

# ***Growth and Productivity of Cut Rose as Related to the Rootstock***

**Ximing Hu**

**Promotor:** Prof. Dr. Ir. H. Challa  
Hoogleraar in de Tuinbouwbedrijfstechnologie

**Co-promotor:** Dr. Ir. P. A. van de Pol  
Universitair Hoofddocent Tuinbouwplantenteelt

**Leden van de promotiecommissie:**

Prof. Dr. L. H. W. van der Plas, Wageningen Universiteit  
Dr. Ir. E. Heuvelink, Wageningen Universiteit  
Dr. Ir. R. Baas, Praktijkonderzoek Plant & Omgeving  
Dr. Ir. W. van Ieperen, Wageningen Universiteit

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# **Growth and Productivity of Cut Rose as Related to the Rootstock**

**Ximing Hu**

## **Proefschrift**

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## **Propositions (Stellingen)**

1. Contrary to what the term suggests, the vigour of a rootstock should be considered as the absence of growth limiting factors, rather than as a production promoting property.  
*This thesis*
2. A rose grower cultivating roses on a rootstock is always right, a rose grower cultivating roses on own roots is sometimes right.  
*This thesis*
3. In research you learn more of a 'bad' than of a 'good' result.
4. A statistically significant difference is not necessarily practically significant, nor the other way around.
5. The sweetness of the rose depends upon the name it bears: things are not only what they are, but, in very important respects, what they seem to be.
6. For the success of a new variety of a crop, marketing is more important than quality.
7. Culture is the DNA of society: in the globalised world, the prosperity of a society depends fundamentally on its culture.
8. Darwin's theory of evolution applies far better to his theory itself than to living nature.

Propositions (Stellingen) attached to the thesis:

**Growth and productivity of cut rose as related to the rootstock**

Ximing Hu

December 3, 2001. Wageningen

*To my parents*  
*my wife and*  
*my son and daughter*

## Abstract

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In contrast to the dramatic improvements in rose varieties over the last 20 years, relatively little progress has been made in the breeding of rootstocks. An important reason is the lack of early selection criteria for rootstock vigour, which has become the most important attribute required for rose rootstocks grown on artificial substrates under greenhouses.

This research examines various rose rootstock effects and the relationships between them, particularly between the effect on flower productivity (defined as rootstock vigour) and the effects on other growing aspects. 5 to 8 rootstocks, both weak and invigorating, were investigated in a series of related experiments. The rootstocks affected flower production mainly by affecting the number of budbreaks in each flush cycle rather than the duration of cycle. The rootstocks also significantly affected external flower qualities in terms of flower weight, stem length and stem diameter. Flower shoots were generally shorter and lighter on weak rootstocks than those on significantly more invigorating rootstocks. However, this observation did not apply to the invigorating rootstocks that have little differences in vigour. This is because the stem density, which was significantly higher on invigorating rootstocks, had a strong impact on flower qualities and, as a result, the relationship between the production (in number of flowers) and the quality parameters was reversed.

The rootstock effects on shoot regeneration of young rose plants in darkness with respect to both the dry weight and the lifespan of the regenerated shoots, though significant, were not correlated with rootstock vigour. The rootstocks affected the capacity of photoassimilation mainly through leaf area. The same was true for respiration. When the size effect is eliminated, neither photoassimilation nor respiration is (closely) correlated with rootstock vigour. There were little differences between the rootstocks in the concentrations of carbohydrates except for starch (at the marketable flower stage of the primary shoots). The rootstocks showed stronger effects on sucrose and starch than on glucose and fructose. In roots, sucrose and starch were generally lower in weak rootstocks than in invigorating ones. In basal stems, however, the situation is reversed. Rootstocks had significant effects on plant water relations. The invigorating rootstocks gave rise to a higher shoot water content as well as higher leaf water potential than the weak rootstocks under normal growing practice and management, but not in phytotron with young plants. The invigorating rootstocks had also a higher water conductivity of the root system as compared to the weak ones. The importance of the rootstock effect on water status in relation to rootstock vigour is addressed and discussed.

**Keywords:** Rosa, rose, rootstock, rootstock vigour, carbohydrate, respiration, photosynthesis, pruning, shoot regeneration, water content, water potential, water conductivity, Natal Briar.

## Preface

This project was financed by Steenks Rosen. The research equipment and facilities were supported by Wageningen University. Most experiments and laboratory works were carried out in the former Horticultural Department of the University. Measurements of photoassimilation and respiration were conducted in the Department of Biology, Utrecht University.

Many people deserve to be acknowledged for their help in assisting me to complete this work. Although not all their names are specifically mentioned here, they all deserve a thank you.

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Ximing Hu



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Wageningen, the Netherlands



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## *Chapter 1*

### **General introduction**

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#### **1.1 The rose industry**

Rose is economically the most important flower crop in the world. In the majority of the temperate countries, rose always has been the top selling flower. Since the 1990's their lead over the other flowers has increased due to a number of factors: a dramatic improvement in the rose varieties, the emergence of new, out of season producing countries and the emergence of a new parallel market (Pertwee, 1995).

As a major rose producer, the Netherlands has played a leading role in research and development of rose cultivation. In the Netherlands, cut roses are nowadays cultivated in greenhouses. In spite of increasing international competition, the rose crop remains on top of the Dutch floriculture. The acreage in 1999 reached 950 hectares with a produce worth € 436 million (auction turnover) (anonymous, 2000). More than half of the acreage is grown on substrates and is provided with supplementary lighting (Van de Salm, 1996).

#### **1.2 Cut rose production under greenhouses**

Cut roses are repeat-flowering perennial woody shrubs. They can continuously form new shoots that are programmed to initiate flowers without requiring a specific photoperiod and temperature (De Vries and Dubois, 1978; Zieslin and Moe, 1985), though unfavourable environmental conditions, such as low light intensity and low temperature, may cause early abortion of flower buds and lead to the formation of the so-called 'blind shoots' (Anonymous, 1998).

In the Netherlands, roses are grown the year around. Unlike most other cut flowers, roses are regularly subjected to disturbances imposed by harvesting. Flowering shoots are the most actively growing part of rose plants and bear a major portion of the leaves. When a rose branch is harvested, the leaf area and, hence, the photosynthetic capacity of

the plant is drastically reduced, resulting in a strong intervention in various functional balances between different parts of the plants, especially between the shoot and the root.

