the experiment the following root pruning treatments were applied to each scion-rootstock combination:

1. control: no root pruning,
2. cutting off half of each individual root,
3. reducing the number of roots by half.

At the end of the experiment (half February) root and shoot fresh weight were determined. The experimental lay-out was a randomized block design of four rootstock genotypes, three pruning treatments and three replications of two plants each.

Root pruning by reducing root length stimulated shoot growth when *R.* 'Motrea' and *R. canina* 'Inermis' were used as rootstock (Table 24). For the other rootstocks no influence was found. Reduction of the number of roots was not effective or decreased shoot weight slightly (*R.* 'Motrea' and *R.* 'Veilchenblau'). Roughly speaking, root fresh weight followed the same pattern. In each of the three pruning treatments the plants with *R.* 'Veilchenblau' as stock showed the highest shoot-root ratio whereas *R. canina* 'Inermis' was much lower. It should be noted that at the end of the experiment the shoot-root ratio in both root pruning treatments had been restored completely, i.e. for all combinations it hardly differed from the unpruned control.

Table 24. *Shoot and root fresh weight (g per plant) and shoot-root ratio of R. 'Sweet Promise' grafted on four rootstock genotypes as influenced by root pruning. Data collected six weeks after pruning (Experiment 9.1.3).*

rootstock	no pruning	decreasing root length	reduction root number
shoot weight:			
R. <i>multiflora</i> 'Aden.'	41.5 A	40.0 A	39.0 A
R. 'Motrea'	33.6 B	40.8 A	29.5 C
R. 'Veilchenblau'	36.9 A	36.6 A	31.7 B
R. <i>canina</i> 'Inermis'	24.1 B	30.8 A	26.9 B
root weight:			
R. <i>multiflora</i> 'Aden.'	8.3 A	8.5 A	8.4 A
R. 'Motrea'	8.6 A	10.5 A	6.6 B
R. 'Veilchenblau'	6.3 A	6.2 A	5.9 A
R. <i>canina</i> 'Inermis'	8.0 C	15.7 A	11.6 B
shoot-root ratio:			
R. <i>multiflora</i> 'Aden.'	5.0 b	4.7 b	4.7 ab
R. 'Motrea'	3.9 c	3.9 b	3.9 b
R. 'Veilchenblau'	5.9 a	5.9 a	5.4 a
R. <i>canina</i> 'Inermis'	3.0 d	2.0 c	2.3 c

(Note: Mean separation for shoot and root weight was made per row and for shoot-root ratio it was made per column.)

9.2 Carbohydrates

Experiment 9.2.1 *Starch content and root activity as influenced by season and genotype*

Referring to Experiment 9.1.2 it may be suggested that better shoot growth found at long days is due to a higher total amount of energy received and the higher root weight at lower temperatures to reduced dissimilation (i.a. Larcher, 1976). In view of the important role of stored carbohydrates in year round rose production (Zieslin *et al.*, 1975), in the present experiment the level of stored carbohydrates and root activity were followed for a number of rootstock cultivars during the winter season. The cultivars were selected on the basis of known differences in 'winter activity'.

The selected cultivars were *R. multiflora* 'Multic', *R. canina* 'Inermis', *R. 'Veilchenblau'*, *R. indica* 'Major' and *R. 'Manetti'*. Three-year-old plants were kept from October 1986 until March 1987 at an unheated greenhouse (set-point 10 °C) in sandy soil on their own roots. At intervals of three weeks five root pieces (length 2.5 cm and diameter 3-8 mm each) were taken from each plant and rated for starch content and bark sticking (as measure for physiological root activity; cf. Materials and Methods, p. 57). The experimental lay-out was a split-plot design with cultivar as main factor and sampling date as side factor. There were five replicates per cultivar and sampling date.

Although the statistical analyses revealed an interaction between rootstock cultivar and time for both starch content and sticking of bark, roughly speaking one could say that in each cultivar the starch level showed the same pattern (Figure 7a). After a gradual decrease of starch content from November until January a rapid increase occurred, culminating in maximum values at the end of February. Thereafter the level dropped again and at the end of March hardly any starch was left. For statistical information refer to Appendix V (Table 1). Root activity, expressed as bark sticking, in *R. multiflora* 'Multic' and *R. 'Veilchenblau'* throughout the experiment, was kept at the same level, whereas for *R. canina* 'Inermis' and *R. 'Manetti'* root activity declined with time (the bark sticking values increased!) and for *R. indica* 'Major' increased as time progressed (Figure 7b). The statistical information is given in Appendix V (Table 2).

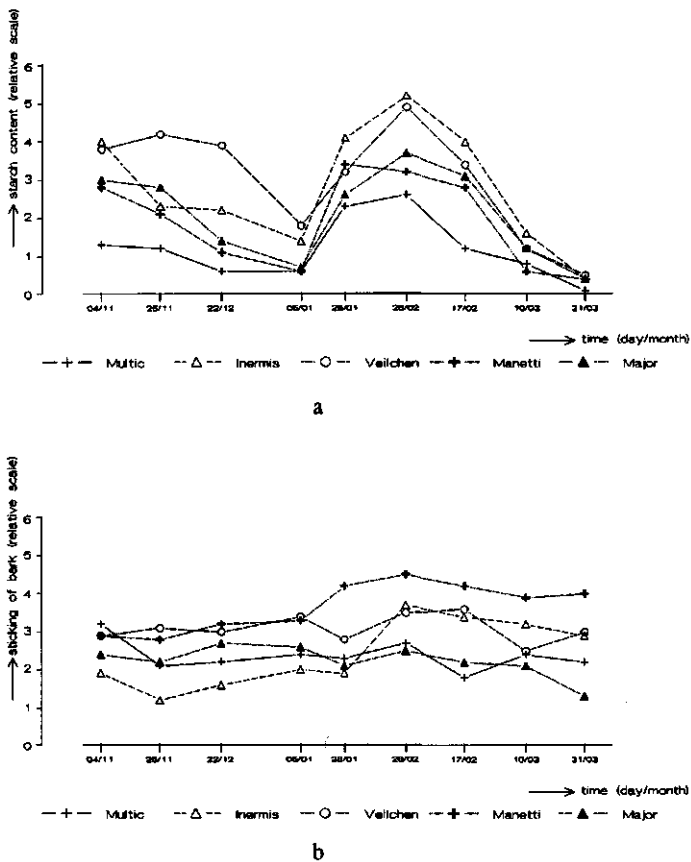


Figure 7. Starch content (a) and sticking of bark (b) of roots of five cultivars throughout the winter (Experiment 9.2.1).

9.3 Root mortality

Experiment 9.3.1 Shoot and root growth as influenced by root genotype and shoot pruning

Preliminary experiments revealed that especially under unfavourable conditions, severe cutting-back of the above ground parts reduced root growth activity to a greater degree than light pruning, suggesting that shortage of assimilates may play a role, as was found for other glasshouse crops (Van der Post, 1968; De Stigter, 1969) and for several crops in the open (Head, 1966 and 1967; Visser, 1969; Kleinendorst and Brouwer, 1969). In Experiment 9.1.3 it was shown that after root pruning the shoot-root ratio was restored within six weeks. In the present experiment a few shoot pruning treatments were applied to rose plants grafted on different rootstocks to find out whether removal of growing points (active sinks) diminishes or enhances root mortality.

Rosa 'Motrea' stented on three different root genotypes, viz. *R. indica* 'Major', *R. 'Veilchenblau'* and *R. 'Fredica'* or having its own roots (cuttings) were grown in soil for three months and then transferred to the hydroculture system. Three months later the pruning treatments were applied. The actual experiment was carried out in the summer of 1984. Each scion/rootstock combination received three pruning treatments:

1. harvest: flowers were harvested in the normal way (stems cut back to the third basal five-foliate leaf) at the beginning of the experiment,
2. harvest + removal of laterals: flowers were harvested in the normal way and in addition, all sprouting buds were removed twice weekly during the first three weeks and once a week during the rest of the experimental period,
3. harvest + leaf removal: flowers were harvested in the normal way and in addition, the second basal five-foliate leaf and half the number of the other basal leaves were removed. Half the number of the newly appearing leaves were cut off at intervals as indicated in treatment 2.

The experimental period lasted until the plants of treatment 1 produced a new harvestable flower (39 days). Root and shoot weights were recorded once weekly. The experimental lay-out was a randomized block design of four genotypes, three pruning treatments and three replications of two plants each.

Root fresh weight

Figure 8 shows that root weights of *R. indica* 'Major' and *R. 'Fredica'* were much higher than those of *R. 'Veilchenblau'* and *R. 'Motrea'*. Except for *R. 'Veilchenblau'*, marked root mortality took place in the second week after pruning but recovery occurred within a few weeks. Harvest + removal of laterals (treatment 2) initially stimulated root growth but thereafter had no noticeable effect (Figure 9). In contrast, normal harvest only (treatment 1) resulted in a marked root

mortality (see also Figure 10) in the second week followed by a rapid regeneration. Harvest + leaf removal (treatment 3) led to a strong reduction of root weight; recovery did not occur. For statistical data refer to Appendix VI (Tables 1 and 2).

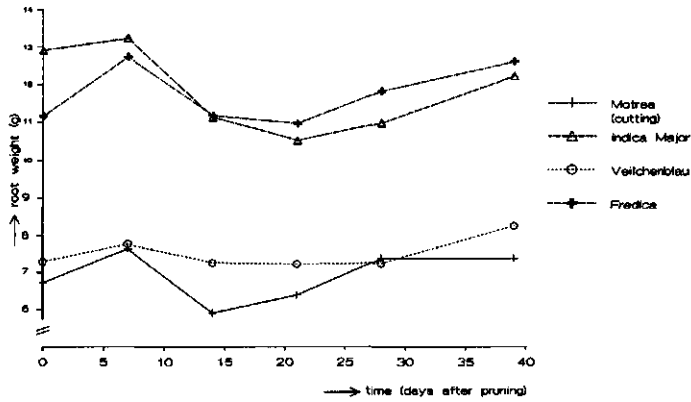


Figure 8. Time course of change of root weight per plant of R. 'Motrea' as influenced by rootstock genotype. Values are means of three shoot pruning treatments (Experiment 9.3.1).

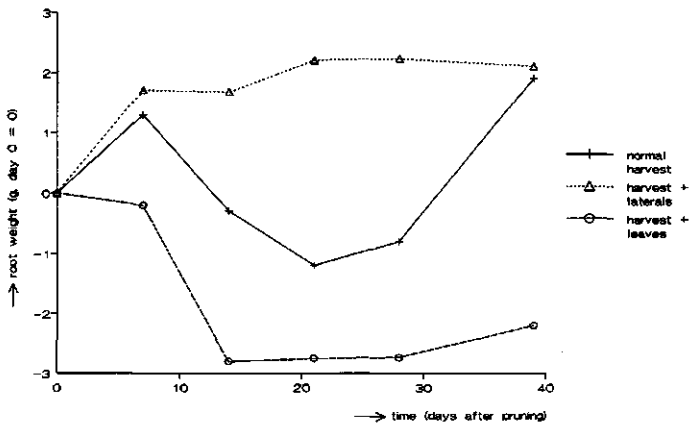


Figure 9. Time course of change of root weight per plant of R. 'Motrea' as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).

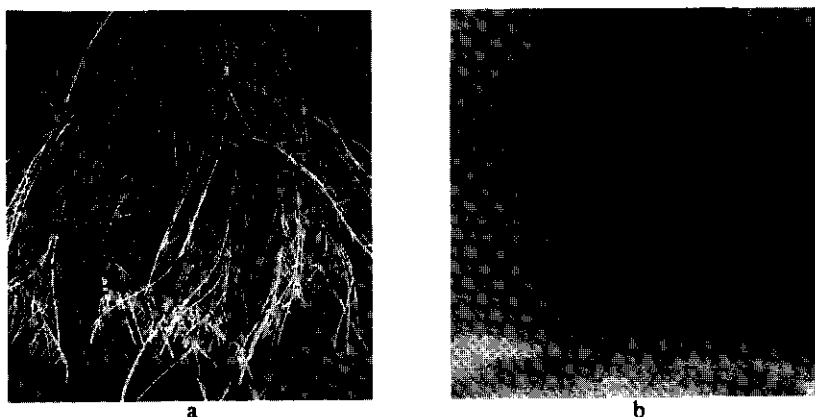


Figure 10. The root system of the same *R. 'Motrea'* plants (on its own roots) (a) just after pruning, showing a lot of new white roots, and (b) 21 days later, almost no root growth activity is seen (Experiment 9.3.1).

Shoot fresh weight

Figure 11 shows that shoot weight (included the cut off parts) of *R. 'Motrea'* on *R. 'Fredica'* was higher than that of the other cultivars; and that its increase with time exceeded that of the others. In particular, shoot weight of *R. 'Veilchenblau'* was low and increased only little during the experimental period. The rootstocks *R. 'Motrea'* and *R. indica 'Major'* occupied an intermediate position. The degree of pruning did affect shoot development (Figure 12). In all treatments shoot weight increased with time but that increase decreased with severity of pruning and was of little importance after normal harvest + removal of laterals (treatment 2). For statistical analysis of the data refer to Appendix VI (Tables 3 and 4).

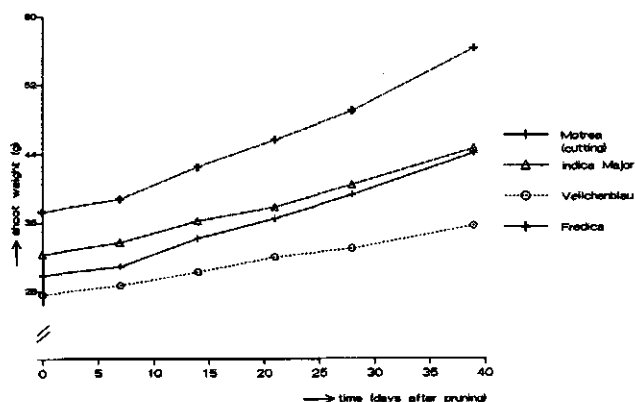


Figure 11. Time course of change of shoot weight per plant of *R. 'Motrea'* as influenced by rootstock genotypes. Values are means of three shoot pruning treatments (Experiment 9.3.1).

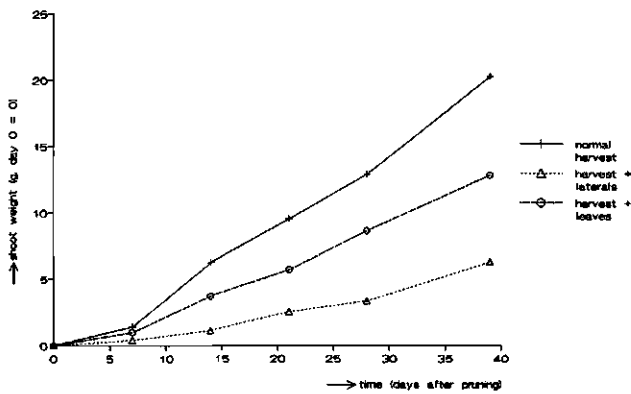


Figure 12. Time course of change of shoot weight per plant of *R. 'Motrea'* as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).

Shoot-root ratio

The shoot-root ratio at the start of the experiment, immediately after pruning, varied between 4.7 for *R. 'Motrea'* on its own roots and 2.5 for *R. indica 'Major'* (Table 25).

Table 25. Shoot-root ratio (g/g fresh weight) of six months old plants of *R. 'Motrea'* grown on hydroculture as influenced by various rootstocks (Experiment 9.3.1).

rootstock	shoot-root ratio
<i>R. 'Motrea'</i>	4.7 a
<i>R. 'Veilchenblau'</i>	3.7 ab
<i>R. 'Fredica'</i>	3.3 bc
<i>R. indica 'Major'</i>	2.5 c

With respect to time course of shoot-root ratio, the four rootstock-scion combinations responded similarly to the various pruning treatments. Therefore, in Figure 13 mean values of four rootstocks are given as influenced by pruning treatment. The shoot-root ratio decreased due to the reaction of the above ground parts on pruning, but in the second week rapidly increased until the original level was reached in treatment 1 (normal harvest) and 3 (harvest + leaf removal). In contrast, the additional removal of laterals (treatment 2) kept the ratio at a low level throughout. Statistical information is given in Appendix VI (Table 5).

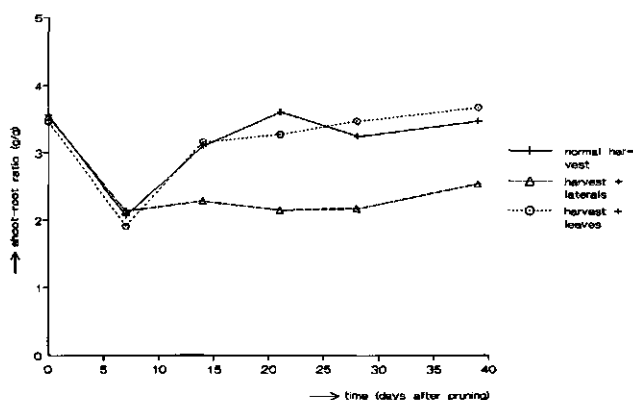


Figure 13. Time course of shoot-root ratio of *R. 'Motrea'* as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).

Experiment 9.3.2

Root growth of plants grown in soil as influenced by shoot pruning

The purpose of this experiment was to study whether roots of plants grown in soil respond to shoot pruning in a similar way to the plants of the previous experiment that were kept in hydroculture. To save time, the roots were not washed free of soil and weighed at the end of the experiment but after lifting the plants root activity was estimated by the light reflection method (cf. General Materials and Methods, p. 57) on the basis of the presence of white, newly formed roots.

Rosa 'Motrea' stented on four different root genotypes, viz. *R. multiflora* 'Multic', *R. 'Veilchenblau'*, *R. indica* 'Major' and *R. 'Fredica'* or *R. 'Motrea'* on its own roots (cuttings), were grown in soil for two years. Then at the start of the experiment each combination received three pruning treatments, increasing in severity:

1. flower bud: all the flowers and the flower buds were removed,
2. flower stems: flower stems were cut back to the second basal five-foliolate leaf (normal harvest),
3. all stems: as 2 and in addition the blind shoots and all growing shoots were cut back to the second basal five-foliolate leaf.

The removed parts were weighed and the leaf area of the removed leaves was determined. The experiment was started in May 1985 and was terminated four weeks later. The experimental layout was a randomized block design of five root genotypes, three pruning treatments and three replications of two plants each.

Table 26 and Figure 14 show that root activity decreased with severity of pruning. Furthermore, a significant negative linear correlation ($p < 0.005$) was found between root activity and removed leaf area (data not given).

Table 26. Root activity of *R. 'Motrea'*, measured by the light reflection method and expressed as percentage of reflected light by the root clod, as influenced by various shoot pruning treatments (Experiment 9.3.2).

root genotype	light reflection (%) after removing of		
	flower bud	flower stems	all stems
<i>R. multiflora</i> 'Multic'	70.3	63.9	62.8
<i>R. 'Veilchenblau'</i>	84.9	77.2	74.4
<i>R. indica</i> 'Major'	71.6	64.2	62.4
<i>R. 'Fredica'</i>	65.4	61.3	60.2
own roots	59.0	57.7	57.7
mean	70.2 a	64.9 b	63.5 b



Figure 14. Root activity of sixteen months old *R. 'Motrea'* plants 12 days after pruning, as influenced by various shoot pruning treatments (see text) (Experiment 9.3.2).

Experiment 9.3.3 Root growth of completely cut back plants

The production of half-year-old plants for greenhouse cultivation, is started with one-year-old rootstock seedlings in March, which are budded in May - June, and cut back completely two weeks later just above the graft union. Therefore, in order to study the effect of very severe pruning on root behaviour, one-year-old seedlings of *R. canina* 'Inermis' (root collar diameter of 6-8 mm) were planted in sandy soil in the open at the beginning of April 1987. In June these seedlings were budded with the scion cultivar *R. 'Jack Frost'* and four weeks later the plants were cut back to just above the graft union. Regular, starting four days before cut back until eighteen days after this pruning, a number of plants were lifted of which the fresh weights of the newly formed (white) roots and the older (brown) roots were determined. The experimental lay-out was a randomized block design of four replications of seven plants each for all the sampling dates.

Figure 15 shows that severe shoot pruning decreased the ratio between newly formed and older roots indicating cessation of root growth. Two weeks later recovery started and three weeks after pruning the original ratio has been re-attained.

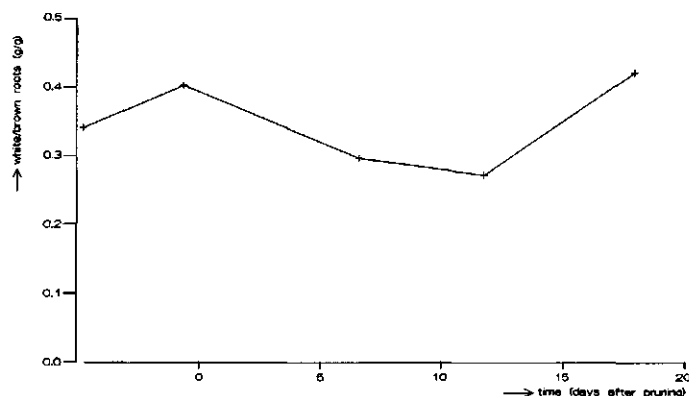


Figure 15. Time course of the ratio between newly formed (white) and older (brown) roots (g/g) after completely cut back the shoots (at day 0) of one year old rootstocks of *R. canina* 'Inermis' (Experiment 9.3.3).

Two months after planting, heavier roots of *R. canina* 'Inermis' showed better root regeneration than roots of lesser weight (Figure 16). The linear correlation coefficient between total root weight and the weight of the newly formed roots was highly significant ($p < 0.005$), i.e. 0.962.

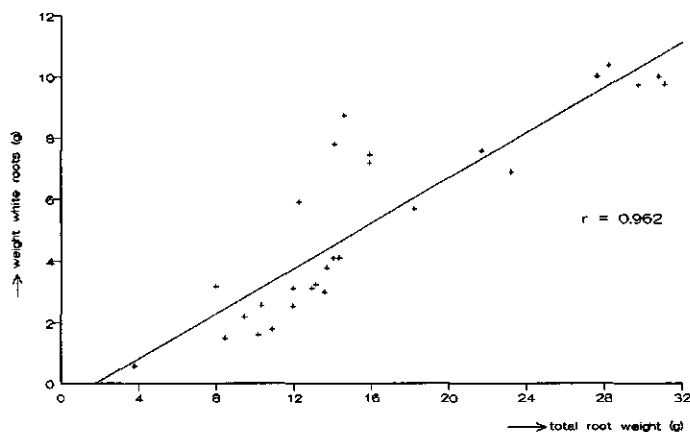


Figure 16. Formation of new roots (g fresh weight per plant) two months after completely cut back of *R. canina* 'Inermis' as influenced by total root fresh weight (g) (Experiment 9.3.3).

Experiment 9.3.4Root and shoot growth as influenced by pruning and application of growth regulators

In the foregoing experiments 9.3.1, 9.3.2 and 9.3.3 the negative effect of shoot pruning on root development was clearly demonstrated. However, initially removing developing axillary buds or shoots prevented root mortality, which suggests that root mortality, as well as recovery of root growth thereafter, is due to shoot-root competition. In the present experiment this aspect will be studied in some detail.

In one treatment, shoot pruning was combined with root pruning, to maintain the original shoot-root ratio. As reported for yellow poplar by Sterling and Lane (1975) and for the tulip tree by Kelly and Moser (1983) this treatment stimulates root growth recovery. Furthermore, in several treatments the effect of auxin and the auxin-transport inhibitor 2,3,5-triiodobenzoic acid (TIBA) on root regeneration was determined. Auxin has long been known to stimulate lateral root formation (Torrey, 1950). In addition, Carlson and Larson (1977) found an increased auxin level in oak roots before the appearance of new roots. In quiescent rose plants root application of auxin (mainly IBA) enhanced root regeneration (Fuchs, 1986a). Finally, since cytokinins usually increase sink activity (Wickson and Thimann, 1958; Van Staden *et al.*, 1981a), a shoot application of a cytokinin was included in the experiment in order to favour sink activity of the shoot. The experiment was carried out in the autumn of 1986 with six-month-old cuttings of *R. 'Motrea'* grown in hydroculture. Supplementary light was provided by SON-T lamps (Philips MGR 102-400, 4.5 Watt/m²); day length was 18 hours. At the start of the experiment the plants, usually having one heavy and one or two minor shoots, were pruned by shortening the main stem to the fourth basal five-foliolate leaf and the minor shoots to half their original length. There were five treatments:

1. control: the roots were soaked in water for 15 minutes and the upper parts were sprayed with the wetting agent monylphenolpolyglycolether (Agral LN, concentration 0.075%) at the start of the experiment and at 3, 7 and 12 days thereafter,
2. root pruning: to restore the original shoot-root ratio all roots were cut back to half their original length at the start of the experiment,
3. root-IBA: the roots were soaked in a solution of indolebutyric-acid (IBA, potassium salt, concentration 250 mg/l) for 15 minutes at the start of the experiment and at 3, 7 and 12 days thereafter,
4. shoot-TIBA: the above-ground part was sprayed until running off with a solution containing 2,3,5-triiodobenzoic acid (TIBA, concentration 250 mg/l) and Agral LN (0.075%) at the start of the experiment and at 3, 7 and 12 days thereafter,
5. shoot-PBA: the above-ground part was sprayed until running off with a solution containing N-(phenylmethyl)-9-(tetra-hydro-2H-pyran-2-yl)-9H-purin-6-amine (PBA, 250 mg/l) with Agral LN (0.075%) at the start of the experiment and at 3, 7 and 12 days thereafter.

Throughout the experiment (50 days) root and shoot weights, the number of released buds and the length of the newly developed shoots on the main stem were recorded weekly. The number of

newly formed roots (>2.5 cm) were counted on day 30, 37 and 44. The experimental lay-out was a randomized block design of five treatments and three replications of three plants each.

Root mortality as a result of shoot pruning was already apparent on day 7 and increased with time (Table 27, control). Root pruning completely prevented root mortality and even stimulated root growth. Soaking the roots in IBA reduced root mortality anyhow on day 21 and 35, whereas sprays of TIBA and PBA had a clear negative effect.

Table 27. *Change of root weight (g fresh weight per plant) of cuttings of R. 'Motrea' with time as influenced by root pruning, root application of IBA, and shoot application of TIBA and PBA (Experiment 9.3.4).*

treatment	change in weight (g) at day		
	7	21	35
control	-0.49 b	-1.80 b	-2.67 c
root pruning	0.40 a	0.15 a	1.11 a
root-IBA	-0.81 bc	-0.54 a	-0.86 b
shoot-TIBA	-1.18 c	-2.61 b	-4.32 d
shoot-PBA	-1.32 c	-2.64 b	-4.46 d

The difference in appearance between the dying off, disintegrating root tips of the control plants and the healthy smooth tips of the root-pruned plant is clearly demonstrated in Figure 17. With respect to the occurrence of newly formed roots the IBA-treatment and to a lesser degree the root-pruning treatment markedly stimulated root development as compared with the control (Table 28). In contrast, TIBA and especially PBA reduced new root growth. Bud release was reduced by IBA applied to the roots but was clearly stimulated by the cytokinin PBA sprayed on the above ground part of the plant. However, average shoot length was reduced by PBA.

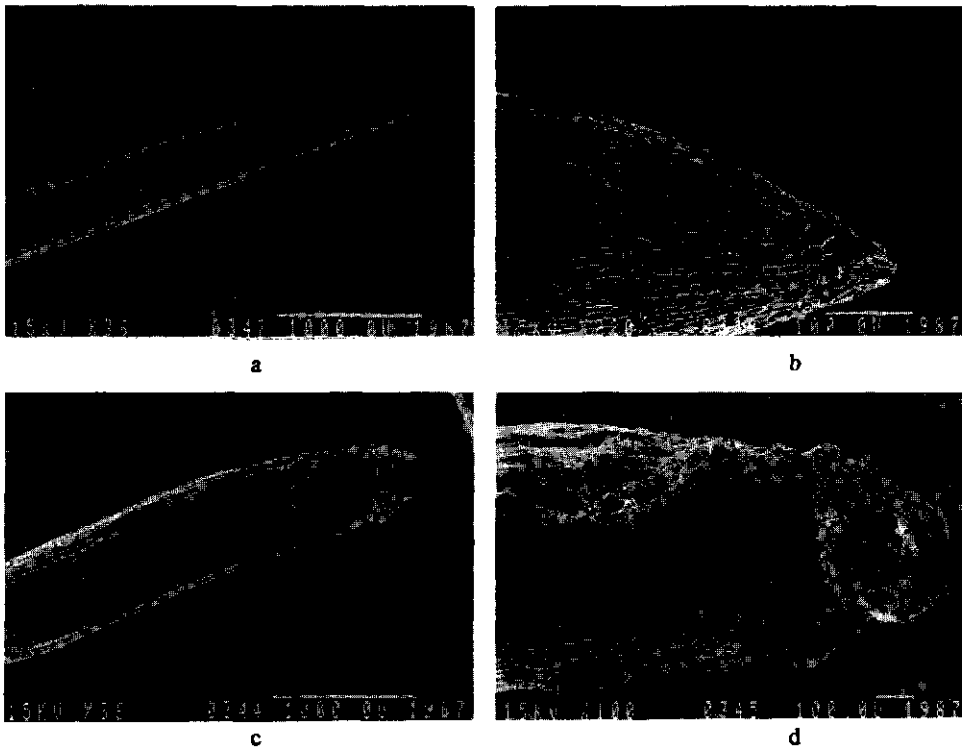


Figure 17. Electron microscopical photographs of healthy (a and b) and disintegrated died off roots (c and d). Magnification 36 (a and c) and 100 (b and d) (Experiment 9.3.4).

Table 28. The occurrence of newly formed (white) roots (>2.5 cm) per plant at day 30, the number of released buds per plant and the average shoot length (cm) at day 35 as influenced by root pruning, root application of IBA and shoot application of TIBA and PBA (Experiment 9.3.4).

treatment	white roots at day 30 (number)	released buds at day 35 (number)	length new shoots at day 35 (cm)
control	24.4 c	8.1 b	17.4 a
root pruning	40.1 b	7.0 b	23.5 a
root-IBA	56.2 a	5.8 c	22.8 a
shoot-TIBA	13.4 d	8.0 b	19.4 a
shoot-PBA	1.3 e	15.2 a	5.1 b

9.4 Root regeneration

Experiment 9.4.1

Shoot growth as influenced by root regeneration

Referring to Experiment 9.3.4 it may be suggested that competition between shoot and root growth is due to competition for assimilates. This could be influenced by growth regulators. In the present experiment the competition for assimilates was studied by promoting root growth by auxin.

Cuttings of *R. 'Sweet Promise'* were taken at the beginning of November 1985 and after soaking the basal end for ten minutes in a solution containing indolebutyric-acid (IBA, potassium salt, concentration 0, 250, 500 or 1000 mg/l) to promote rooting, were kept in propagation benches at 26 °C for eighteen days. The plants were then lifted and after washing the roots free of soil transferred to the hydroculture system. Supplementary light was provided by SON-T lamps (Philips MGR 102-400, 4.5 Watt/m²), day length was 18 hours. From day 20 after the start of the experiment number, weight and length of shoots and roots were recorded throughout the experiment (six weeks). The experimental lay-out was a randomized block design of four IBA treatments and two replications of seven plants each.

Initially, the shoot-root ratio was high for 0 mg/l IBA as well as for the highest IBA concentration (1000 mg/l) (Figure 18). After 54 days the shoot-root ratio was about the same for all IBA treatments except for 1000 mg/l which remained behind.

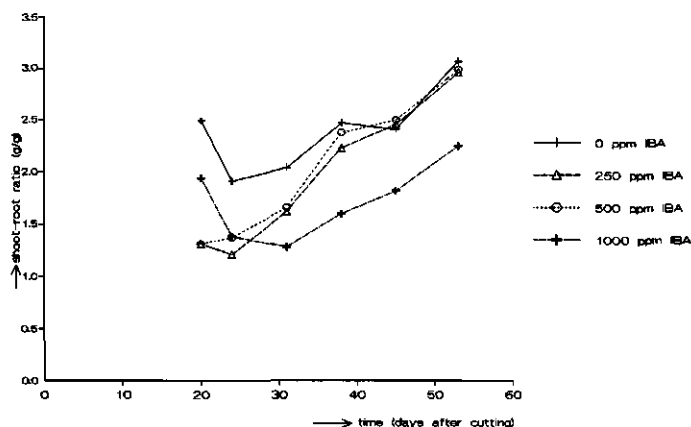


Figure 18. Time course of shoot-root ratio (g/g) for young cuttings of *R. 'Sweet Promise'* as influenced by IBA (Experiment 9.4.1).

Figure 19 shows that the cuttings treated with 500 mg/l IBA showed the highest root weight, especially in the beginning. As time progressed the effect of auxin concentration decreased. The

number of new roots increased with auxin concentration (Figure 20), whereas for shoot weight the effect was less pronounced except at 1000 ppm where a clearly lower value was found (Figure 21). For statistical analysis of the data refer to Appendix VII.