Traditionally, flower shoots are cut above the first or the second full-grown leaf from below. The remaining part of the stem bears several axillary buds from which new shoots can be formed. In recent years, the so-called knot-growing system (Van der Meer, 1994) has become the leading cultivation system. In this system, plants are grown on raised benches (usually 60-70cm from the ground). The flowering shoots are cut at the base to get the maximum length of the stem. The non-marketable shoots are bent down so that their assimilation capacity can be utilised for the development of new flowering shoots.

Typically, a rose crop lasts 5-7 years. After this period, the flower quality and the yield usually decrease to such an extent that it is more economic to replace the old plants rather than to continue production. However, drops in productivity and quality are not the only reason. The need for early introduction of new varieties often results in an earlier renewal of a crop.

### **1.3 Propagation, growth and development of rose plants**

Rose varieties were normally obtained from hybridisation of other rose hybrids or hybrid varieties (Hollis, 1974). Being highly heterozygous for most characters, rose varieties must be propagated vegetatively in order to keep their desired characters. A number of methods of vegetative propagation have been developed for roses, including layering (suckering), budding, bench grafting, stenting, root grafting, cutting and in vitro culture. Plants that are produced by these methods fall into two categories: (1) own-rooted plants, *i.e.*, those that grow on their own roots, *e.g.* plants propagated by layering, cutting and in vitro culture are own-rooted plants; (2) grafted (or combination) plants, *i.e.*, those that grow on an alien rootstock. Grafted plants are obtained by bench grafting, budding, stenting and root grafting. In the Netherlands, large-scale propagation of greenhouse roses is almost exclusively by means of cutting, stenting (for clonal stocks) or bench grafting (for seedling stocks). Although propagation by cuttings was getting increasingly popular in the last decade due to its low cost, a considerable portion of cut roses is still grafted on only few rootstock clones, of which Natal Briar is the most popular one.

Regardless of the propagation method, growth and development of rose is more or less the same, except for in vitro culture where plants often show more branching than with other methods (De Vries, 1993; Marcelis-Van Acker, 1994; Kool, 1996). Generally, only the most developed axillary bud will break and develop into the so-called primary shoot. It is, however, not unusual that more axillary buds break and lead to the formation of

two or even three primary shoots, depending on the variety, the propagational conditions and (in case of grafting) the rootstock. The primary shoot is normally pinched at bud stage to promote growth of lateral shoots from usually few distal axillary buds. After one or two weeks, the primary shoot is bent down to promote breaking of the basal quiescent buds. Shoots growing from these buds are termed 'basal shoots' or 'bottom breaks' and are usually more vigorous than the primary shoot.

## **1.4 Rootstocks**

Rootstocks have been widely used in many crops and their use stems from an old tradition. Especially for fruit crops like apple and citrus, the use of rootstocks is extremely important and it still is the most powerful and the most economic means of manipulation of plant vigour.

Rootstocks have played a vital role in modern rose cultivation. They have been an effective means of quick, large-scale production of marketable rose plants. Both clones and seedlings have been used as rootstocks. The former were popular around the Mediterranean region and in the United States, while the latter flourished in Middle and North-western Europe, and in Japan (De Vries, 1993).

A rootstock can influence growth and development of the scion in various ways. These effects have been investigated in relation to the functions of the root system. The most important are water uptake and transport, nutrient uptake (Byrne and Furuta, 1967; Jones, 1971; Gammon and McFadden, 1979; Johansson, 1979;), hormone (esp. cytokinins) production (Lockard and Schneider, 1981; Zieslin and Ziv, 1986).

### *The history*

In Europe, grafting roses on rootstocks has been practised for many centuries (Edwards, 1955). The main reason for using rootstocks was timesaving. The use of rootstocks dramatically shortened the time that was usually needed for the production of saleable plants raised from cuttings. It would take at least three years to produce a plant comparable with a one-year-old budded plant (Norman, 1953). Contrary to current view, roses were originally grafted for the purpose of getting them on their own roots (Buck, 1951). For slowly growing or developing varieties, using rootstocks seemed to be the first choice (Edwards, 1955). Because own-rooted cultivars were considered more true to the type in the early days (De Vries, 1993), it was originally intended to use rootstocks only temporarily as nurse roots. However, the advantages of grafted plants over cuttings were soon recognised in early commercial rose production. In addition to timesaving, other beneficial rootstock effects, such as adaptations to certain pH values

and drainage conditions of the soil (Grueber and Hanan, 1980), tolerance for salinity (Singh and Chitkara, 1983), climatic factors such as frost resistance or winter hardiness (Meiss, 1985), disease resistance (Buck, 1951; Coolen and Hendrickx, 1972; Schneider *et al.* 1995), plant longevity, vigour, productivity and flower quality (Edwards, 1955), were also too important to ignore. Gradually, grafting rose varieties, both difficult and easy to root, on rootstocks became common practice.

### *The present state*

Unlike the rose varieties, which were dramatically improved in the last two decades, there has been relatively little progress in the breeding of rootstocks. This lack of development has become more evident when artificial growing media were introduced and the measures to increase rose productivity and quality by improving growing conditions seemed gradually exhausted.

Until 1980, soil was the only substrate used in rose cultivation in greenhouses in the Netherlands where usually (seedling) Edelcaninas were used as rootstocks (De Vries, 1993). The introduction in the early 1980's of artificial substrates, of which rockwool was the most important one, resulted in significant changes in growing practice. Seedling rootstocks were immediately found unsuitable for roses grown on artificial substrates, not only because of the danger of carrying soil-borne diseases, but also because of their big size. In soil culture, big rootstocks were usually appreciated. On artificial substrate, however, they turned out to be undesirable as starting material. Cuttings were easier to handle on artificial substrates and therefore preferred. On the other hand, the growing environment of roots in artificial substrates is very different from that in soil. Most greenhouses are equipped with automatic irrigation systems. With well-balanced nutrient solution and a carefully formulated irrigation scheme, theoretically there should never be a shortage or an excess of water in the growing medium. Soil-borne diseases could also be controlled to a large degree. These improvements, together with the use of artificial lighting and heating during the winter period, made most of the seedling rootstock characters that were considered important unnecessary. The use of seedling rootstocks, which have only a mediocre vigour, has therefore lost its significance. Despite the effort by the Dutch horticulturists to select super lines from the existing rootstocks (such as the Stur<sup>1</sup> project), seedling stocks were rapidly phasing out in the rose-culture industry in the Netherlands.

Nevertheless, the rootstock effect on flower production under greenhouse conditions has been examined. Interestingly, significant effects on both yield and quality were reported (Pollock, 1983; Miller, 1986; Van de Pol *et al.*, 1988; De Vries, 1990; Vonk

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<sup>1</sup> Stichting ter verbetering van uitgangsmateriaal kasrozen.