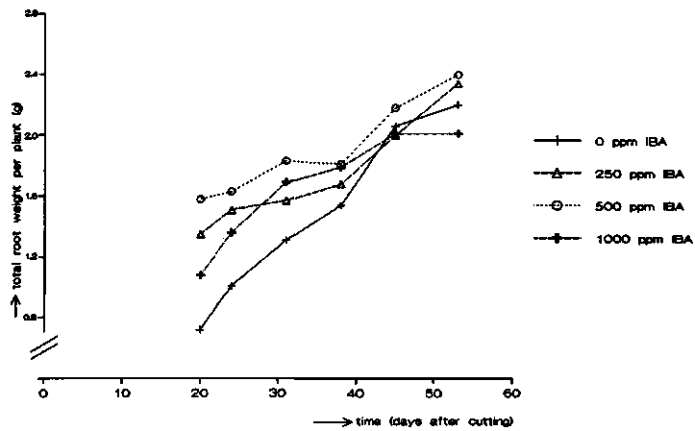


Figure 19. Time course of root weight (g fresh weight per plant) of cuttings of *R. 'Sweet Promise'* as influenced by IBA (Experiment 9.4.1).

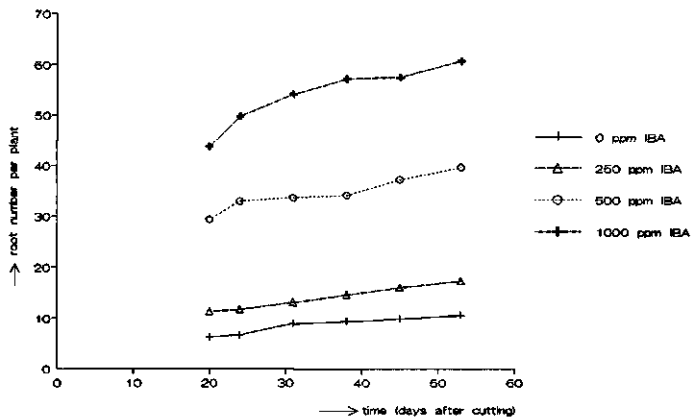


Figure 20. Time course of root number (per plant) of *R. 'Sweet Promise'* as influenced by IBA (Experiment 9.4.1).

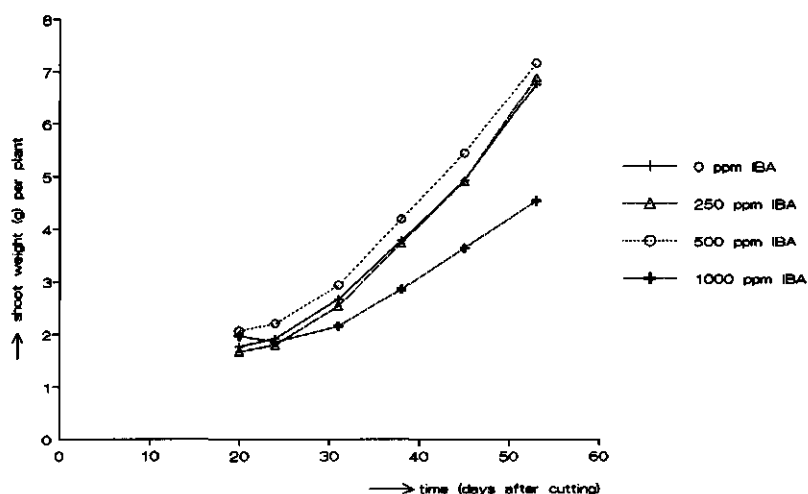


Figure 21. Time course of shoot weight (g fresh weight per plant) of cuttings of *R. 'Sweet Promise'* as influenced by IBA (Experiment 9.4.1).

Experiment 9.4.2

Root regeneration and bud release as influenced by pH

When a rose culture starts with transplanted (quiescent) material, plant survival depends on ready root regeneration. Referring to the literature cited in the Introduction (p. 52) the degree of root regeneration varies with species and cultivar and the physiological stage of the shoot. Apart from factors such as root pruning and application of auxin, propagation practice suggests that pH of the root medium could also be a relevant factor. In a preliminary experiment (data not given) it was found that root growth in particular was retarded at a lower pH level but that root regeneration was hardly affected. In the present experiment the effect of pH on the course of root regeneration and on bud release was followed throughout the first two weeks after planting.

One-year-old cold-stored dormant seedlings of *R. canina* 'Inermis' (root collar diameter 3-5 mm) were transferred to the hydroculture system (tap water) and kept there for fifteen days. The roots had previously been pruned to a length of fifteen cm and subsequently been soaked for ten minutes in different solutions of IBA (potassium salt, concentration 0, 100 or 250 mg/l). Then, in separate units, five pH values were realized, viz. 7.5 (normal tap water), and by adding various amounts of H_2SO_4 , 5.8, 5.4, 3.5 and 2.7. The experiment was carried out in February 1985. Temperature was about 24 °C; no supplementary light was given. The number of new roots (length > 0.3 cm) and root primordia (< 0.3 cm) were recorded at intervals. After fourteen days, at the end of the experiment, the percentage of released buds was also recorded. The experiment was not replicated. There were 15 plants per pH treatment.

There was no interaction between pH optimum and IBA pre-treatment, which means that the IBA pre-treatment the effect of pH on root regeneration not affected (data not given). As Figures 22 and 23 show, the pH of 5.8 was optimal for root regeneration (irrespective of their IBA pre-treatment). At that pH the ratio between roots and primordia is about 10, whereas at lower values root primordia predominate (data not given).

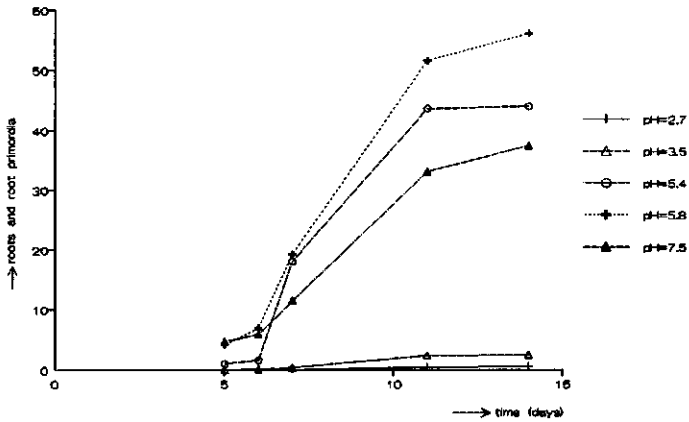


Figure 22. Number of roots per plant including root primordia of *R. canina* 'Inermis' as influenced by pH of the root medium. Values are means of three IBA pre-treatments (Experiment 9.4.2).

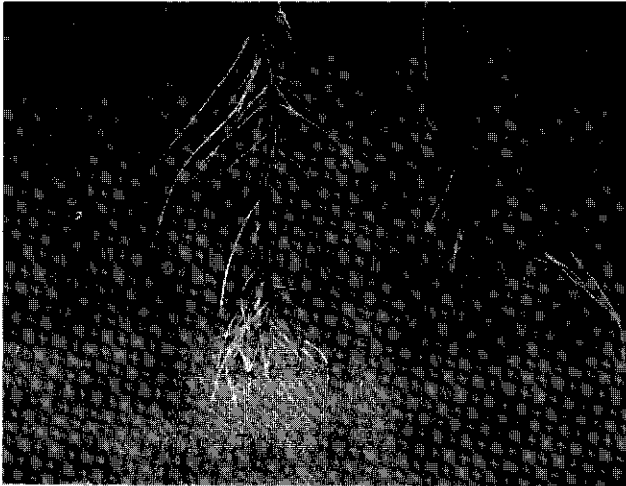


Figure 23. The root system of plants of *R. canina* 'Inermis', pre-treated with 100 mg/l IBA and kept for 11 days at (from left to right) pH values of 3.5, 5.8 and 7.5 (Experiment 9.4.2).

At the end of the experiment the plants kept at pH 2.7 were transferred to pH 5.8 and vice versa. Within three hours the newly formed roots of the plants transferred to the low pH turned blue and rapidly deteriorated during the following three days. In contrast, the plants transferred to pH 5.8 showed a ready new root production (data not tabulated).

Broadly speaking, the pattern for bud release in response to root medium pH followed that for root regeneration but was less pronounced; the optimum pH value for bud release was also 5.8 (Figure 24).

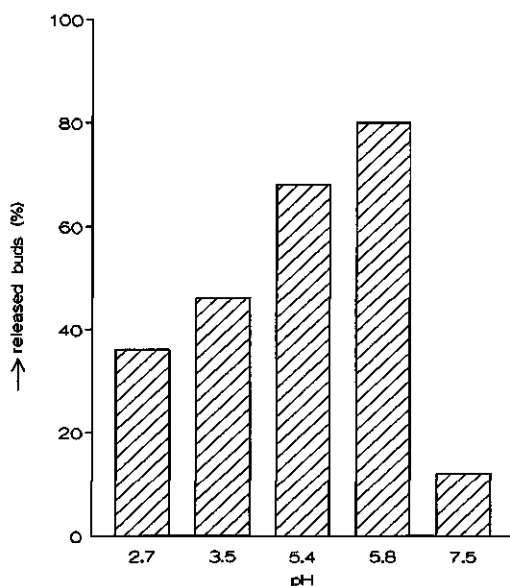


Figure 24. Bud release (percentage of released buds per plant) of *R. canina* 'Inermis' after the plants were kept for 14 days at different pH values (Experiment 9.4.2).

Experiment 9.4.3

Root regeneration in dormant plants as influenced by auxin

In Experiment 9.3.4 it was shown that auxin favoured new root formation in shoot-pruned plants. In the present experiment the auxin effect was further evaluated by varying the type of auxin, its concentration and the method of application.

Plants of *R. 'Motrea'*, T-budded in June (1985) on one-year-old seedlings of *R. canina* 'Inermis' were lifted in November 1985 and stored at 2 °C for four weeks. Then the plants were divided into ten groups and given the following treatments:

1. control: no treatment,
2. root pruning: all roots pruned to a length of 15 cm,
3. tap water: as 2 and thereafter the roots were soaked in tap water for 1 hour,

4. IAA 50: as 2 and thereafter soaked in a solution containing 50 mg/l IAA for 1 hour,
5. IAA 500: as 2 + 500 mg/l IAA,
6. IBA 50: as 2 + 50 mg/l IBA,
7. IBA 500: as 2 + 500 mg/l IBA,
8. NAA 50: as 2 + 50 mg/l NAA,
9. NAA 500: as 2 + 500 mg/l NAA,
10. IBA 0.4% in talcum powder: as 2; before planting the roots were dipped in talcum powder containing 0.4% IBA.

After treatment the plants were planted in a sandy clay in a greenhouse and kept at 18 °C without supplementary light for another four weeks. Then the plants were lifted and the number of roots longer than 0.5 cm were recorded. The experimental lay-out was a randomized block design of ten treatments and two replications of five plants each.

Table 29 shows that the best root regeneration occurred when IBA at 500 mg/l was applied. The results were also positive when 0.4% IBA in talcum powder was given and in lesser degree when NAA at 500 mg/l was used. IAA proved to be ineffective in both concentrations. It should be noted (data not given) that high NAA concentration induced more root primordia than the other auxins and that all auxin applications reduced individual root length.

Table 29. *Root regeneration (number of new roots per plant), as influenced by various root-applied auxin treatments of R. 'Moiree' on R. canina 'Inermis' four weeks after treatment (Experiment 9.4.3).*

treatment	number of new roots	
control	32.4	de
root pruning	17.2	e
tap water	13.5	e
IAA 50	20.7	e
IAA 500	21.5	e
IBA 50	59.1	cd
IBA 500	177.7	a
NAA 50	44.8	cde
NAA 500	68.0	c
IBA 0.4% in talcum powder	108.8	b

Experiment 9.4.4 Root regeneration in dormant plants as influenced by auxin and temperature

In the previous experiment IBA proved to be the most effective auxin to stimulate new root formation in young rose plants under greenhouse conditions. It may be expected that temperature affects rose root regeneration as was also found for pine roots by Abod *et al.* (1979). In the present experiment the effect of various combinations of IBA concentration and temperature on root regeneration was studied.

Plants of *R. 'Sweet Promise'*, T-budded in June (1985) on one year old seedlings of *R. canina* 'Inermis' (root collar diameter about ten mm) were lifted in November 1985 and stored at 2 °C for six weeks. Subsequently, the roots were pruned to a length of 15 cm. Shoot and root weight were recorded separately. The plants were treated by soaking the roots in 0, 100, 250 or 250 mg/l IBA (potassium salt) for one hour. In January 1986 the plants were planted into plastic trays (50*30*20 cm) filled with standard pot soil, that were placed in a phytotron under natural daylight conditions at 9, 13, 17, 21, 25 °C or in a greenhouse at 5 °C. Six weeks later, at the end of the experiment, root and shoot weights were determined again. The experimental lay-out was a split-plot design with temperature as the main factor (six levels, without replications) and auxin concentration as the side factor (four levels, two replications).

Table 30 shows that below 17 °C root weight increased with increasing IBA-concentration but that at higher temperatures a maximum occurred at 250 mg/l. Furthermore, the optimal temperature for root regeneration was affected by the concentration of IBA. Although the differences were less marked, broadly speaking the pattern for shoot weight in response to temperature and auxin concentration followed that for root weight (data not given).

Table 30. *Root regeneration, expressed as increase of root fresh weight (g) per plant, as influenced by auxin concentration and temperature (°C) of R. 'Sweet Promise' on R. canina 'Inermis' six weeks after treatment (Experiment 9.4.4).*

IBA (mg/l)	temperature					
	5	9	13	17	21	25
0	0.7 b	0.4 b	1.2 c	1.3 b	1.0 b	0.2 c
100	2.8 ab	3.9 a	5.0 b	5.9 a	9.1 a	4.2 ab
250	3.5 a	4.8 a	9.4 a	9.9 a	10.9 a	5.2 a
500	5.2 a	5.6 a	9.6 a	8.3 a	3.2 b	2.1 bc

Experiment 9.4.5

Root regeneration of bare root segments as influenced by applied auxin and sugar

In Experiment 9.3.1, 9.3.2 and 9.3.4 it was shown that root mortality after shoot pruning was due to shortage of assimilates and lack of competition capacity (sink activity) of the roots. In the present experiment root regeneration as influenced by application of auxin and sugar in various concentrations was estimated.

Six dormant four-year-old plants of *R. multiflora* 'Kanagawa', growing in the open in sandy clay, were lifted in February 1984. From each plant a number of root segments (length 7.5 cm, diameter 1-2 mm) were collected and soaked for five minutes in 0% or 5% solution of sucrose in water, supplemented with 0, 10, 100 or 1000 mg/l IBA (potassium salt). Subsequently, as was described in detail in Chapter 8, the segments were placed polarly in plastic cups. Root

regeneration (RRP) was recorded after 21 days at 21 °C in climate rooms of the phytotron (cf. General Materials and Methods, p. 58). The experimental lay-out was a randomized block design of eight treatments and three replications of five root segments each.

Table 31 shows that application of IBA (100 or 1000 mg/l) promoted RRP, as was reflected in a larger number of new roots, as well as in a greater total new root length per segment. Addition of sucrose 5% enhanced the promoting effect of auxin at least at the higher concentration.

Table 31. Root regeneration (number of new roots and total new root length (mm) per regenerated segment) of *R. multiflora* 'Kanagawa' as influenced by various auxin concentrations to which sucrose 5% had or had not been added (Experiment 9.4.5).

<u>treatment</u>	<u>number of new roots</u>		<u>total new root length</u>	
no sucrose:				
0 mg/l IBA	3.7	d	13.3	f
10 mg/l IBA	3.6	d	15.2	ef
100 mg/l IBA	7.4	c	41.6	d
1000 mg/l IBA	11.4	b	49.5	c
sucrose 5%:				
0 mg/l IBA	3.8	d	13.8	f
10 mg/l IBA	2.1	d	20.5	e
100 mg/l IBA	8.4	c	53.1	b
1000 mg/l IBA	14.4	a	78.2	a

Experiment 9.4.6 Root regeneration as influenced by genotype and stored carbohydrates

In Experiment 9.4.5 it was shown that RRP could be enhanced by applied sucrose. In Experiment 9.3.1 it was shown that the degree of root mortality after shoot pruning depended on root genotype. Experiment 9.2.1 showed that the amount of stored carbohydrates depended on season and genotype. In a preliminary experiment (data not given) it was seen that young rose plants grown at high light intensity showed a higher root mass and a higher relative root growth rate compared with plants grown under low light intensity. The present experiment was carried out to study the importance of carbohydrate storage in explaining differences in degree of root mortality and regeneration between genotypes.