Noordegraaf, 1990; Kool and Van de Pol, 1991, 1992). In the early 1990's some clonal rootstocks such as *Moneyway* and *Natal Briar*, which were of higher vigour than the seedling rootstocks, were introduced for roses cultivated on artificial substrates. In addition to these developments, the new grafting technique—stenting (grafting a leafy scion on a piece of rootstock stem, usually internode) was developed for rose by Van de Pol and Breukelaar (1982). This simple but effective technique allows to efficiently produce combination plants (called stentlings) that are of a size comparable with cuttings. Encouraged by these developments, the Dutch horticulturists suggested that better rootstocks should and could be developed for future improvement of flower quality and productivity of cut roses since the potential by improving growing conditions had almost reached its limit (De Vries, 1993; Van de Salm, 1996).

### *The problems*

In spite of the experts' vision, the use of own-rooted cuttings was increasing steadily during the 1990's. The most important reason was the low propagation cost of own-rooted cuttings as compared to grafted plants. However, the fact that grafted plants, particularly those on traditional rootstocks, did not show clear superiority over the own-rooted cuttings under greenhouse conditions (as they did in the open field) was another important reason. In the Netherlands some efforts were made to breed and to select vigorous clonal rootstocks in order to improve the productivity. Most work was carried out on the basis of empirical knowledge and was hitherto unsuccessful. The major obstacle that was encountered in these attempts was the lack of early selection criteria (Kool and Van de Pol, 1992; De Vries, 1993). The conventional breeding of cultivars usually yields a large number of candidates in the early stages of selection. Because the chance of getting a successful new variety is very low (for scion variety it was estimated only one out of a million), the population of candidates has to be reasonably large. Unlike the screening of candidates for scion cultivar, direct selection of rootstock based on the seedling's external characteristics was unfortunately rather ineffective (De Dood and Rademaker, 1990). The problem is the difficulty to judge a candidate's performance as rootstock in the absence of a standard scion. In a seedling population in which each individual represents a particular genotype, the genetic variation in productivity is brought about by genetic variation in both roots and shoots. It is generally, however, difficult to distinguish root and shoot effects. Most characteristics found in shoots are not graft-transmittable when the material is used as a rootstock. On the other hand, it is predictably laborious, time-consuming and expensive to test a large number of candidates for productivity under commercial conditions because of the long crop life, the high variation in flower production and the high production cost. To cope with the expectable large number of candidates, either rootstock seedlings or clonal material of different genetic background, early selection criteria for high productivity should first be

made available. The knowledge of the background of the rootstock-induced variation of flower productivity is therefore the key to the problem.

## 1.5 Terminology

The rootstock effect on flower productivity is usually attributed to the character of 'rootstock vigour'. The term 'rootstock vigour' was originally used for describing the characteristic of vegetative growth (usually in a relative sense) in fruit rootstocks (Ferre and Carlson, 1987). It is a vague though nevertheless useful term. It is usually related to plant weight, plant height, trunk diameter, growth rate, etc. (Vyvyan, 1955; Bryndum, 1965; Renaud *et al.*, 1991; De Vries, 1993). Despite the different parameters, the general meaning of the term was well understood. More importantly, the evaluation of relative vigour among a range of rootstocks (such as the established famous Malling rootstocks of apple) by different parameters usually gave consistent result. With roses, however, the term causes some confusion. It is often used as a synonym for the rootstock's productivity, which might be inconsistent with the implied meaning for fruit rootstocks. Generally, the rootstocks that induce high flower productivity are said to be of high vigour and vice versa. De Vries (1993), for instance, used the flower shoot yield (number) in a certain period as a parameter of rootstock vigour. In order to incorporate quality aspects into the parameter and provide an operational basis for comparison of different rootstocks, the rootstock vigour is defined here as a relative concept relating flower productivity of a given cultivar of the scion to flower productivity of on a reference rootstock and the flower fresh weight production rate over a 'long period' is used to measure the flower productivity. The term has therefore a horticultural rather than a physiological interpretation.

It is worth noting that there is a major difference between the vigour of a rootstock and that of a plant. For rootstock vigour, it is not the growth of the rootstock itself, neither root nor shoot, that matters. The vigour of a rootstock is judged only by the growth response (the flower productivity) of a cultivar that is grafted on the rootstock, not by the characteristic of vegetative growth of the rootstock itself. Therefore, a vigorous rootstock, by definition, does not have to be a vigorous plant, nor is a vigorous plant necessarily a vigorous rootstock, although they are almost certainly related.

Throughout this thesis the term quality is used to indicate specifically the external quality. The most important determinants of external quality are flower weight, stem length and stem diameter.



## 1.6 Aim of the thesis

The objective of the present research is to investigate the rootstock effect on flower productivity and some underlying horticultural and physiological principles and thereby to gain insight into the potentials and limitations of the use of rootstocks in the production of cut roses.

## 1.7 Approach

From a genetic point of view, the flower productivity of a rootstock is most probably a quantitative trait. It is, therefore, very likely that it depends on many genes that define both morphological and physiological characteristics of the rootstock. Practically, however, one could only choose few supposedly important factors (or characteristics) for investigation, such as shoot regeneration (De Vries, 1993), root carbohydrate reserves (Loescher *et al.*, 1990; Zieslin *et al.*, 1976; Fuchs, 1986, 1994), photosynthesis (Schechter, *et al.*, 1991; Sharma and Chauhan, 1992) and root respiration (Werner and Young, 1982; Wutscher *et al.*, 1993), and water relations (Olien and Lakso, 1984; Agbaria *et al.*, 1995). In order to be able to compare different rootstock effects, a number of rootstocks, both weak and vigorous, were selected and used in all the experiments. Although the subjects to be investigated were selected on the basis of literature study and of the empirical knowledge from preliminary rootstock experiments, it is difficult not to be arbitrary and subjective since the nature of rootstock performance was largely unknown. Besides, some factors such as endogenous hormones were excluded in the investigation for practical reasons, though they are considered extremely important.

## 1.8 Outline of the thesis

In Chapter 2, the effects of seven rootstocks on flower productivity and on other growing aspects on the knot growing system are examined. Relative rootstock vigour is quantitatively defined for each of the seven rootstocks on the basis of flower productivity. The result serves as a basis for the comparison of various rootstock effects with rootstock vigour (flower productivity). Chapter 3 deals with the rootstock effects on the carbohydrate reserves at the moment of and after the harvesting (pruning) of the flowering primary shoots. The results are discussed in relation to pruning resistance of the rootstocks. In Chapter 4, the shoot regeneration in terms of dry weight and of lifespan in darkness on different rootstocks is investigated after the primary shoots were complete pruned. The results are discussed in relation to the two pruning types applied (pruning at the same date vs. pruning at the same stage). In Chapter 5, the effects of six

rootstocks on photosynthesis and respiration of both roots and shoots are studied and the results are compared with rootstock vigour. In Chapter 6, rootstock effects on shoot water content and on leaf water potential are examined. The results are compared with the water conductivity of different root systems and that of different graft unions. In the general discussion, an attempt is made to reconcile the current theory with new facts of rootstock effects and to come to an evaluation of the potential of rootstocks in cultivation of cut roses.

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## Chapter 2

### **Growth of rose cultivar 'Frisco'® as affected by rootstocks in the knot-growing system**

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Ximing Hu and Peter A. van de Pol

#### **Abstract**

The effects of seven rootstocks of contrasting vigour (one weak, one medium weak and five vigorous) on the flower production of *Frisco*® (*Rosa hybrida* cv. 'Korflapei') on knot-growing system were examined on a weekly basis during a period of 15 months. The rootstocks showed significant effects on the release of axillary buds during propagation, the growth of the primary shoots and the flower production. The length of primary shoots in the early developmental stage was positively correlated with the total flower production in the whole period. The rootstocks significantly affected the number of flowers harvested in each flush cycle, but not the duration of cycle (the time between two successive flushes), suggesting that rootstocks affect flower production mainly by affecting the number of budbreaks rather than the growing time from budbreak to harvest. The rootstocks also affected shoot weight and shoot length (therefore, they must have affected the growth rate in these terms). In general, vigorous (productive) rootstocks produced flowers with better quality. However, a negative correlation between flower productivity in number and flower quality was observed within the vigorous rootstocks. It is suggested that the reverse relationship was caused by the high stem densities on vigorous rootstocks rather than the productivity (vigour) per se. The levels of the relative vigour of the rootstocks were quantified according to the fresh weight of flower shoots produced in the period (the result will serve as a reference of vigour for the rootstocks and will be used for correlation analysis with various root parameters, either in this or other experiments).

**Keywords:** Frisco®, rose, rosa, rootstock, vigour

## 2.1 Introduction

In recent years, the rose industry in the Netherlands has experienced a number of changes in the growing practice. Apart from a sharp increase in own-rooted cuttings and new growing media (such as coconut peat), a new growing system, known as 'Knot' growing system in the Netherlands (Van der Meer, 1994) and 'Arching Cultivation Technique' (ACT) in Japan (Pertwee, 1997) has been introduced by the Dutch growers. Under the new system, rose bushes are not built up like in the traditional way. The flowering shoots are cut at the base to get the maximum length of the stem. The non-marketable shoots are bent down so that their assimilation capacity can be utilised for the development of new flowering shoots. Popular rootstocks, such as *Natal Briar*, have been used in the system. The new system is said to have other advantages over the traditional system as well (such as labour-saving) and has been adopted quickly in the Netherlands. So far, little is known about the rootstock behaviour on this system. It becomes therefore important to know how rootstocks would affect flower productivity and other growing aspects on this new system.

A rose rootstock may influence the flower production by affecting: (1) the number of buds to be released from inhibition after shoot harvest; (2) the growth rate of broken buds and developing shoots; (3) the percentage of blind shoots. In previous rootstock experiments, the comparison is usually made among rootstocks with a limited range of vigour. Owing to the inherent high variability in flower production of rose crops (Raviv *et al.*, 1993), assessment of performance of different rootstocks that cover a narrow range of vigour is difficult. In this experiment, specially selected weak as well as vigorous rootstocks have been used to increase the range of vigour. Currently, information of how a weak rootstock affects rose growth and development is not available. Large and long time trials of rootstock effects are also scarce, especially under the condition of the recently introduced knot-growing system. The primary objectives of this experiment were: (1) to investigate rootstock effects on greenhouse rose production on the new knot-system; (2) to quantify relative rootstock vigour of a group of rootstocks (seven) and provide a basis for the evaluation of early selection criteria for rootstocks in later experiments.

## 2.2 Materials and methods

This experiment was carried out in the greenhouse at the Department of Horticulture, Wageningen Agricultural University. At the end of September 1995, combination plants of seven rootstocks were made by stenting (Van de Pol and Breukelaar, 1982). Marketable flower shoots of *Frisco*<sup>®</sup>, which were taken from a commercial greenhouse, were used as scion material. Only 3-5 nodes, below the upper-most five-leaflet leaf,

were selected for making the combination plants (stentlings). Stock materials were taken from the greenhouse of the Department. In order to increase the range of vigour, both good and poor clone stocks were included in this experiment. Of the seven rootstocks, three were existing rootstocks (*Natal Briar*, *Helena*, *Moneyway*), and the other four were new hybrids (code numbers: 20—10, 12—06, 18—23, 15—13). In a preliminary experiment carried out in a commercial greenhouse on a conventional growing system, 20—10 and 12—06 performed good as rootstocks while 18—23 was poor and 15—13 was the poorest (data not shown).

Stented plants were propagated on rockwool cubes (7×7×6cm, Grodan) under 100% humidity. The rockwool cubes were isolated by plastic from the beds of the propagation benches, which were heated to 21°C. Within three weeks, most of the stentlings formed roots. Those with visible roots at the bottom of the rockwool cubes were then subjected to hardening and those without visible roots were hardened a few days later. Transplantation onto rockwool slabs took place on November 1. Since much more material was propagated than actually needed, only stentlings with good roots (as well as good shoots if possible) were selected from each rootstock combination and transferred to the experimental compartment of the greenhouse.