The cultivars were chosen on the basis of divergent differences in 'winter activity'. The plants, aged 2.5 years, received no supplementary light. The plant material consisted of two batches, caused by the difference in average winter temperature, scion-rootstock combination and regularity of harvest. The first batch consisted of plants of *R. multiflora* 'Multic', *R. canina* 'Inermis', *R. indica* 'Major' and *R. 'Veilchenblau'*, grown on their own roots. The selected plants had been randomly pruned and remained in a greenhouse at an average winter temperature of about 7 °C. The second batch consisted of *R. 'Varlon'* plants of the same age stented on *R. multiflora* 'Multic', *R. canina* 'Inermis', *R. indica* 'Major' or *R. 'Veilchenblau'* and were grown

at a moderate winter temperature of about 17 °C. They had been harvested regularly. At the beginning of February 1985 roots (diameter 4 mm, length 6 cm) were collected from both batches and used as rootstock for *R. 'Sweet Promise'* applying the method of root grafting of Van de Pol (1986). After three weeks the RRP (number of new roots and their length) was measured. In another batch of similar roots, starch and the sugars glucose, fructose and sucrose were determined (cf. General Materials and Methods, p. 56). The experimental lay-out was a randomized block design of four genotypes and eight replications of two plants each.

As Tables 32a and 32b show, in both batches RRP is low for *R. multiflora* 'Multic' and for *R. indica* 'Major'. *Rosa multiflora* 'Multic' shows about the same regeneration capacity irrespective of its origin. The number of newly formed roots of *R. 'Veilchenblau'* was remarkably high (Table 32b).

Table 32a. Root regeneration per root segment of various rootstocks grown previously at 7 °C with their own leaves, three weeks after root grafting with *R. 'Sweet Promise'* (Experiment 9.4.6).

rootstock	new roots (number)	length new root (mm)	total length (mm)
<i>R. multiflora</i> 'Multic'	1.9 c	30.9 abc	58.7
<i>R. canina</i> 'Inermis'	4.5 bc	38.1 ab	171.5
<i>R. indica</i> 'Major'	2.5 c	21.8 cd	54.5
<i>R. 'Veilchenblau'</i>	3.5 bc	27.0 bc	94.5

Table 32b. Root regeneration per root segment of various rootstocks grown previously at 17 °C with *R. 'Varlon'* as scion, three weeks after root grafting with *R. 'Sweet Promise'* (Experiment 9.4.6).

rootstock	new roots (number)	length new root (mm)	total length (mm)
<i>R. multiflora</i> 'Multic'	1.8 b	42.1 a	75.8
<i>R. canina</i> 'Inermis'	2.1 b	27.0 b	56.7
<i>R. indica</i> 'Major'	0.7 b	36.0 ab	25.2
<i>R. 'Veilchenblau'</i>	7.7 a	33.1 ab	254.9

The roots of *R. multiflora* 'Multic' from both batches had a low starch content (Tables 33a and 33b). With scion *R. 'Varlon'*, grown under moderate temperature, the rootstock *R. 'Veilchenblau'* had a relatively high amount of starch (Table 33b). Further, there was a significant correlation between the number of new roots, their length and total new root length on the one hand and starch content of the roots on the other hand. The amount of the other carbohydrates is relatively less important, except for sucrose in plants grown under moderate temperature.

Table 33a. Carbohydrates content (% of dry weight) of root segments from various rootstocks grown with their own leaves at 7 °C (Experiment 9.4.6).

rootstock	starch	glucose	fructose	sucrose
<i>R. multiflora</i> 'Multic'	1.5 b	0.04 NS	0.13 NS	0.76 b
<i>R. canina</i> 'Inermis'	11.4 a	0.03	0.12	1.42 a
<i>R. indica</i> 'Major'	9.3 a	0.13	0.16	1.04 ab
<i>R. 'Veilchenblau'</i>	12.7 a	0.07	0.12	1.33 ab

Table 33b. Carbohydrates content (% of dry weight) of root segments of various rootstocks grown with *R. 'Varlon'* as scion at 17 °C (Experiment 9.4.6).

rootstock	starch	glucose	fructose	sucrose
<i>R. multiflora</i> 'Multic'	1.8 b	0.01 NS	0.11 NS	1.38 NS
<i>R. canina</i> 'Inermis'	3.4 b	0.02	0.11	1.60
<i>R. indica</i> 'Major'	2.0 b	0.09	0.12	1.62
<i>R. 'Veilchenblau'</i>	13.0 a	0.03	0.07	1.30

Experiment 9.4.7 Root and shoot growth of intact plants as influenced by applied sugar

As found in Experiment 9.4.5, the application of sucrose favoured root regeneration in isolated root segments. The aim of the present experiment was to evaluate this effect for intact rose plants.

In July 1986 one year old plants of *R. canina* 'Inermis' seedlings (root collar diameter 4-6 mm) were transplanted from the open to the hydroculture system and kept there for about five weeks. No supplementary light was given. The plants were cut back completely. Only a 2-3 cm stump of one shoot bearing a well-developed bud (without a leaf) was left. On the decapitated shoot an inverted flower tube (volume 6 ml) was placed containing sucrose solutions of 0, 10, 25, 100 or 200 g/l in water (Van de Pol and Marcelis, 1987). When after four weeks the tubes were removed, the average absorption was 3.6 ml per plant. Throughout the experimental period root weight, number of new roots (>0.5 cm), number of new shoots and shoot length were recorded at regular intervals. The experimental lay-out was a randomized block design of five treatments and three replications of three plants each.

As found previously, some root mortality occurred while root fresh weight reached a minimum after three weeks (data not given). However, after about two weeks root regeneration started (Table 34). Root regeneration as well as shoot growth was promoted by sucrose; an optimum occurred at 100 g/l (Tables 34 and 35). The promotive effect of applied sucrose started after about two weeks and was most pronounced at the end of the experiment. It should be noted that none of the plants treated with 25 or 100 g/l sucrose died but that at 10 and 200 g/l sucrose the percentage of dead plants reached 40% (data not given).

Table 34. Time course of number of new white roots (>0.5 cm) per plant of almost completely cut back *R. canina* 'Inermis' plants as influenced by applied sucrose (Experiment 9.4.7).

sucrose (g/l)	number of new white roots at day			
	12	19	26	33
0	0.3 NS	1.4 NS	2.5 b	5.3 d
10	0.2	1.2	3.8 b	12.4 cd
25	1.3	5.0	30.1 a	41.8 ab
100	1.2	5.6	30.3 a	59.9 a
200	1.9	7.9	36.0 a	36.4 bc

Table 35. Time course of number of developing shoots per plant and their average length (mm) of almost completely cut back *R. canina* 'Inermis' plants as influenced by applied sucrose (Experiment 9.4.7).

sucrose (g/l)	day							
	12		19		26		33	
	number	length	number	length	number	length	number	length
0	0.8 NS	16.0 b	1.0 NS	18.6 b	1.0 c	27.7 bc	1.0 c	59.9 bc
10	0.6	20.0 b	1.3	17.8 b	1.5abc	19.9 c	1.9abc	30.7 c
25	0.9	21.3ab	1.8	26.9ab	2.2ab	46.3ab	2.4ab	73.1 b
100	0.9	29.9ab	2.0	39.5a	2.6a	66.5a	2.6a	108.2a
200	0.2	42.5a	0.8	31.2ab	1.3 bc	37.4abc	1.6abc	49.7 bc

Experiment 9.4.8 Root and shoot growth of young plants as influenced by various pruning treatments

In Experiments 9.3.1, 9.3.2, 9.3.4 and 9.4.1 it was shown that, at least in the short term, shoot and root competed for assimilates. In addition, higher assimilate levels were reflected in better shoot and root growth (Experiment 9.3.1 and 9.4.7). However, root pruning (removing half their length) (Experiment 9.1.3) promoted root growth without negative consequences on shoot development. In the present experiment these aspects were studied in more detail.

Cuttings of *R. 'Sweet Promise'* having two buds and subtending leaves were rooted in propagation benches in two weeks and subsequently transferred to the hydroculture system. After another two weeks the plants were selected for uniformity, viz. one shoot emerging from the uppermost bud. The following pruning treatments were applied:

1. no pruning: no pruning at all,
2. root pruning length: cutting off half of each individual root,
3. root pruning number: reducing the number of roots by half,
4. shoot pruning: removing the shoot just above the subtending leaf,

5. shoot + leaf: as 4 including the subtending leaf,

6. shoot + new shoots: as 4 and removing all releasing buds throughout the experiment.

The experiment was carried out in winter 1986 and lasted about five weeks. The plants received supplementary light (SON-T, Philips MGR 102-400, 4.5 Watt/m²) for 18 hours daily. Weights of shoot and root, number of released buds and length of the developing shoots were recorded weekly. The experimental lay-out was a randomized block design of six treatments and six replications of three plants each.

Figure 25 shows that *R. 'Sweet Promise'* on its own roots re-established its initial shoot-root ratio within one month irrespective of root pruning. The same applied to the effect of shoot pruning, if not too severe (treatment 4), but it took more time to reach the original balance. When shoot pruning was very severe as in treatments 5 and 6, the original ratio was not attained within the experimental period.

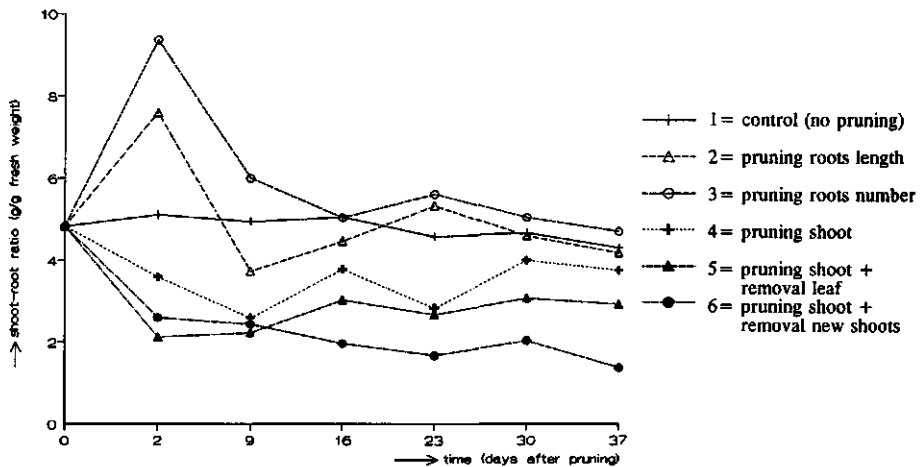


Figure 25. Time course of shoot-root ratio (g/g fresh weight) of 1 month old plants of *R. 'Sweet Promise'* as influenced by various ways of root and shoot pruning (Experiment 9.4.8).

Root pruning resulted in the highest increase of root fresh weight (Table 36), whereas the effect of shoot pruning was much less marked and even led to a decrease as in treatment 5 (complete defoliation).

Table 36. *Time course of change in root weight (g fresh weight per plant) from day of treatment (= day 0) of one month old plants of R. 'Sweet Promise' as influenced by various ways of pruning (Experiment 9.4.8).*

treatment	change in root weight at day			
	9	16	23	30
1 no pruning	0.20 bc	0.47 b	0.97 bc	1.30 b
2 root pruning length	1.20 a	1.23 a	1.49 ab	2.43 a
3 root pruning number	0.78 ab	1.28 a	1.67 a	2.16 a
4 shoot pruning	0.46 b	0.28 bc	0.64 c	0.52 cd
5 shoot + leaf	-0.09 c	-0.16 c	-0.14 d	-0.08 d
6 shoot + new shoots	0.21 bc	0.63 b	0.83 c	0.65 bc

With respect to the influence of root pruning on shoot growth, reducing the root length promoted shoot growth, whereas reducing the root number had little effect (Table 37). Shoot pruning reduced new shoot weight in all cases, especially when the attending leaf (treatment 5) was also removed and, of course, also when the new developing buds were removed regularly (treatment 6).

Table 37. *Time course of change in shoot weight (g fresh weight per plant) from day of treatment (= day 0) of one month old plants of R. 'Sweet Promise' as influenced by various ways of pruning (Experiment 9.4.8).*

treatment	increase in shoot weight at day			
	9	16	23	30
1 no pruning	1.62 a	3.22 ab	5.45 b	7.50 b
2 root pruning length	1.23 ab	3.45 a	6.67 a	9.25 a
3 root pruning number	0.86 b	2.35 b	4.60 b	7.08 b
4 shoot pruning	0.08 c	1.16 c	2.17 c	3.53 c
5 shoot + leaf	0.18 c	0.60 c	1.26 c	1.81 d
6 shoot + new shoots	0.33 c	0.29 c	0.30 d	0.40 d

Experiment 9.4.9 *Bush development as influenced by auxin*

Referring to other experiments (i.a. 9.4.1 and 9.4.3) root regeneration of young rose plants could be enhanced by auxin. Due to competition between shoot and root for carbohydrates this enhancement could result in an inhibition in shoot growth as was found in Experiments 9.3.1, 9.3.4, 9.4.1 and 9.4.8. However these experiments were only of short duration. Since for practical rose growing more or better roots are only of interest if they result in more flowers, in the present auxin experiment plant development was followed for a longer period.

Plants of *R. 'Motrea'* bench-grafted on *R. canina* 'Inermis' were planted on 21 January 1985 in a commercial greenhouse at a density of 30*20 cm. Air temperature was 21 °C during the day and 19 °C at night; relative humidity was 80% and the CO₂ concentration was enriched to a

maximum of 1500 mg/l (set-points). The primary and axillary shoots were cut back to the uppermost five-foliolate leaf on 11 February and 11 March 1985 respectively. The bottom-breaks were pruned back to a length of 30-40 cm as soon as the flower bud appeared (soft pinched).

Before planting the plants were treated as follows:

1. control: roots were left unpruned; roots soaked for 30 minutes in tap water,
2. roots pruned: roots were pruned back to a length of 12 cm and thereafter soaked for 30 minutes in tap water,
3. roots pruned + IBA: pruning as 2 and thereafter soaked for 30 minutes in a solution containing 50 mg/l IBA.

Throughout a period of six months data on the development of primary shoots, axillary shoots and bottom-breaks was recorded. The experimental lay-out was a randomized block design of three treatments and 29 replicates of one plant each.

Table 38 shows that at first plant development was somewhat retarded after root pruning. Later on, and especially for plants soaked in IBA, no differences were found.

Table 38. Some plant development parameters per plant in relation to time as influenced by root pruning and applied auxin, *R. motrea* on *R. canina* 'Inermis' (Experiment 9.4.9).

treatment	primary shoots at day 20		axill. shoots at day 36		bottom-breaks at day			
	length (cm)	diam. (mm)	length (cm)	diam. (mm)	64		167	
					number	diam. (mm)	number	diam. (mm)
control	29.4 a	3.8 a	4.4 NS	3.5 a	1.3 NS	4.8 NS	2.3 NS	8.0 NS
root pr.	23.2 c	3.6 b	5.0	3.0 b	1.0	4.3	2.2	7.8
r.p.+IBA	25.5 b	3.7 b	5.0	3.2 ab	1.2	4.0	2.4	7.4

Experiment 9.4.10

Root and shoot growth of older plants as influenced by regular application of auxin

In Experiment 9.3.4 it was shown that root mortality after cutting back could be reduced by application of auxin to the roots. The aim of the present experiment was to study whether application of low concentration auxin over a longer period, could be of interest in practical rose production for preventing root mortality. In that case the development of slow release auxin was considered (Sierra Chemicals, De Meern).

Three-year-old plants of *R. 'Motrea'* stented on *R. 'Fredica'* or grown on their own roots, were grown in 5-l containers in a greenhouse. Temperature was about 20 °C during the day and 18 °C at night. No supplementary light was given. At the start of the experiment all the shoots were pruned back to the third basal five-foliolate leaf. There were four treatments:

1. control: untreated plants,
2. IBA*5: plants received 50 ml water with 50 mg/l IBA weekly, for five weeks,
3. IBA*10: plants received 50 ml water with 50 mg/l IBA, for five weeks twice a week,
4. IBA*1: plants received 50 ml water with 250 mg/l IBA at the beginning of the experiment.

The experiment was carried out from the end of January until the beginning of March 1986. At the end of the experiment the number of flowers, their weight and the weight of blind shoots were recorded. Also, a visual judgement was made concerning root activity, measured as the amount of white roots on the outside of the clod (0=no white roots visible, ..., 2=numerous white roots visible). Two weeks later the number of released buds (> 1 cm) was recorded. The experimental lay-out was a randomized block design of two root genotypes, four auxin treatments and five replications of five plants each.

Because both root genotypes responded similarly, the average for both is given (Table 39). Auxin, irrespective of the method of application, promoted shoot development as well as root activity, especially when it was given at frequent intervals. There was no effect on bud release.