The growing system was a knot system with growing benches oriented from north to south. There were six benches in total. Each had two parallel lines of eight rockwool slabs (133×15×9cm) laid in gutters at a height of approximately 65 cm above the ground level. The layout of the experiment was a randomised Latin square. On slabs at both ends of the benches, the outside half was filled with border plants and the other half with the stentlings of *Moneyway* rootstock. Each rootstock had six sub-plots (except *Moneyway* which had 12 half sub-plots) which consisted of two parallel rockwool slabs. On each rockwool slab there were eight plants (occupying ground area of 1.125 m<sup>2</sup>). Therefore, each rootstock had a total number of 96 (=6×16) plants. Supplementary light, provided by high-pressure sodium lamps (SON-T; 400W; 36.5μmolm<sup>-2</sup>s<sup>-1</sup> PAR, 18hd<sup>-1</sup>), was used when the global radiation outside the greenhouse dropped below 100Wm<sup>-2</sup>. The lamps were removed on March 15. In the following winter, no supplementary light was used. Bending of the primary shoots started in mid December with all rootstocks except 15—13 because of delayed development. Bending of the primary shoots was carried out when they were blooming out and started to form side shoots. The first and the second (sometimes the third) bottom-breaks were bent so that every individual plant of all rootstocks had more or less the same leaf area before the first harvest. Flowers were harvested three times a week from February 2 onwards. The number, fresh weight and stem length of flowers produced by each rootstock were recorded. Most growing practices not mentioned here were more or less the same like in commercial greenhouses.



## 2.3 Results

### 2.3.1 Rootstock effects on root development and bud release

In the stage of propagation, considerable variations in root initiation and in bud release were observed. Generally, stentlings of 15—13 and 18—23 took longer time than the other rootstocks to form visible root primordia and to have visible roots at the bottom of the rockwool cubes. In the mean time, bud break of the scion was much slower on 15—13 and 18—23 than those on *Natal Briar*, *Moneyway* and 20—10. There was a positive correlation ( $r = 0.85$ ) between the percentage of stentlings with visible roots at the bottom of rockwool cubes and that of budbreaks across the rootstocks (Table 2.1).

**Table 2.1** The root development and the bud release of *Frisco*<sup>®</sup> (*Rosa hybrida* cv. 'Korflapei') as affected by the rootstocks during propagation.

Rootstock	12—06	15—13	18—23	20—10	Helena	M'way	N. Briar
% of stentling with visible roots *	77.2 ±2.9	18.0 ±2.9	8.9 ±2.1	93.3 ±1.9	66.2 ±3.3	85.1 ±2.6	85.9 ±2.0
% of stentling with budbreaks **	82.3 ±2.7	34.0 ±3.5	63.5 ±3.6	95.5 ±1.5	90.5 ±2.0	98.2 ±1.0	82.8 ±2.2

\* Visible roots at the bottom of rockwool cubes three weeks after stenting.

\*\* Outgrowing buds four weeks after stenting.

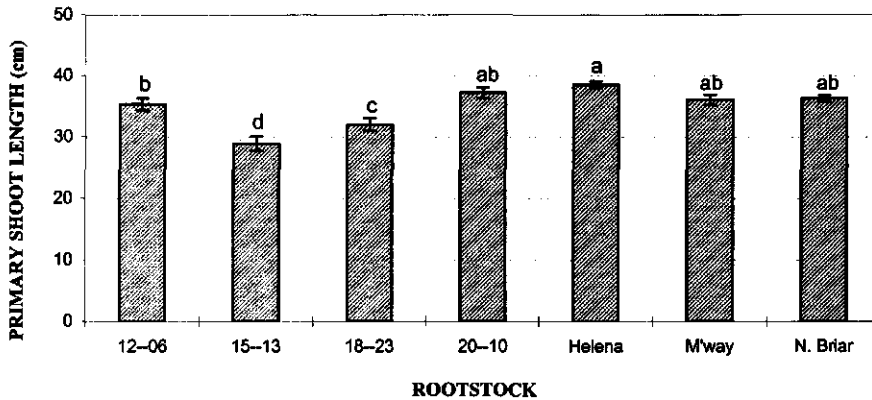
### 2.3.2 Rootstock effect on primary shoot development

Differences in stem length of the primary shoots appeared soon after bud break, primarily because the axillary bud of scion did not break at the same time in different rootstocks. After the stentlings were transferred into the compartment for production trials, the differences in primary shoot development were still clearly visible. Figure 2.1 shows the rootstock effect on primary shoot development one month after the transplantation. The primary shoots on 15—13 and 18—23 were significantly shorter than those on the other rootstocks.

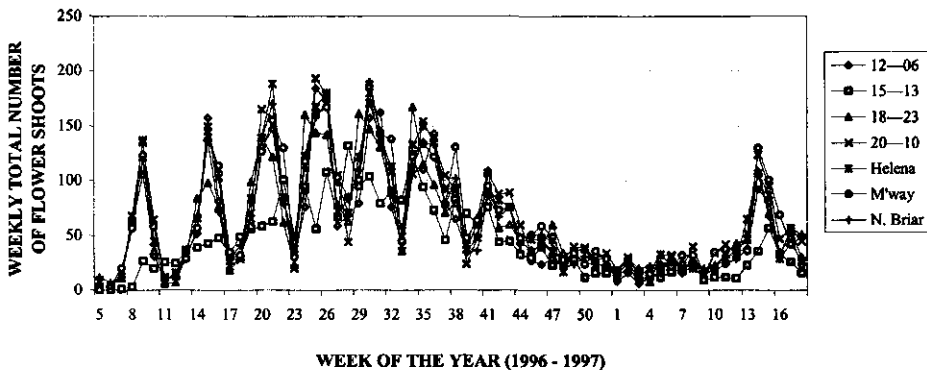
### 2.3.3 Rootstock effect on flower production

There were no significant differences in the duration of flush cycle (*i.e.* from cut to cut) between the rootstocks. Flower production on all rootstocks except for 15—13 showed a clear and regular fluctuation with a period of approximately 6 weeks, indicating that the duration of cycle is not affected by the rootstocks (Figure 2.2 and 2.3). However, as indicated by different height and width of peaks between the rootstocks in these figures,

there were clear differences in flower production either in number or in total fresh weight in each cycle as well as in the whole period. As expected, there is a dramatic seasonal effect on flower production. From the beginning of February (the 5<sup>th</sup> week) until late July (the 28<sup>th</sup> week), the flower production gradually increased over time irrespective of the rootstocks, and then declined to a minimum in January in 1997. No significant interaction between the rootstocks and the seasons was observed.



**Figure 2.1** Effect of rootstock on the primary shoot development of *Frisco*® (*Rosa hybrida* cv. 'Korflapei') two months after propagation by stenting. Vertical bars indicate the standard error of mean. Mean separation by DMRT at 5% level, indicated by different letters.



**Figure 2.2** Time course of flower production of *Frisco*®, as affected by 7 rootstocks, from the 5<sup>th</sup> week, 1996 to the 18<sup>th</sup> week, 1997. Each point on the lines represents the total number of shoots harvested from 96 plants in the indicated week.