Table 39. *Number of flowers, harvest weight (g fresh weight), root activity and number of released buds per plant of R. 'Motrea' as influenced by auxin application. Values are means of two rootstocks (Experiment 9.4.10).*

treatment	flowers	harvest weight			visual root activity	released buds
		flowers	blinds	total		
control	1.2 b	14.2 b	24.0 NS	38.3 b	0.6 NS	9.4 NS
IBA*5	1.4 ab	21.5 ab	26.1	47.3 a	0.8	8.7
IBA*10	2.0 a	23.0 a	23.2	46.6 a	0.9	10.0
IBA*1	1.5 ab	18.1 ab	25.2	43.3 ab	1.0	8.9

10 Discussion

Root characteristics

The weight of rose roots originating from different rootstocks with *R.* 'Varlon' as scion cultivar differed markedly after three years (Table 22). The same was found for crops such as apple, where even differences in root characteristics occur between combinations of different scions grafted on the same rootstock (Hartmann *et al.*, 1990). These authors even stated that "nurseryman propagating apples can often identify many of the scion cultivars by the appearance of the root system of the grafted rootstock". For several woody species Tamási (1986) enumerated a number of root characteristics that may be influenced by the scion, viz. rootlet formation, habitus of the root system, root distribution and rooting depth.

Although we did not find statistical difference in root fresh weight between plants made by bench-grafted and root-grafted plants, there was a tendency that the latter weighed less and had fewer, but longer, roots (Table 22). Obviously, the propagation technique plays a role in root development. In the literature, information is scarce in this respect, Van de Pol *et al.* (1988b) reported differences in root behaviour between rose plants made by different propagation techniques.

Shoot-root ratio

One of the widely used plant characteristics, the shoot-root ratio, may be considered as a result of mutual influence of shoot and root. The shoot-root ratio of 3 to 6 (Tables 24 and 25 and Figures 13 and 18) found in the present study is about the same as reported by Zieslin *et al.* (1976c) for young rose plants. For older plants we found this ratio to be about 10 to 15 (Figure 4). This is in line Kramer and Kozłowski (1979), who stated that each species has a characteristic shoot-root ratio, which remains constant in a stable environment and increases progressively with plant age and size.

More precisely, the shoot-root ratio proved to be dependent on the chosen combination of rootstock and scion cultivar. For instance, when *R.* 'Motrea' was used as rootstock for *R.* 'Varlon' (Figure 4) and for *R.* 'Sweet Promise' (Table 24) the shoot-root ratio was relatively low. However, a high ratio was found for *R.* 'Motrea' used as a cutting (own roots) (Table 25). *Rosa* 'Veilchenblau' as rootstock gave a rather high shoot-root ratio in all cases (Figure 4, Tables 24 and 25), whereas *R.* 'Fredica' was in between (Figure 4, Table 25). Further, this ratio was relatively high for the combination *R.* 'Varlon' on *R. indica* 'Major' (Figure 4) but low for *R.* 'Motrea' on *R. indica* 'Major' (Table 25). Obviously, the mutual influence of shoot and root with respect to partitioning of assimilates between shoot and root, depends on the combination; it is difficult to predict which predominates. However, one should keep in mind that this data was found for plants under different climatic conditions and of different age. Hence, as was found for

radish (Waisel and Breckle, 1987), variations in growth and behaviour, and therefore also for shoot-root ratio, among these rose plants should be expected.

In the long term experiment with *R. 'Varlon'* (Part I), the close relationship between the final shoot-root ratio and the ratio between flower weight produced over three years and final root weight, may suggest that a fixed share of assimilates of the upper parts is used for flower formation, independent of root genotype (Figure 4). This means that the root genotype plays no role in partitioning of assimilates within the shoot, but that better growth of the upper parts is directly reflected in more flowers. The absence of rootstock influence on partitioning of assimilates within the above-ground part of the plant is in contrast with the role of rootstocks in apple trees, where a greater share of assimilates is allocated to the fruits when weaker rootstocks are used (Preston, 1970).

Broadly speaking, in the event of fewer sinks the remaining sink(s) can take a greater share of the available amount of assimilates. Eliasson and Brunes (1980) found after a light period more starch in leaves of stem cuttings of *Populus* that failed to root than in rooted cuttings. Therefore it is supposed that in the absence of any shoot system, as in leaf cuttings, the (over)produced assimilates will be directed to the roots, the only active growing sites (sinks). Following this line of thought, it is not surprising that leaf cuttings growing under a longer photoperiod produced more root mass than under short days (Figure 5). However, whether more root weight also means more stored carbohydrates remains a matter of conjecture. Increased root growth (expressed in root regeneration) with increasing light intensity was found by Abod *et al.* (1979) for *Pinus*. In several herbaceous cuttings (Carpenter *et al.*, 1973) and in aspen and willow (Eliasson and Brunes, 1980) improved rooting occurred when extra light was given. However, the photoperiod as such can also influence root mass, as was mentioned by Carpenter *et al.* (1973) for cuttings of some herbaceous species.

The greater root mass produced under lower soil and air temperature regimes (Figure 5) is in accordance with data of Shanks and Laurie (1949a,b) for roses and for a number of other plants (Cooper, 1973). This may be the result of higher net-photosynthesis due to reduced dissimulation (Larcher, 1976). The occurrence of thicker roots of roses at lower temperature (Figure 6) was also reported by Shanks and Laurie (1949b) and for other woody crops like pine by Stupendick and Shepherd (1979).

Figure 5 may suggest that the photosynthetic apparatus of *R. 'Sweet Promise'* is more efficient than that of *R. 'Golden Wave'* respectively *R. 'Tekla'* or, alternatively, the differences found are due to a genetically different rooting capacity. The poor root regeneration of *R. 'Golden Wave'* compared with other scion cultivars grafted on *R. 'Manetti'* reported by Lee and Zieslin (1978), was also supposed to be due to its relatively low photosynthetic activity.

Removing the leaves by harvesting flower stems, as well as harvesting in combination with removal of extra leaves, implicates that both the photosynthetic potential and the shoot-root ratio decrease. The plant responds immediately so that, despite the different reaction in root growth (Figure 9), within a few weeks after harvesting the initial shoot-root ratio is reached (Figure 13).

As a consequence, the shoot reaction was also different (Figure 12). A ready recovery to the same shoot-root ratio also occurred when not the shoot system but the root system was pruned, irrespective of the type of rootstock and the slightly different shoot and root reactions (Table 24). As long as pruning was not too severe, the same was true for very young plants that were shoot- and root-pruned in various degrees (Figure 25). Nevertheless, the rate of regrowth of root and shoot differed markedly between various pruning treatments (Tables 36 and 37). The attempt to re-establish a stable shoot-root ratio attuned to the given situation is generally according to the literature (Brouwer, 1962a,b; Kramer and Kozlowski, 1979). The time needed to restore the root-shoot balance varies greatly and depends on various environmental factors and on plant species, as was reported by Geisler and Ferree (1984a).

When a frequently repeated intervention was made, i.e. by removing active laterals after emergence, the ratio of shoot to root mass reached a new stable balance at a different, lower level (Figure 13), a situation similar to that found for grass by e.g. Troughton (1977). It is suggested here that the lower shoot-root ratio after regular shoot pruning is due to the fact that the root takes over some functions from the shoot, such as storage of reserves. Further, one may conclude from the practice of clipping grass, collecting propagation material and removing branches from several trees and shrubs in e.g. low willow-grounds and public gardens, that depending on age, plant condition, plant species, frequency of interference and so on, many plants can withstand this operation pretty well for years.

In conclusion it may be said that the shoot-root ratio in roses depends on a number of factors and, furthermore, may vary within certain limits. Important factors are plant age, the chosen scion-rootstock combination, the sink-source relationship between below and above ground parts, environmental conditions such as light and temperature, and plant management (pruning). The plant reacts in order to find the optimal shoot-root ratio attuned to the given situation. This means that there is an interdependence of roots and shoots which is based on the function and not simply on their mass or extent. Therefore, shoot-root ratio may be better expressed, for example, by the ratio of surface areas such as root area to leaf area, as was suggested by Van Noordwijk and De Willigen (1987).

Carbohydrates

It is not surprising that in roses the surplus of carbohydrates varies with the time of year, plant activity and cultivar. The effect of the seasons on carbohydrate content of plant parts (Brandon, 1939) is likely due to the plant's development and the degree of photosynthetic activity, as can be concluded from the results of Blanc *et al.* (1976), Van de Pol *et al.* (1986) and Zieslin *et al.*, (1976c). The role of stored carbohydrates in year round production of roses is stressed by Zieslin and co-workers (Zieslin *et al.*, 1975) and for woody plants in general by Loescher *et al.* (1990).

In Experiment 9.2.1, carried out with a number of cultivars, the starch content of roots in autumn decreased until a minimum was reached in January. A maximum occurred at the end of

February, whereafter it decreased again (Figure 7a). It is suggested here that this course is correlated with the development of the shoot (sink) on the one hand and the photosynthetic activity of the leaves (source) on the other. By this reasoning, the low (Table 33) and constant level of starch (Figure 7a, Appendix V (Table 1)) in roots of *R. multiflora* 'Multic' during winter is owing to its constant and high physiological activity (estimated as degree of bark sticking) (Figure 7b), in contrast with the other cultivars in that period (see also Appendix V). This is in line with practical experience with scion cultivars grafted on *R. multiflora* 'Multic' (Van de Pol *et al.*, 1988a).

The extremely high content of starch in roots of *R. 'Veilchenblau'* (Tables 33a,b) especially with *R. 'Varlon'* as scion (Table 33b) must be related to less use of stored carbohydrates and/or a higher production of new assimilates by the scion. For *R. canina* 'Inermis' roots more variation occurred (Tables 33a,b and Figure 7a) and an additional factor, probably its ability to redistribute the stored carbohydrates, may be involved since own-rooted *R. canina* 'Inermis' plants drop their leaves under the low temperature regime. *Rosa indica* 'Major' had generally fewer stored carbohydrates in winter (Figure 7a, Table 33) which could be an explanation of the observations of Van Marsbergen (1980) and Kool and Van de Pol (1991a) which state that plants grafted on *R. indica* 'Major' produce more flowers in autumn (less storage) and fewer in late winter and early spring (reserves no longer available) than do plants grafted on *R. canina* selections.

Broadly speaking, Experiment 9.4.6 showed that roots from plants grown under a lower temperature regime had a relatively high amount of starch and a low amount of glucose, fructose and sucrose (Table 33). However, it should be kept in mind that in this experiment the scion cultivars were not the same at the two temperatures.

In conclusion it may be said that starch content in rose roots varies with the chosen scion-rootstock combination and with physiological plant activity controlled by the season.

Root mortality

From the foregoing it will be clear that good growth and development of rose plants is possible if sufficient carbohydrates are supplied either from storage or from fresh production. For root growth, the presence of leaves was important (Figures 9, 10, 14 and 15 and Table 36). The more leaves were removed, the more root growth was inhibited and even root mortality may occur. Reduced root growth after defoliation has been observed in other crops such as apple (Head, 1966 and 1967), ryegrass (Ennik, 1966; Kleinendorst and Brouwer, 1969), tea (Visser, 1969), sour cherry (Maurer, 1972) and citrus (Eissenstat and Duncan, 1992). Loss of leaf area, viz. the reduction of assimilate production, leads to a change in the state of equilibrium between root and shoot mass which must be restored. However, one should keep in mind that after partly defoliation the remaining leaves may photosynthesize more efficiently than the leaves from intact plants, as was found for wheatgrass (Painter and Detling, 1981).

Partial canopy removal in roses caused diminished root growth and even root mortality within one to two weeks for older plants (Figures 8, 9, 15 and Table 27) depending on severity of shoot pruning, genotype and likely time of year. In young rose plants root mortality was observed as

soon as two days (Figure 25). A similar close relationship between leaf development and root growth in roses was demonstrated by Zieslin *et al.* (1976c). For grasses root growth ceased within one to four days following canopy removal, depending on the species and the amount of shoot removed (Davidson and Milthorpe, 1966). For woody crops like plum and apple, shoot pruning induced diminished root growth within one to three weeks (Head, 1967) and for black currants within one week (Atkinson, 1972).

Severity of root mortality depended in some degree on rootstock (Figure 8 and Appendix VI (Table 1)). Broadly speaking one could say that plants on *R. indica* 'Major' stored relatively few carbohydrates (Figure 7a and Table 33) and had a high root mass (Figure 8), and will therefore possess strong internal competition between individual roots. As a result, root mortality after shoot pruning was heavy. Conversely, it was shown that *R. 'Veilchenblau'* suffered less from root mortality (Figure 8) probably because of its high amount of stored carbohydrates (Table 33). However, the data concerning storage of carbohydrates on the one hand and root mortality on the other hand were obtained at different times of the year; plants grew in different rooting media and the graft cultivar was not (always) the same. Furthermore, Eissenstat and Duncan (1992) stated that in citrus only current photosynthates are important to prevent root mortality, starch being of minor importance and if only after three weeks.

In Experiment 9.3.4 where sink activity was manipulated, it could be clearly shown that root and shoot growth counteracted each other (Tables 27 and 28). In addition, the demand for carbohydrates by developing shoots in roses is high until flower buds appear (Mor and Halevy, 1979). In the present experiments (9.3.1 and 9.3.4) sink activity of developing shoots was so large that roots not only stop growth but even decreased in mass. Root mortality was less marked when competition was lowered by removing sinks like active laterals (Figure 9). Removing extra leaves additionally, resulted in a dramatic decrease in root mass; regrowth started later and final root weight was lower compared to normal harvested plants (Figure 9). The delay in root growth later on in the plants without laterals could have been caused by the absence of certain factor(s) from the active buds or apices, as was concluded from root regeneration experiments with other crops (Lee and Hackett, 1976). Among these factors, auxin could be important (Lee *et al.*, 1974), as it actually enhanced root regeneration in several perennials like pear (Looney and McIntosh, 1968) and oak (Struve *et al.* 1984). In the present study with roses, reduction of root mortality also occurred by applying auxin (IBA) immediately after shoot pruning, whereas preventing auxin transport by TIBA promoted root mortality (Tables 27 and 28).

Kramer and Kozlowski (1979) stated that after reduction of the shoot-root ratio by root pruning recovery occurs via stimulated root growth by directing more assimilates to the roots. Our present results support this view: pruning of roots stimulated root growth and prevented root mortality even after shoot pruning (Tables 27, 28 and 36). It should be realised that at least part of root mortality can be ascribed to the removal of weak roots sensitive to root mortality. Maggs (1964) for young apple trees also found increased root activity and growth rate after root pruning. Notwithstanding this increased root activity, Geisler and Ferree (1984b) found reduced

photosynthesis after root pruning. Similarly, in bean leaves decreased photosynthetic rates occurred after root pruning (Carmi and Koller, 1978). In transplanting experiments with a number of tree species Sterling and Lane (1975) and Kelly and Moser (1983) demonstrated that plant recovery and establishment was optimal if shoot and root pruning was carried out without disturbing the original shoot-root ratio. However, it is remarkable that in Experiment 9.3.4 growth and development of the upper parts, expressed as number of released buds (Table 28), was not influenced by root pruning when compared to the control.

Summarizing the foregoing, root mortality in roses depends on type of rootstock, competition for carbohydrates within the plant and, related to the latter, intervention in the shoot-root ratio by e.g. hormone application, root pruning and defoliation (harvesting).

Root growth and root regeneration

Although in most cases the prevention of root mortality is difficult to distinguish from root regeneration, from a physiological point of view it is worthwhile to consider them as separate phenomena.

Root weight in roses appeared to recover completely within three to five weeks after shoot pruning (Figures 8, 9), depending on the degree of pruning and the rootstock cultivar. In other woody crops recovery varied from nine weeks (citrus: Eissenstat and Duncan, 1992) to one year (black currant: Atkinson, 1972). In experiments with apple it was shown that the time of year has a large effect on the time required for root density to recover its pre-pruning level (Head, 1967).

The significant correlations between the number of new roots, their length and total new root length on the one hand and starch content of the roots on the other, suggest that availability of carbohydrates plays an important role with respect to regeneration capacity (Experiment 9.4.6). However, genetic factors are involved, as was shown by Young and Werner (1982) for apple rootstocks. The importance of stored carbohydrates for regrowth of above-ground parts is indicated by plants of ryegrass; plants having a large root mass show a better regrowth and this may explain the difference in regrowth between two clones of ryegrass (Kleinendorst and Brouwer, 1969). Nevertheless, the role of available reserves is not restricted to shoot growth but also known for root growth and regeneration as found for several woody species by Rogers and Head (1968), Lathrop and Mecklenburg (1971) and Blakeley *et al.* (1972). The important role of carbohydrates in root regeneration was also clear from Tables 31 and 34, which show that the application of sucrose to roots enhanced their regeneration. The promotive effect of sucrose on root regeneration was reflected in an increase in number, and especially elongation, of new roots (Table 31). Applied sucrose may increase auxin efficiency in stimulating root formation, as was found by Nanda *et al.* (1968) for *Populus*. Figure 16 shows a positive relationship between total root mass and root regeneration for young rose plants. The same was found by Tamási (1986) for intact root systems of apple in which the thicker roots (diameter between 5 and 20 mm) showed the best regeneration. However, the available literature is not univocal. Van de Pol (1986) found no difference in new root formation of roses after root grafting of root segments ranging from 2

to 8 mm with a scion having one leaf. In the work of Lee and Zieslin (1978), also with roses, the highest number of new roots per segment occurred in bare root segments with a diameter of 1 to 2 mm and the greatest length of new roots when segment diameter was at least 4 mm. It is suggested here that these varying results are due to differences in availability of carbohydrates. Thus, as Table 29 shows, root regeneration was reduced after pruning of dormant plants (i.e. removal of stored carbohydrates). Furthermore, rootstocks of *R. canina* 'Inermis' appeared to produce a higher mass of new roots and shoots and a higher percentage of flowering of primary shoots, when root mass was higher (unpublished results Van de Pol and Fuchs).

The importance of competition for carbohydrates between shoot and root in roses has already been discussed (p. 97). This importance also becomes clear from the results of Hoad and Abbott (1984) who found that in root-pruned apple trees a large fruit load diminished root regeneration as compared with a light crop. The level of available carbohydrates will influence the degree of competition between shoot and root and therefore root regeneration as well. This is demonstrated in a light intensity experiment where after shoot pruning the least root regrowth was found at the lowest light intensity (Fuchs, data not published).

Since growth regulators influence shoot-root competition, they may affect root regeneration as well. Application of auxin to the roots promoted root development (Figures 19 and 20, Table 27) and therefore may have inhibited shoot growth (Table 28). Conversely, cytokinin favoured shoot development and reduced root growth (Tables 27 and 28). However, inhibition of bud release by auxin was not found when auxin had been added regularly (Table 39). If all flowers are harvested at once (harvesting in flushes), this opens possibilities for decreasing root mortality by the application of auxin to the canopy. Furthermore, in a long term experiment (data not given) it was even found that auxin (IBA) applied to half year old dormant *R. 'Motrea'* plants on *R. canina* 'Inermis' improved production with one flush of flowers in the first year (Fuchs, 1986c), in this case due to a higher temperature given immediately after planting.

Auxin enhanced root regeneration in very young plants (Figures 19 and 20), in roots of older dormant plants (Tables 29, 30 and 31) as well as in active plants (Tables 27 and 28). However, for the latter it was difficult to make a distinction between diminished root mortality and root regeneration. Carlson and Larson (1977) showed that auxin activity in pruned oak roots sharply increased in the first 24 hours after pruning, and subsequently decreased to pre-pruning levels in the next one to two days. Further, stimulation of root regeneration by auxin was found to occur in several woody crops like pear (Looney and McIntosh, 1968), tulip tree (Kelly and Moser, 1983) and oak (Struve and Moser, 1984). The best root regeneration in roses occurred after application of the auxin IBA, rather than IAA or NAA (Table 29). IAA seemed to be least effective; NAA only initiated a large number of roots, but elongation was less than when IBA was used. It is likely that differences in the rate of breakdown between the various auxins play a role. The positive effect of auxins on rose roots was mainly due to an increased number of newly initiated roots. The increase in length may be caused by their advanced development. For oak and several other woody perennials, it was found that in autumn the improved root regeneration after auxin

application was almost exclusively due to elongation, whereas in spring regeneration concerned both initiation and elongation (Struve and Moser, 1984; Struve *et al.*, 1984). The auxin IBA affected root regeneration in the whole range of tested temperatures from 5 to 25 °C, but optimal concentration was dependent on temperature (Table 30). The lower the temperature, the higher the optimal concentration. If the mode of action of phytohormones is related to transport mechanisms through the cell membrane and tissue (Maan, 1985) it is not surprising that response curves of phytohormones change with temperature.

According to Moore (1974) soil pH values between 4 and 8 do not usually limit root growth of most plants. We were able to confirm this for rose plants grown in soil (data not given), whereas for *R. canina* 'Inermis' on hydroculture an optimal pH of about 6 was found (Figures 22 and 23). From the results of Experiment 9.4.2 it was clear that at a pH of 2.7, dormant roots remain inactive but were not damaged, whereas young active roots transferred to the same pH disintegrated within a few hours. The latter is in line with the findings of Findenegg (personal communication) and others (Moore, 1974). Banko and Boe (1975) found for *Coleus blumei* that at low pH, the production of cytokinin was inhibited. This probably explains why bud release in roses was inhibited at low pH (Figure 24). It should be noted however, that optimal pH for root growth varies with species and cultivar (Gilliam *et al.*, 1985).

Temperature greatly influences root regeneration in woody crops (Geisler and Ferree, 1984a). For pine seedlings the most favourable air and root temperature for root regeneration was between 20 and 30 °C (Stone and Schubert, 1959; Stupendick and Shepherd, 1979). However, for pine Abod *et al.* (1979) found that root temperature had a greater influence on regeneration than air temperature. It is notable, that temperature also affects bud release, which may in turn interfere with root regeneration. Root regeneration was optimal in the range of 13 - 21 °C (Table 30), dependent on the auxin concentration used and time of observation. In a preliminary experiment with root segments of *R. multiflora* 'Adenochæata' the best temperature for root regeneration proved to be 21 °C (Fuchs, data not published).

The significance of reduced root growth on plant growth depends on the general plant vigour and on the period in which root growth is reduced. A short period is not necessarily damaging for the plant, as was demonstrated by Brouwer (1981), who reported that under favourable conditions shoot growth of *Zea mais* and *Phaseolus vulgaris* was not inhibited by removing a part of the root system. Obviously, the remaining roots were able to compensate for the loss. Nevertheless, reduced root growth during a longer period will decrease shoot growth (Experiment 9.3.1). Explaining factors may be limited water absorption (water stress), reduced mineral absorption, reduced storage of assimilates and reduced hormone (cytokinin) synthesis. In our experiments, the fact that plants suffering severe root mortality wilted readily under water stress conditions, indicated that the absorption of water was actually reduced. The negative effect of root mortality was further demonstrated by the fact that plants with severe root mortality were more heavily infected with mildew (*Sphaerotheca panosa*) (data not published). Another reason for both poor

shoot and root growth after root mortality may be the increase of oxygen consumption due to increased bacterial activity (Nonnen, 1980).

Although in the beginning reduced shoot growth enhanced root growth induced by i.a. auxin or root pruning, later shoot growth made up the arrears (Tables 37, 38 and 39) due to recovery of the so-called "functional equilibrium" between shoot and root (Brouwer and De Wit, 1968). After some time root and shoot growth are more 'in line' with each other (Tables 24, Table 34 vs. 35 and Table 36 vs. 37). Buttrose and Mullins (1968) for grapes and Larson (1975) for oak seedlings, found that reduced root growth inhibited shoot growth.

Root pruning by removing half the length of each root promoted root growth (Tables 24, 27, 28 and 36), the degree being dependent on rootstock, whereas root pruning by removing half the number of roots generally resulted in less root growth (Table 24). For the effect on shoot growth, root pruning by length proved to be better or at least equal to root pruning by number or no pruning at all (Tables 24 and 37). Better root and shoot growth after root pruning was also observed by Maggs (1965) and Richards and Rowe (1977) for young apple and peach trees respectively. Removing roots by length induced more lateral roots than the untreated control (Table 28). More lateral roots implicates a higher number of root apices, the main sites of cytokinin production (Van Staden and Davey, 1979) and it is well-known that cytokinins stimulate shoot development. The results of Richards and Rowe (1977) and Richards (1980) in their root manipulation studies, with peach and apple respectively, support this reasoning. According to this, in grapevines better shoot growth occurred if root density increased (Swanepoll and Southey, 1989). Similarly for roses, in Experiment 9.1.1 was found that production and quality of flowers was correlated with number of roots. This is recently confirmed by De Vries (1993), who found a positive correlation between branching of the root system and number of produced rose shoots. In conclusion it may be said that for optimal root growth and regeneration the availability of sufficient carbohydrates is essential. In the normal situation these carbohydrates are produced by the plant itself and allocated to the roots, but application of sugars may be helpful. Root growth and regeneration can further be effected by i.a. manipulating the shoot-root competition (hormones), pH and temperature. A balanced root growth is necessary for good establishment of the plant over a longer period.

11 General discussion

For the experiment described in Part I, plants with *R.* 'Varlon' as scion, were grown in soil at a relatively low winter temperature and this should be kept in mind. However, in contrast with most other publications about shoot-root relationships in roses, the present results are from a long term experiment in which a genetically broad range of rootstocks was used. Therefore, it is my opinion that the general concept about the mutual influence of shoot and root for glasshouse roses during continuous production presented in this study will hold also for other combinations and growing conditions. Furthermore, this assumption is in line with results found for apple in various experiments (Tubbs, 1980) and recently confirmed for roses by De Vries (1993).

In Part I it was shown that for glasshouse roses differences in production and quality caused by rootstock were restricted and most pronounced in winter. The same applied to parameters for bush development (Tables 2 - 7). Evidence that these bush development parameters play a role in determining production and quality was given in Chapter 5, where bush development parameters were used as regressors to predict production (Tables 14 and 15) and quality (Tables 18 and 19). In addition, it became clear that root behaviour, directly via differences in winter activity but also indirectly through the influence on bush development, was an important factor. Therefore, behaviour of the rootstock under the influence of unfavourable conditions was the main topic in Part II.

It was expected that the detailed information about root behaviour provided in Part II would explain shoot behaviour. However, in Part II no univocal information was obtained: sometimes indeed root activity in winter was in line with production and quality in that season, whereas in other situations this was not the case and the balance between shoot and root development was of especially important. In addition, it could be argued that root mortality and root regrowth thereafter, both influenced by carbohydrate content, hormonal balance and shoot development, were also connected to production and quality in winter. These conclusions and their practical consequences will be discussed in more detail hereafter.

Root activity

The importance of root activity in winter for good production and quality becomes clear when the data of the *R.* 'Varlon' experiment are combined with the known 'winter activity' of the rootstocks used (cf. Materials and Methods, Part 1, p. 21). Plants of *R.* 'Varlon' on *R. indica* 'Major' are more active during winter than on *R. canina* 'Inermis' which was reflected in better production (Table 8). For quality (Tables 9 and 10) the same tendency was found. Another example of the importance of rootstock activity was shown in Experiment 9.1.3; it demonstrates that during winter the behaviour of the scion (*R.* 'Sweet Promise') and the rootstock itself was influenced by the chosen combination. This resulted in low activity when *R. canina* 'Inermis' was used as rootstock and higher activity when more winter active rootstocks such as *R. multiflora*

'Adenochaeta', *R.* 'Veilchenblau' and *R.* 'Motrea' were chosen. Only when *R. canina* 'Inermis' was forced to be active (by root pruning) did a relatively good development for both shoot and root occur.

As a practical consequence, selection of rose cultivars should be focussed primary on properties of the scion (such as shape, colour, resistance). The real judgement of the cultivar for vigour and adaption to stress conditions (especially production in winter but probably also to other stress conditions such as harvesting in flushes, as will be discussed later) may take place only after grafting on rootstocks adapted properly to that situation. Therefore, judgement of new cultivars propagated on rootstocks of *R. canina* selections, the practical situation nowadays in The Netherlands, is undesirable for cultivars destined for year round production.

The necessity of winter activity of the rootstock for satisfactory winter production is underlined by the results of Pollock (1983), Miller (1986) and Van de Pol *et al.* (1988a). It can be concluded that for year round production (quantity as well as quality) rootstocks of sub-tropical origin are superior to the more winter-hardy ones, mainly because of their improved winter activity. Results obtained from the tender rootstock *R.* 'Natal Briar', a popular rootstock in The Netherlands nowadays, confirmed this conclusion (Van de Pol, unpublished results).

For year round production, the 'winter rest' inducing genes in interesting rootstocks should probably be removed in a biotechnological way. This also indicates that a specific selection of rose rootstocks, apart from scion cultivars, will be valuable. Separate selection programmes for scion cultivars and rootstocks are also common practice in top fruits (Rom and Carlson, 1987). These separate selection programmes has recently been stressed for roses by De Vries (1993).

Balanced development between shoot and root

In addition to rootstock activity other factors are involved in good production and quality. Root mass is correlated with mass of the above ground parts as found for perennial fruit crops (Hartmann *et al.*, 1990) as well as for herbaceous crops like tomato (Zijlstra and Den Nijs, 1987) and cucumber (Zijlstra and Groot, 1988). Figure 4 shows that in the long term experiment with *R.* 'Varlon', actual shoot weight and fresh root weight at the end of a three-year period depended on rootstock. This indicates that the shoot-root ratio in roses has not a fixed value but depends on the chosen combination as we have seen in the discussion on page 94. Absence of a fixed relation between shoot and root in the present experiment with *R.* 'Varlon' is probably due to the continuous production throughout the year. From Experiment 9.1.2 it can be concluded that activity of the plant is reflected in root mass i.e. amount of carbohydrates. Therefore, it is not illogical that year round production hampers the storage of carbohydrates throughout the year (Figure 7a). As a consequence, factors such as an efficient use of carbohydrates and the balance between shoot and root development become more important. The latter implies that winter active rootstocks are able to give a good production and quality but only if sink activity of shoot and root are in balance. This requirement is met for example by *R. indica* 'Major' and *R.* 'Veilchenblau'. Contrary to this, when *R.* 'Motrea', in which the root weight is relatively high

(Table 24) and root activity is high (a relatively good recovery after root mortality: Figure 8), is used as rootstock, because of its too strong root sink activity, production and quality are reduced. Too many assimilates are directed to the roots, whereby shoot development is neglected.

For practical growing this means that good plant management is essential, especially during stress situations and in case of a (relatively) small root mass. As a consequence different growing conditions (artificial substrate, lighting) may need specific plant management and/or may need another rootstock. Furthermore, plant management (such as pruning) should be in harmony with plant behaviour for optimal production and quality as was actually demonstrated by Kool and Van de Pol (1993). In addition, for optimal year round production the right plant management should be carried out. That means that *R. canina* types are not suitable for modern rose culture due to their genotypic variation (Kool *et al.*, 1991; De Vries, 1993), their recalcitrant vegetative propagation (De Vries, 1993) and their mediocre vigour.

Root mortality and root regeneration

In the various experiments in which flowers were harvested, or other ways of shoot pruning were carried out, root mortality often occurred probably due to the strong competition for assimilates between shoot and root growth (Experiment 9.3.1, 9.3.2, 9.3.3, 9.3.4). Taking into account the competition between the developing shoots (Mor and Halevy, 1979; Khayat and Zieslin, 1982), the high sensitivity of roses to low light intensity (Halevy, 1986) and the production throughout the year, it is obvious that problems occur especially when the need for carbohydrates is high and their availability is low. If shoot development was poor in, for instance, a less active scion cultivar and/or under a low temperature regime, the starch content of the roots remained at the same level (Table 33a,b: *R. 'Veilchenblau'*). However, it decreased when the plant was grown under a higher temperature regime or an active scion cultivar was used, which needed more assimilates than it was able to produce (Table 33a,b: *R. multiflora* 'Multic', *R. canina* 'Inermis' and *R. indica* 'Major') (Blanc *et al.*, 1976; Van de Pol *et al.*, 1986). Thus, some rootstocks retain a high amount of stored carbohydrates under unfavourable conditions (winter) which can be useful to prevent root mortality or to stimulate recovery thereafter (Tables 31, 32 and 34), but may be a disadvantage for good flower production and quality. In other words, rootstocks that apparently do not need or use their stored starch for shoot development, like *R. 'Veilchenblau'* (Table 33), suffer less from root mortality after pruning than *R. indica* 'Major' (Figure 8, Appendix VI (Table 1)). In the long term this could be an advantage for good production and quality of flowers, as was discussed on p. 98 and 99. Rootstocks like *R. 'Fredica'* are able to provide satisfactory production (Table 8) and quality (Tables 9 and 10), possibly because they suffer relatively less from root mortality and if so they recover easily (Figure 8, Appendix VI (Table 1)). The reason for this may be the hormone balance of the plant in which auxin plays an important role (i.a. Experiment 9.3.4, 9.4.3 and 9.4.4). Although in practice the ideal combination will depend on plant management and growing conditions, for rootstock breeding a certain amount of storage capacity should be a valuable selection criterion.