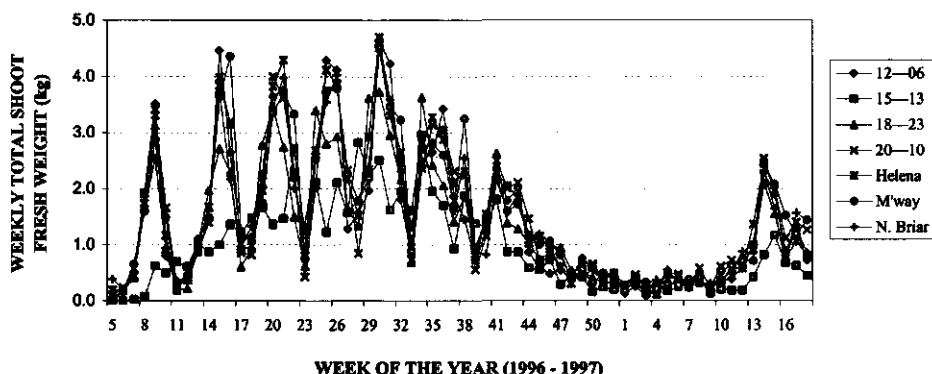


Figure 2.3 Time course of flower production of *Frisco*®, as affected by 7 rootstocks, from the 5th week, 1996 to the 18th week, 1997. Each point on the lines represents the total fresh weight of shoots harvested from 96 plants in the indicated week.

The quality of flower was also significantly affected by the rootstocks. As shown in Figure 2.4 and 2.5, the peaks of weekly average shoot weight and the weekly average shoot length, which fluctuated in the same flush cycle as production, correspond to the lowest production figures (Figure 2.2, 2.3), suggesting a negative correlation between the flower production at a moment and the quality of these flowers. Obviously, it was because that the fresh shoot weight and length were adversely influenced by the number of shoots produced in the week. The less shoots produced (*i.e.* the lower stem density during their growth), the heavier as well as longer the shoots became.

Compared to shoot length, shoot weight was more affected by the production in the same week (the coefficient of variance over the time, regardless of the rootstock types, is 4.5% for stem length and 15.6% for shoot weight). Effects of rootstock and season on both parameters were observed. On average, 12—06 and Natal Briar produced flowers with the longest stem, while 15—13 produced the shortest (Figure 2.6). There was also a clear difference between 15—13 and the other rootstocks in the distribution of flower production (in % of total number) over shoot length (Figure 2.7). The same was true for fresh shoot weight.

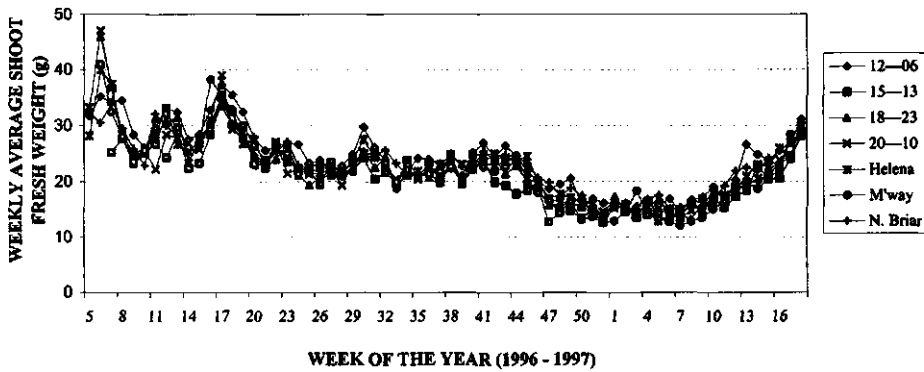


Figure 2.4 The time course of fresh shoot weight of *Frisco*® as affected by 7 rootstocks from the 5<sup>th</sup> week, 1996 to the 18<sup>th</sup> week, 1997. Each point on the lines represents the average fresh weight per piece of shoot in the indicated week.

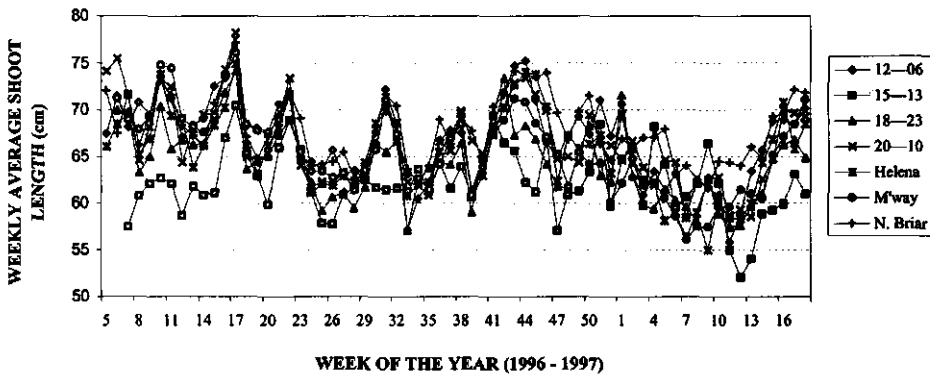
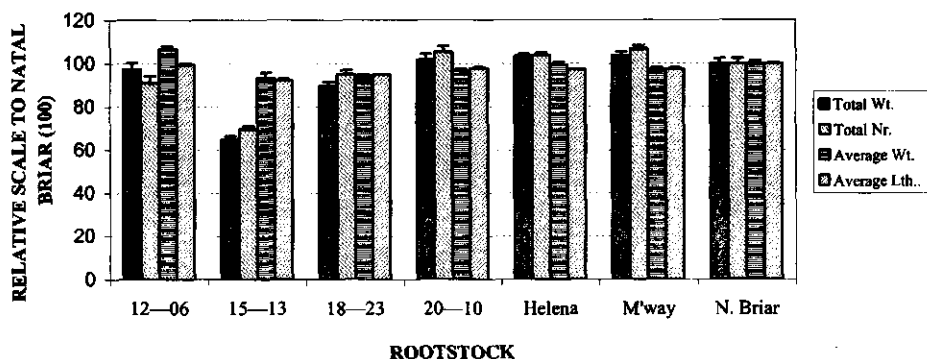
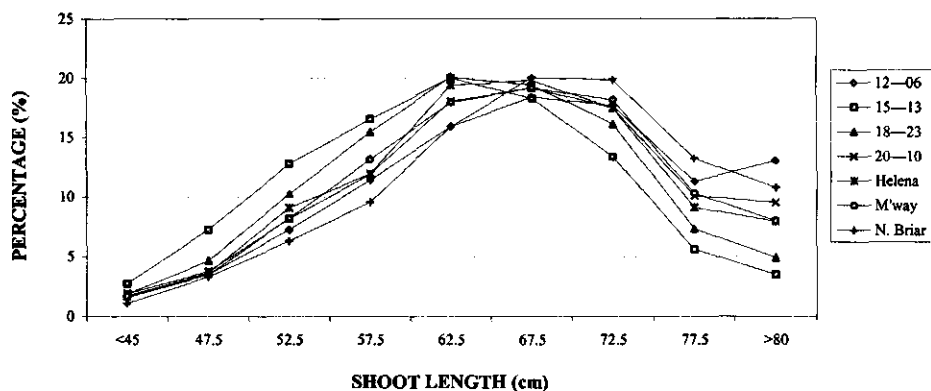