In all the above mentioned cases the availability of sufficient carbohydrates is essential for good growth and development of roses throughout the year. This is in line with the observation that production is better if thicker parent shoots are available (more stored carbohydrates) (Chapter 5) (Mor and Halevy, 1979) or when (more) leaves are present (production of new assimilates) (Section 4.2). However, in the case of stored carbohydrates one should keep in mind that redistribution of these is essential. More carbohydrates enhanced bud release and shoot development (Table 12). It may be concluded therefore that the good flower production and quality of rootstocks as e.g. in *R.* 'Bobby James', *R.* 'Mme Alfred Carrière' and *R.* 'Lecenstiana', are especially due to their good bush development in combination with a moderate root activity in winter, a balanced development between shoot and root, a not too dramatic root mortality and sufficient root growth recovery thereafter.

Here again, it will be clear that obtaining optimal production and quality in roses can be achieved only when thick parent shoots are available, whether the result of correct plant management (Kool and Van de Pol, 1993) or of the correct choice of rootstock and/or cultivar.

It is obvious that good year round production and quality in roses depend on a number of factors and that the rootstock influence is not based on one feature only. An optimal combination of all characteristics in one of the tested rootstocks, i.e. winter activity, a balanced development between shoot and root, little root mortality and a quick recovery thereafter, was not found, but can probably be obtained through breeding.

For a rose grower, an attractive system would be to harvest all roses at the same time (harvesting in 'flushes' such as 'growing for holidays'). The advantages are irrefutable (use of energy and pesticides depending on plant's stage of ontogeny, better planning of labour) but it should be taken into account that root mortality would become a problem. The question remains whether genetic variations occur between rose rootstocks with respect to the frequent root mortality and recovery thereafter. The selection of rootstock(s) focussed on these characteristics may be helpful to reduce the problems caused by repeated root mortality in such a system.

In conclusion it may be said that the production of roses is influenced by competition between upper parts and roots. For good rose production it is not sufficient to have a good assimilation system (leaves). A good storage capacity is also necessary, as well as a well balanced redistribution of the stored assimilates, especially under unfavourable conditions. Assimilates can be stored in roots as well as in shoots. Further, for optimal production throughout the year, the roots should also be active and after mortality, a quick recovery is required to ensure the correct balance between shoot and root.

Realisation of the above features and the others mentioned by De Vries (1993) such as broad graft-compatibility, resistance to specific diseases, readily adventitious rooting and adaptation to various growing media in a future 'ideal' rootstock will enhance production as well as quality. Growing cultivars on their own roots is nowadays becoming more popular in The Netherlands.

These cultivars on their own roots should satisfy such a tremendous number of selection criteria for scion requirements as well as for rootstock requirements that the cultivar put into practice will be 'only' a compromise between the ideal scion and rootstock. Therefore, it will be more practical to select rootstock and scion cultivars in separate programmes and to combine them by grafting.

Samenvatting

Scheut-wortel relaties en wortelgedrag bij kasrozen

In Nederland wordt bij de teelt van snijrozen in de kas meestal een onderstam gebruikt. De meeste rozen worden geteeld voor jaarrondproductie. In het eerste gedeelte van dit onderzoek werden verschillende type onderstammen onderzocht op hun mogelijkheid om de productie en de kwaliteit tijdens deze jaarrondproductie te beïnvloeden. De onderlinge beïnvloeding van de bovengrondse ent en het ondergrondse wortelstelsel werd daartoe gevolgd. De beoordeelde rozestruiken waren geplant in de kasgrond en werden niet belicht. De uitgevoerde teelthandelingen waren zoals gebruikelijk bij een dergelijk gewas. Getracht werd de fysiologische achtergrond van de wederzijdse beïnvloeding gedurende de groei en ontwikkeling van de plant te achterhalen. In het tweede gedeelte van dit proefschrift worden verschillende experimenten beschreven die uitgevoerd werden om meer inzicht te krijgen in de scheut-wortel verhouding, de afsterving en regeneratie van wortels en de rol hierin van de in de wortels opgeslagen koolhydraten.

In het eerste gedeelte werd in een driejarig experiment het effect bestudeerd van 17 verschillende wortelstelsels op het gedrag van de bovengrondse delen van de ent *Rosa* 'Varlon' (Ilona[®]) geteeld in de grond van een kas waar een relatief laag temperatuurregime werd aangehouden, er vond geen bijbelichting plaats. Het werd duidelijk dat het wortelstelsel een invloed had op de struikopbouw, die vooral gedurende het eerste jaar na het planten plaatsvond.

Alleen kijkend naar de planten die via stenting werden verkregen, varieerde het aantal grondscheuten per plant tussen 1,5 voor planten op *R.* 'Motrea' en 2,3 voor planten op *R. indica* 'Major'. Ongeveer 90% van alle grondscheuten werd gevormd in de eerste maanden na het planten. De kwaliteit van deze grondscheuten, uitgedrukt als diameter op het moment van oogsten, was voor de planten op de in dit opzicht beste onderstam, *R.* 'Mme Alfred Carrière', 15 procent hoger vergeleken met de planten op de slechtste, *R.* 'Paul's Lemmon Pillar'. Het percentage secundaire diktegroei van de grondscheuten na drie jaar varieerde enigszins per onderstam maar was gemiddeld ongeveer 20%. Aan het eind van deze drie jaar was het verschil in diameter van grondscheuten tussen de planten met verschillende onderstammen ongeveer gelijk aan het verschil dat reeds aanwezig was bij de oogst van deze grondscheuten.

Rosa 'Varlon' produceerde na drie jaar op *R.* 'Moonlight' het hoogste aantal zijscheuten per grondscheut, namelijk 2,4, terwijl de grondscheuten op *R. zigrii* slechts gemiddeld 1,4 zijscheuten vormden. De diameter van deze zijscheuten varieerde van 10,2 mm op *R.* 'Fredica' tot 8,6 mm op *R.* 'Paul's Lemmon Pillar'.

Het aantal scheuten op 60 cm hoogte boven de grond dat dikker is dan 0,5 cm, de zogenaamde structurele scheuten, was op *R.* 'Moonlight' 6,6 per plant, hetgeen 60% meer was dan op de slechtste onderstam *R. zigrii*. Dit betekent dat hier dezelfde tendens aanwezig was als

die werd waargenomen voor het aantal zijscheuten per grondscheut. Het werd bovendien duidelijk dat concurrentie bestond tussen de structurele scheuten van de plant onderling; naarmate meer scheuten werden geproduceerd, waren meer scheuten na drie jaar afgestorven. De diameter van de structurele scheuten was het hoogst voor planten op de onderstam *R. 'Mme Alfred Carrière'* en het laagst op *R. 'Paul's Lemmon Pillar'*. Ook deze tendens is vergelijkbaar met wat eerder gevonden was voor de diameter van de grondscheuten.

De methode van enting bleek een belangrijke factor te zijn voor de struikopbouw; planten vermeerderd door zetten op *R. canina 'Inermis'* produceerden weliswaar het hoogste totaal aantal grondscheuten maar hun diameter, secundaire diktegroei en gewicht bleef achter in vergelijking met alle andere wortelstelsels, inclusief de planten die waren gewortelent op *R. canina 'Inermis'*.

Uit ditzelfde experiment bleek verder dat gedurende de periode met de laagste produktie (de winter) tussen de planten met verschillende onderstammen, ongeacht hun vermeerderingsvorm, produktieverschillen werden gevonden van ruim 100%. Over het gehele jaar gezien waren de verschillen in produktie kleiner (maximaal 60%). De hoogste produkties werden gevonden wanneer *R. 'Varlon'* op eigen wortel werd geteeld en wanneer *R. indica 'Major'* als onderstam werd gebruikt. De laagste produkties werden behaald wanneer de planten op beide *R. canina* types werden geteeld, ongeacht de gebruikte manier van vermeerdering, en voor de planten op *R. zigrii*. Verder bleek dat bepaalde onderstammen gedurende het hele jaar beter produceerden, terwijl er ook onderstammen waren die slechts in één of enkele perioden van het jaar meer produceerden. De hoge produktie van *R. 'Varlon'* op eigen wortel zou mede te danken kunnen zijn aan de afwezigheid van een entplaats.

Behalve het aantal axillaire knoppen per plant en het aantal uitgelopen axillaire knoppen, zijn ook de snelheid van knopuitloop en vervolgens de tijd die de uitlopende knop nodig heeft om zich tot een oogstbare bloem te ontwikkelen, belangrijke factoren in de bloemproduktie. In dit onderzoek werd aangetoond dat het verschil dat gedurende het jaar werd gevonden in snelheid van axillaire knopuitloop, in belangrijke mate bijdraagt tot de gevonden verschillen in produktie tussen de onderstammen en tot verschillen tussen de seizoenen van het jaar. De gebruikte onderstam bleek eveneens van invloed te zijn op de snelheid van ontwikkeling van de bloemstengel na knopuitloop. Het belang van de aanwezigheid van het bij de axillaire knop behorende blad op de snelheid van uitloop en ontwikkeling hangt af van de gebruikte onderstam. De oorzaak van vermelde verschillen tussen onderstammen is waarschijnlijk te verklaren uit de wijze waarop de knop aan de benodigde koolhydraten kan komen (via actuele fotosynthese of via redistributie vanuit opslag) die nodig zijn voor de uitloop en de verdere ontwikkeling van de scheut.

Het effect van de onderstam op zowel produktie (aantal bloemen) als kwaliteit van de geoogste bloem (lengte en gewicht) was in de winter groter dan in de zomer. De gebruikte kwaliteitsparameters zijn onderling goed gecorreleerd. Het seizoen had minder invloed op lengte van de bloemstengel dan op het bloemgewicht.

Tenslotte werden met behulp van de verkregen cijfers van het langdurige experiment met *R. 'Varlon'* de produktie en kwaliteit gekwantificeerd door middel van lineaire regressiemodellen. Hiertoe werden de waarnemingen die gebruikt werden als parameters voor de struikontwikkeling, ongeacht de onderstam, gehanteerd als verklarende variabelen voor produktie en kwaliteit. Voor elk seizoen bleek zowel produktie als kwaliteit (gedeeltelijk) verklaard te kunnen worden uit de gemiddelde oppervlakte van de dwarsdoorsnede van de zijscheuten van de grondscheuten. Het aantal grondscheuten was minder belangrijk voor de produktie, zelfs minder belangrijk dan het aantal vertakkingen van de grondscheuten. Het aantal grondscheuten bleek alleen een belangrijke verklarende variabele voor de produktie in voorjaar en zomer. Het belang van de oppervlakte van de dwarsdoorsnede van een scheut is waarschijnlijk te danken aan het feit dat deze maat een indicatie geeft van de opslagmogelijkheid van reserves en de transportcapaciteit van de scheut. Daarmee is ook de betere uitloop verklaard waarmee axillaire knoppen uitlopen op dikkere ouderscheuten en zich vervolgens sneller tot oogstbare bloemen ontwikkelen. De belangrijke rol van de oppervlakte van de dwarsdoorsnede van de scheuten werd bevestigd door hun grotere aandeel (ten opzichte van andere parameters) in de verklaring van de produktie in de winter en van de produktie door oudere planten.

Door vergelijking van de cijfers die de struikopbouw van jonge planten van *R. 'Varlon'* weergeven en dezelfde parameters aan het eind van de driejarige teelt, kon worden gesteld dat de ontwikkeling van de plant vooral gedurende de eerste zes maanden na het planten belangrijk was voor de uiteindelijke struikopbouw van de plant en daarmee tevens voor de produktie en kwaliteit van de plant gedurende de gehele teeltperiode.

Uit het tweede gedeelte van dit proefschrift bleek dat het versgewicht van de wortels van een jonge rozeplant sterk afhing van het gekozen wortelsysteem. De wortels van *R. 'Mme Alfred Carrière'* waren 40% lichter dan die van *R. 'Moonlight'*. Verder werden enkele aanwijzingen gevonden dat de vermeerderingstechniek een rol zou kunnen spelen bij het tot stand komen van wortelkarakteristieken als aantal en gemiddelde lengte van de wortels.

In dit onderzoek bleek dat de scheut-wortel verhouding van jonge rozeplanten (jonger dan één jaar) varieerde van 3 tot 6 en afhankelijk was van de gebruikte teelttechniek, milieufactoren en de combinatie van ent en onderstam. Bovendien nam de scheut-wortel verhouding toe met de leeftijd van de plant; planten die ruim drie jaar oud waren, hadden een scheut-wortel verhouding van 10 à 15, afhankelijk van de gebruikte onderstam. Gesteld mag worden dat de wederzijdse beïnvloeding van scheut en wortel, met betrekking tot verdeling van de assimilaten tussen scheut en wortel, afhangt van de gekozen combinatie en beïnvloed kan worden door de gebruikte klimatologische teeltomstandigheden, de leeftijd van de plant en de toegepaste teelttechniek.

Bij *R. 'Varlon'* op verschillende wortelstelsels, bleek een significante correlatie te bestaan tussen de scheut-wortel verhouding van de plant na drie jaar en anderzijds de verhouding tussen het totaal aantal geproduceerde bloemen gedurende de drie voorafgaande jaren en het

wortelgewicht na drie jaar. Hieruit werd geconcludeerd dat een bepaald, vast aandeel van de assimilaten die in de bovengrondse delen van de plant terechtkomen, worden gebruikt voor bloemproductie, en dat de onderstam op dat vaste aandeel geen invloed heeft.

Uit verschillende experimenten werd duidelijk dat verstoring van de balans tussen scheut en wortel, of door scheut- of door wortelsnoei, werd gevolgd door een herstel van de oorspronkelijke scheut-wortel verhouding. Dit gebeurde ongeacht de gebruikte combinatie van ent en onderstam en de leeftijd van de plant. Een regelmatig herhaalde verwijdering van bovengrondse delen leidde tot een scheut-wortel verhouding die op een lager niveau lag maar eveneens stabiel was.

Verondersteld werd dat het regelmatig verwijderen van bovengrondse delen aanleiding geeft tot opslag van een groter deel van de reserves in de wortel, waardoor deze relatief zwaarder wordt.

Uit experimenten met beworteld blad werd duidelijk dat een overmaat aan assimilaten leidde tot een hogere wortelmassa. Aan de andere kant werd ook gevonden dat een hogere wortelmassa het gevolg kan zijn van een hogere sinkactiviteit en/of een grotere opslag van reserves in de wortel.

De hoeveelheid opgeslagen koolhydraten in de wortels van een rozeplant gedurende het jaar is gerelateerd aan de ontwikkeling van de scheut en de wortel en bovendien aan de fotosynthetische activiteit van de bladeren. Er werd aangetoond dat, los van de tijd van het jaar, ook de combinatie van ent en onderstam een uitgesproken effect had op de hoeveelheid opgeslagen koolhydraten in de wortel. Voor wat betreft dit laatste werd duidelijk dat onderstammen die afkomstig zijn van 'winteractieve' planten, zoals *R. multiflora* 'Multic' en *R. indica* 'Major', in de winter een duidelijk geringere variatie in hoeveelheid opgeslagen koolhydraten vertoonden dan de meer winterharde onderstammen zoals de *R. canina* types. Verder werd aangetoond dat aspecten als verschil in opslagcapaciteit, sinkactiviteit, mate van redistributie en klimaatfactoren een rol kunnen spelen in de opslag van koolhydraten in wortels.

Wortelgroei was gerelateerd aan de aanwezigheid van blad. Dit betekende ook dat verwijdering van blad door het oogsten van bloemscheuten of andere methoden van scheutsnoei resulteerden in minder wortelgroei binnen één of twee weken. Na sterke snoei kon zelfs wortelsterfte optreden. De mate van wortelsterfte was in zekere mate afhankelijk van de gebruikte onderstam. De gevoeligheid voor wortelsterfte hing af van de hoeveelheid opgeslagen koolhydraten en van de heersende competitie zowel binnen de wortel als tussen scheut en wortel.

Nadat wortelsterfte is opgetreden, werd een betere wortelregeneratie gevonden naarmate meer reserves ter beschikking stonden. Dit betekende dat planten met een wortelsysteem dat een grote reserve-opslagmogelijkheid bezat (in het algemeen wil dit zeggen dikkere wortels), planten met meer blad, planten die groeiden onder betere lichtomstandigheden, of planten die kunstmatig extra suiker kregen toegediend, een betere wortelregeneratie vertoonden. De wortelregeneratie werd ook verbeterd nadat de sinkactiviteit van de wortels werd gestimuleerd door toediening van auxine. De optimale concentratie van het toegediende auxine voor wortelregeneratie was afhankelijk van de temperatuur waarbij de plant groeide. De beste wortelregeneratie vond plaats bij een temperatuur (grond en lucht) van rond de 17 °C.