Figure 2.5 The time course of stem length of *Frisco*® as affected by 7 rootstocks from the 5<sup>th</sup> week, 1996 to the 18<sup>th</sup> week, 1997. Each point on the lines represents the average stem length in the indicated week.



**Figure 2.6** Number of shoots, fresh shoot weight, average shoot weight and average stem length in the period from the 5th week, 1996 to the 18th week, 1997 as affected by 7 rootstocks. The values are relative, expressed as percentage of the values induced by *Natal Briar*. Vertical bars indicate the standard error of mean.



**Figure 2.7** Percentage distribution of number of flowers over shoot length as affected by seven rootstocks.

### 2.3.4 Relative rootstock vigour index

The ranking of vigour of the rootstocks depends on the criterion. When the total fresh weight production during the experimental period is used as a criterion (see Figure 2.6), the ranking of the rootstocks from the most to the least vigorous is as follows:

*Helena* (103), *Moneyway* (103), *20—10* (102), *Natal Briar* (100), *12—06* (98) >  
*18—23* (90) >  
*15—13* (65)

The numbers in parentheses are the levels of fresh weight production as compared to that of *Natal Briar*, which is defined as 100. The differences between the first five rootstocks, which are separated by ',', do not reach statistical significance (LSD,  $p < 0.05$ ). The vigour of the rootstocks are therefore only in three distinct levels, *i.e.* *Helena*, *Moneyway*, *20—10*, *Natal Briar* and *12—06* are the most vigorous rootstocks, *15—13* is the least and *18—23* is in between.

## 2.4 Discussion

Similar to that found in our preliminary experiment which was carried out on the conventional growing system, the rootstocks showed significant effects on flower production and on flower quality on the knot growing system. The relative performances with regard to flower productivity of the rootstocks are the same (data not shown), suggesting that the assessment of rootstock vigour using the conventional system is also valid for the new system and vice versa.

In agreement with the results of Zieslin *et al.* (1973) and those of De Vries (1993), the rootstock effect on flower fresh weight production was achieved mainly by affecting the number of budbreaks rather than the growth rate of the developing shoots. There were indeed differences in growth rate (either in weight or in length), which lead to differences in average shoot weight as well as in average stem length, but not in the duration of flush cycle. These differences had no effect on the number of flowers produced and had relatively small effect on the total flower fresh weight produced. However, the growth rate of developing shoots on poor rootstocks, which was only slightly affected, might have been achieved at the expense of the number of developing shoots. Therefore, it remains a question whether the growth rate could still be sustained if the budbreak was not affected.

Compared to the fluctuation in fresh shoot weight and shoot length over each flush cycle and over the seasons, the rootstock effects were relatively small. In general, the vigorous

rootstocks produced flower with better quality. The weak rootstocks produced not only less, but also inferior (shorter and lighter) flower shoots ( $r=0.80$  for all the rootstocks), the same effect as found for dwarfing rootstocks of fruit trees. This is contrary to the results from De Dood and Rademaker (1991) and De Vries (1993), who concluded that shoots tend to be shorter on vigorous than on weak rose rootstocks. However, among the vigorous rootstocks, the correlation between the flower production (flower number) and quality was indeed negative ( $r=-0.85$ ). The reverse relationship was probably due to the counteractive effect of stem density (*i.e.*, the number of shoots of the same or similar developmental stage per  $m^2$ ), which was significantly higher on the vigorous rootstocks than on the weak ones. As has been shown in the results, there was a strong negative correlation between flower quality (either shoot length or shoot weight) and stem density, especially in high density. When the density of shoots is low, as in the case of the two weak stocks, the number of shoot will not significantly affect the shoot length. The effect of the vigour of rootstock on shoot length will then be observed without significant interference.

It is worth noting that the significant rootstock effect on the flower production found in this experiment was basically due to the presence of the two weak rootstocks, *i.e.* 18—23 and 15—13. The differences in yield (especially fresh weight) among the other five rootstocks were not significant. The fact that they had the same flower productivity (thus the same vigour by definition) does not necessarily mean that they have the same functional capabilities that pertain to rootstock vigour since the production could be limited by factors other than roots and the five invigorating rootstocks are of quite different genetic background and with very different root morphology. The negative correlation between the flower yield (in number) and flower quality found within the vigorous rootstocks suggests that the stem density rather than the vigour *per se* was playing an important role under the experimental circumstances and, as a consequence, the effect of these rootstocks has reached its limit.

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## Chapter 3

# The effect of rootstocks and severe pruning on non-structural carbohydrates of cut rose

Ximing Hu and Peter A. van de Pol

### Abstract

Five rootstocks of contrasting vigour were compared with respect to the concentration and the amount of the non-structural carbohydrates that were accumulated in both roots and basal stems<sup>2</sup> at the flowering stage of primary shoot. The dynamics of root carbohydrates during the stress period following the removal of the blooming primary shoot was investigated. The rootstocks were grafted with *Madelon*<sup>®</sup> (*Rosa hybrida* cv. 'Ruimeva') and grown on hydroponics under controlled conditions similar to those in a commercial greenhouse. The results show that the carbohydrate reserves were generally low. The concentration of the carbohydrates in roots dropped fast in the beginning of the stress period following the shoot removal and then gradually approached to depletion. The pattern of this process was more or less similar in all the rootstocks. There were little rootstock effects on the concentrations of the carbohydrates except the starch in roots. However, the total amount of each of the four carbohydrates varied significantly among the rootstocks due primarily to the differences in the size of the root system. In general, sucrose and starch were mostly affected by the rootstock. In roots, the total amount of the carbohydrates and, to a less degree, the concentration of sucrose and starch were higher in the vigorous rootstocks than in the weak ones. In the basal stem, however, a reversed relationship between the rootstock vigour (measured as flower productivity) and the concentration of sucrose and starch was observed. The results suggest that the carbohydrate reserves in roots are mainly affected by the rootstock via its effect on root and shoot development.