De wortelgroei van *R. canina* 'Inermis' (in turf) werd niet beperkt door pH-waarden tussen de 4 en 8. De wortelgroei van planten op hydrocultuur was optimaal bij een pH van ongeveer 6. Planten in rust bleven enkel en alleen inactief bij pH-waarden van 3,5 of lager, maar jonge, actieve wortels desintegreerden binnen enkele uren bij deze lage pH-waarde. Knopuitloop werd geremd bij pH-waarden die de wortelgroei belemmerden; waarschijnlijk veroorzaakt door een achterblijvende cytokinineproductie.

Beperkte wortelgroei gedurende een korte periode of in geringe mate was niet noodzakelijkerwijs schadelijk voor de plant. In feite werd scheutgroei zelfs gestimuleerd indien de wortelmassa afnam door eenmalige verwijdering van de worteltopjes. Het na enige tijd verschijnen van een groot aantal nieuwe worteltopjes suggereerde dat deze betere scheutgroei te danken was aan een hogere productie van cytokininen. Een sterkere reductie van wortelgroei leidde echter wel tot mindere scheutgroei, meer waterstress en een hogere gevoeligheid voor ziekten.

Concluderend kan worden gesteld dat de groei en ontwikkeling van de rozeplant, en daarmee bloempromotie en bloemkwaliteit, beïnvloed wordt door de competitie tussen de bovengrondse en ondergrondse delen. Voor een goede ontwikkeling van de plant is niet alleen een adequaat assimilatiesysteem noodzakelijk, maar ook een goede opslag- en redistributiecapaciteit. De opslag- en redistributiecapaciteit is speciaal van belang gedurende ongunstige omstandigheden. Voor een optimale productie gedurende het hele jaar, moeten de wortels actief zijn. Na eventuele afsterving van wortels is een snelle hergroei noodzakelijk om een juist evenwicht tussen scheut en wortel te verzekeren. De onderstam speelt hierbij een belangrijke rol.

Voor de praktijk betekent dit dat een juiste beoordeling van nieuwe entcultivars alleen kan gebeuren nadat deze zijn geënt op een onderstam die, onder de later (door de teler) toegepaste teeltomstandigheden en plantbehandeling, een optimale groei en ontwikkeling geeft. Bij het gebruikswaarde-onderzoek van cultivars die jaarrond geteeld worden, zou daarom het gebruik van *R. canina* selecties moeten worden vermeden (matige groei-inductie, vooral in de winter).

De plant moet op een zodanige wijze worden behandeld dat een juist evenwicht tussen ent en onderstam wordt bereikt. De juiste wijze hangt af van de milieu-omstandigheden, het wortelmedium, de combinatie van ent en onderstam en de plantconditie zelf.

De eisen welke aan een onderstam worden gesteld ter verkrijging van een optimale groei, kwaliteit en productie van de ent zijn hoog. Omdat ook de eisen die aan een entcultivar gesteld worden talloos zijn, lijkt het noodzakelijk dat voor selectie van onderstam en entcultivar afzonderlijke veredelingsprogramma's worden opgezet. Uiteindelijk kunnen de voor de beoogde teeltomstandigheden juiste ent en onderstam door middel van enting worden gecombineerd.

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Appendices

Appendix I

Percentage of dead plants (%) and number of dead bottom-breaks and branches (per plant) on 60 cm above ground level of *R. Varlon* after three years as influenced by various rootstocks.

rootstock	dead plants (%)	number of dead shoots per living plant	
		bottom-breaks	60 cm above ground
Var	5.0 bc	1.3 a	1.0 ab
In-b	5.0 bc	1.1 ab	0.6 ab
In-r	12.6 bc	0.6 ab	0.4 ab
Br-r	5.0 bc	0.4 b	0.6 ab
Bob	0.0 c	0.5 ab	0.6 ab
Maj	7.5 bc	0.5 ab	0.9 ab
Fre	12.6 bc	0.7 ab	0.7 ab
Lav	7.5 bc	0.5 ab	0.5 ab
Lec	5.0 bc	0.5 ab	0.4 ab
Mac	0.0 c	0.8 ab	0.6 ab
Mad	12.6 bc	0.6 ab	0.5 ab
Moo	30.0 b	0.7 ab	0.7 ab
Mot	5.0 bc	0.5 ab	1.1 a
Kan	62.5 a	0.5 ab	0.2 b
Pau	12.6 bc	0.7 ab	0.6 ab
Pin	0.0 c	0.4 b	0.6 ab
Vei	0.0 c	0.6 ab	1.1 a
Zig	5.0 bc	0.6 ab	0.6 ab
average	10.4	0.6	0.7

Appendix II

Linear correlation coefficients between bush development parameters.

	BBN	BBD	BBL1	BBL2	BBW	RCN	RCD	RCL1	RCL2
BBN									
BBD	-0.157								
BBL1	0.244	0.732**							
BBL2	0.061	0.782**	0.863**						
BBW	-0.109	0.936**	0.737**	0.807**					
RCN	-0.131	0.449*	0.285	0.398	0.449*				
RCD	0.315	-0.048	0.264	0.086	-0.048	-0.168			
RCL1	0.125	0.261	0.578**	0.403*	0.261	0.115	0.628**		
RCL2	0.263	0.203	0.507**	0.268	0.203	-0.003	0.763**	0.573**	
RCW	-0.069	0.328	0.374	0.166	0.328	0.197	0.595**	0.487**	0.805**

(r is significant at $p < 0.05$ (indicated by *) or at $p < 0.01$ (indicated by **).)

2 Scion-rootstock relationships and root behaviour in glasshouse roses

Appendix III

Linear correlation coefficients between quality parameters of the flowers per harvest period.

	weight				length		
	spring	summer	autumn	winter	spring	summer	autumn
weight:							
summer	0.641**						
autumn	0.450*	0.579**					
winter	0.328	0.179	0.546**				
length:							
spring	0.791**	0.770**	0.705**	0.445*			
summer	0.291	0.659**	0.714**	0.377	0.711**		
autumn	0.313	0.484*	0.809**	0.576**	0.729**	0.874**	
winter	0.209	0.173	0.368	0.913**	0.348	0.308	0.409*

(r is significant at $p < 0.05$ (indicated by *) or at $p < 0.01$ (indicated by **).)

Appendix IV

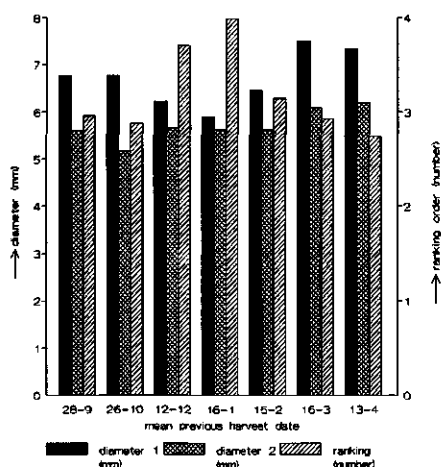


Figure 1a. Diameter of the old (diameter 1) and the new flower stem (diameter 2) and the ranking order (number) of the old stem as influenced by season. Values are means of fifteen rootstocks in six replicates, R. 'Varion'.

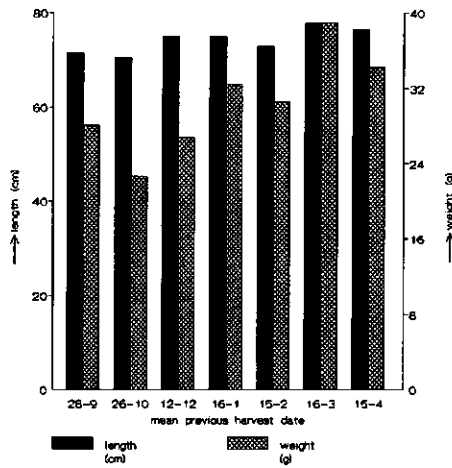


Figure 1b. Length (cm) and weight (g) of the newly developed flowers and the day (days) to flowering as influenced by season. Values are means of fifteen rootstocks in six replicates, R. 'Varlon'.

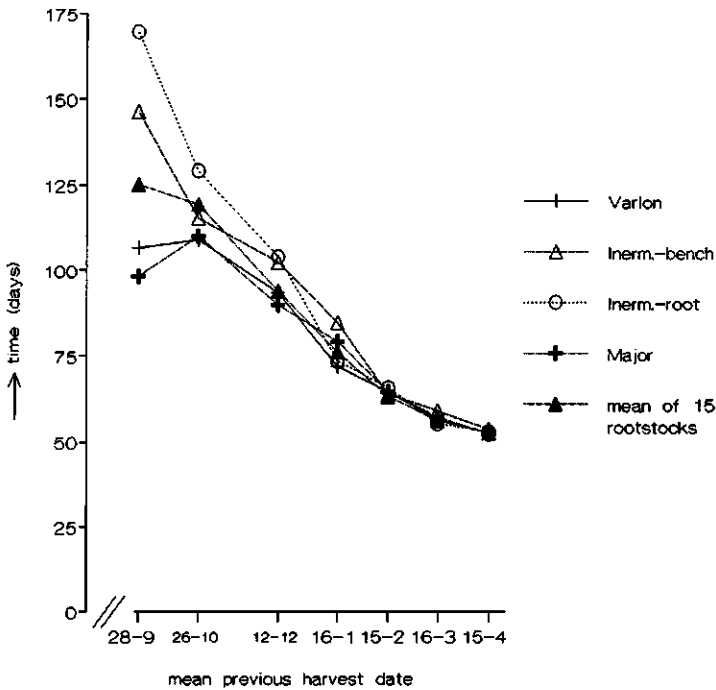


Figure 2. Time between two successive harvests for the most widely rootstocks as influenced by season. Values are means of six replicates, R. 'Varlon'.

Appendix VTable 1. Significant components ($p < 0.05$) of the equation describing the course of starch content during the winter in roots as influenced by various varieties grown with own leaves (Experiment 9.2.1).

cultivars	components of calculated course of starch content			
	mean level	linear	quadratic	cubistic
<i>R. multiflora</i> 'Multic'	1.19	-	-	-
<i>R. canina</i> 'Inermis'	4.90	-1.054	0.1134	-0.0032
<i>R. 'Veilchenbl.'</i>	4.58	-0.413	0.0428	-0.0013
<i>R. 'Manetti'</i>	3.51	-0.722	0.0750	-0.0021
<i>R. indica</i> 'Major'	2.78	-0.052	-	-

(- = no significant value)

Table 2. Significant components ($p < 0.05$) of the equation describing the course of sticking of bark during the winter in roots as influenced by various varieties grown with own leaves (Experiment 9.2.1).

cultivars	components calculated course		
	mean level	linear	quadratic
<i>R. multiflora</i> 'Multic'	2.37	-	-
<i>R. canina</i> 'Inermis'	1.31	0.085	-
<i>R. 'Veilchenbl.'</i>	3.09	-	-
<i>R. 'Manetti'</i>	2.87	0.060	-
<i>R. indica</i> 'Major'	2.11	-0.104	-0.0051

(- = no significant value)

Appendix VITable 1. Calculated course of growth curve (g fresh weight per plant) of roots of *R. 'Motrea'* as influenced by various rootstocks. Values are means of three pruning treatments (Experiment 9.3.1).

root genotype	components calculated growth curve		
	mean level	linear	quadratic
<i>R. indica</i> 'Major'	13.9 a	-0.20 b	0.004 NS
<i>R. 'Veilchenblau'</i>	8.0 b	-0.05 a	0.002
<i>R. 'Motrea'</i>	7.2 b	-0.05 a	0.002
<i>R. 'Fredica'</i>	12.0 a	-0.04 a	0.002

Table 2. *Calculated course of growth curve of roots (g fresh weight per plant) of R. 'Motrea' as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).*

pruning treatment	components calculated growth curve		
	mean level	linear	quadratic
normal harvest	11.4 a	-0.17 b	0.005 a
harvest+laterals	8.5 b	0.16 a	-0.003 b
harvest+leaves	10.7 a	-0.23 c	0.004 a

Table 3. *Calculated course of growth curve (g fresh weight per plant) of shoots of R. 'Motrea' as influenced by various rootstocks. Values are means of three pruning treatments (Experiment 9.3.1).*

root genotype	components calculated growth curve		
	mean level	linear	quadratic
R. indica 'Major'	37.5 ab	0.32 bc	0.0025 b
R. 'Veilchenblau'	31.2 b	0.21 c	0.0005 b
R. 'Motrea'	35.7 b	0.37 b	0.0027 b
R. 'Fredica'	44.9 a	0.49 a	0.0054 a

Table 4. *Calculated course of growth curve (g fresh weight per plant) of shoots of R. 'Motrea' as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).*

pruning treatment	components calculated growth curve	
	mean level	linear
normal harvest	42.4 a	0.53 a
removed laterals	32.3 b	0.18 c
removed leaves	37.2 ab	0.34 b

Table 5. *Calculated course of shoot-root ratio (g/g fresh weight) of R. 'Motrea' as influenced by various pruning treatments. Values are means of four rootstocks (Experiment 9.3.1).*

pruning treatment	components calculated course		
	mean level	linear	quadratic
normal harvest	3.13 a	0.016 a	0.001 b
harvest+laterals	2.45 b	-0.016 b	0.003 a
harvest+leaves	3.12 a	0.022 a	0.001 b

Appendix VII**Table 1** *Time course of shoot-root ratio (g/g) of cuttings of R. 'Sweet Promise' as influenced by IBA (Experiment 9.4.1).*

IBA	days after cutting					
	20	24	31	38	45	53
0	2.49 a	1.91 NS	2.04 a	2.46 a	2.41 NS	3.08 a
250	1.31 b	1.21	1.62 ab	2.23 ab	2.46	2.96 ab
500	1.31 b	1.37	1.66 ab	2.38 a	2.50	2.99 a
1000	1.94 ab	1.38	1.28 b	1.61 b	1.82	2.25 b

Table 2 *Time course of root weight (g fresh weight per plant) of cuttings of R. 'Sweet Promise' as influenced by IBA (Experiment 9.4.1).*

IBA	days after cutting					
	20	24	31	38	45	53
0	0.72 c	1.01 b	1.31 b	1.54 NS	2.06 NS	2.20 ab
250	1.35 a	1.51 a	1.57 ab	1.68	2.00	2.34 ab
500	1.58 a	1.63 a	1.83 a	1.81	2.18	2.40 a
1000	1.08 b	1.36 a	1.69 a	1.79	2.01	2.01 b

Table 3 *Time course of root number per plant of cuttings of R. 'Sweet Promise' as influenced by IBA (Experiment 9.4.1).*

IBA	days after cutting					
	20	24	31	38	45	53
0	6.3 c	6.7 c	8.9 c	9.4 c	9.4 c	10.6 c
250	11.3 c	11.7 c	13.1 c	14.6 c	16.0 c	17.3 c
500	29.3 b	32.9 b	33.6 b	34.1 b	37.2 b	39.6 b
1000	43.7 a	49.7 a	54.1 a	57.1 a	57.4 a	60.6 a

Table 4 *Time course of shoot weight (g fresh weight per plant) of cuttings of R. 'Sweet Promise' as influenced by IBA (Experiment 9.4.1).*

IBA	days after cutting					
	20	24	31	38	45	53
0	1.76 NS	1.92 NS	2.67 NS	3.79 NS	4.93 ab	5.31 bc
250	1.67	1.80	2.54	3.74	4.92 ab	6.89 ab
500	2.07	2.21	2.94	4.20	5.45 a	7.17 a
1000	1.97	1.85	2.16	2.86	3.65 b	4.54 c

Curriculum vitae

Hendricus Wilhelmus Maria Fuchs werd op 24 oktober 1956 in Guttecoven geboren. Hij bezocht het Bisschoppelijk College St-Jozef in Sittard. Van augustus 1975 tot juni 1982 studeerde hij aan de Landbouwwuniversiteit in Wageningen, studierichting Tuinbouw. Tijdens de studie werd vooral aandacht besteed aan de gewaskundige kant van de tuinbouw met als bijvakken fytopathologie en plantenfysiologie.

In september 1982 trad hij in dienst van de Landbouwwuniversiteit, vakgroep Tuinbouwplantenteelt. Daar begon hij aan een onderzoeksproject met als doel de energie-efficiency in de kasrozenteelt te verbeteren. Gedurende het academische studiejaar 1983-1984 werd het onderzoekswerk gecombineerd met het docentschap (fruitteelt) bij dezelfde vakgroep. Het daaropvolgende jaar werd dit docentschap voortgezet als deeltijdaanstelling bij de toenmalige Rijks Hogere Tuinbouwschool in Utrecht, nu Agrarische Hogeschool Delft. Vanaf 1986 heeft hij hier een volledige aanstelling als docent fruitteelt en plantenfysiologie en is daarnaast belast met diverse organisatorische taken bij de studierichting Tuinbouw en Akkerbouw.