**Keywords:** Rose, rosa, rootstock, vigour, carbohydrate, Madelon<sup>®</sup>

<sup>2</sup> The stem (below a graft union) that originates from mother rootstocks.

### 3.1 Introduction

Carbohydrates are the most important forms of reserves for most woody perennials (Loescher *et al.*, 1990). The content of carbohydrate reserves depends on the organ and the time of the year. The highest content is usually found in roots by the end of a growing season (Loescher *et al.*, 1990). This is common to almost all woody perennials, especially in deciduous plants growing outdoors in northern countries. The fact that high carbohydrate reserves are associated with the adverse climate conditions in the winter has led to the hypothesis that these reserves may play an essential role in survival or stress resistance of trees (Loescher *et al.*, 1990).

The importance of stored carbohydrates for cut rose production was demonstrated by Zieslin *et al.* (1975, 1976), Van de Pol *et al.* (1986) and Kool *et al.* (1996). Physiological processes in roses grown in greenhouses proceed in many respects similar to those in woody perennials outdoors (Zieslin *et al.*, 1975). However, growing environment and particularly crop management have a great impact on the seasonal change of carbohydrate reserves. During the year-round production in greenhouses, the regular harvesting and pruning impose severe stresses on the roots and dramatically change the natural course of growth. As a consequence, the carbohydrate level, which is closely associated with plant growth, is affected. Zieslin *et al.* (1975) found that in Israel maximum starch level of normally managed greenhouse rose *Baccara* (*Rosa hybrida*) occurred in May, after which the level gradually dropped to a minimum in September-December. Thereafter, it increased again to the spring maximum. The same pattern was observed by Kool *et al.* (1997) in the Netherlands. However, spring pruning considerably reduced starch content and postpone the date of maximum accumulation from May to August (Zieslin *et al.*, 1975). Fuchs (1994) showed that starch content of *Motrea* (*Rosa hybrida*) roots fluctuated during the winter period. After a gradual decrease of starch content from November until January a rapid increase occurred, culminating in maximum values at the end of February. He also found that normal harvesting resulted in marked root mortality and stated that root mortality was inversely related to rootstock's ability to store carbohydrates. The question of interest is: assume that carbohydrate reserves are essential for survival and/or recovery during the stress period, as they supposedly are during the winter, then to what extent could the level of the carbohydrate reserves during that period be affected by rootstocks and how is this property related to rootstock vigour. In fruit trees, it was found that rootstocks differed in carbohydrate accumulation and carbohydrate utilisation (Brown *et al.*, 1985; Oliveira and Priestley, 1988). Brown *et al.* (1985) found that the effect of a particular scion on an apple tree's dry weight and carbohydrate content was not altered by different rootstocks and vice versa. The same was found by Oliveira and Priestley (1988), who concluded that carbohydrate accumulation and carbohydrate utilisation are largely determined

genetically and consequently are a characteristic of scion and rootstock. In greenhouse roses, Fuchs (1994) showed that rootstocks indeed differed significantly in carbohydrate content (but not the pattern of its changing course). However, the carbohydrate reserves in root and stem of rootstocks of very different vigour have not yet been evaluated. Especially during the stress period of shoot harvest, it would be interesting to compare it.

The objectives of this research were to investigate how rootstocks influence the carbohydrate reserve formation in roots and basal stems and how they change during the period following shoot removal in relation to rootstock vigour.

## **3.2 Materials and methods**

### **3.2.1 Experimental set-up and treatment**

Experiments started on May 22, 1996. Five rootstocks, i.e. 15—13, 18—23, 20—10, 12—06, and *Natal Briar* were grafted with *Madelon*<sup>®</sup> (*Rosa hybrida* cv. 'Ruimeva') by stenting (Van de Pol and Breukelaar, 1982). Plants were initially propagated in a mixture of peat and sand (1:1 v/v) in a propagation bench in a greenhouse at Wageningen University. In the bench, saturated humidity was maintained and the soil was heated when the temperature dropped below 22°C. After 10 days (June 3), when root primordia appeared, the plants were lifted from the propagation bench. They were cleaned with tap water and then transferred to a phytotron. The hydroponic growing system was composed of two vertically arranged water containers. Plants were grown in the upper container. Solution was pumped from the lower into the upper container and fell back to the lower container through an overflow pipe, and was thus aerated. The temperature was set at 21°C during the daytime (16 hours) and 19°C during the night. Humidity was 70%–75%. Photosynthetic active radiation supplied by fluorescent lamps (TLD 50W 84HF, Philips) was approximately 40Wm<sup>-2</sup>. The nutrient solution was standard for roses (De Kreij and Kreuzer, 1989), with pH and EC adjusted to 5.8 and 1.6 respectively. After transplanting, plants were initially kept under saturated humidity, using a transparent plastic cover and a light screen. After two weeks, the light screen was removed. In the third week, the humidity was gradually lowered. One week later, the plastic cover was removed. The plants remained under the specified climate conditions until the end of the experiment. When most primary shoots reached the marketable stage, they were all cut back to just 1 cm above the basal bud crown. The fresh shoot weight was recorded. The fresh weight of both the shoots and the roots was used as an indicator of vegetative growth and development for each rootstock. The layout of the experiment was a randomised block design. There were three culture units in total. Each culture unit served as a block with 12 plants for each rootstock combination.

### 3.2.2 Sampling

Samples were taken at 0, 2, 4, 8, 12 and 16 days after cutback of the primary shoot. For each rootstock, 6 whole roots ( $\approx 2 \times 3$  blocks) and 6 pieces of basal stem ( $\approx 2.5$  cm) below the grafting union were collected at each time. The materials were immediately immersed in liquid nitrogen, freeze-dried and weighed, and thereafter kept at  $-20^{\circ}\text{C}$  until analysis. The samples were ground just before analysis.

### 3.2.3 Carbohydrate Determination

#### *Soluble sugars*

Approximately 17 mg freeze-dried sample material (powder) was used for both soluble sugar and starch determination. Soluble sugar was extracted by 5 ml 80% ethanol with an internal standard (melezitose) in a shaking waterbath at  $80^{\circ}\text{C}$  for 20 minutes. After centrifuging (5 minutes, 8000 rpm), 1 ml of the supernatant was put in an Eppendorf tube and dried in a vacuum concentrator (SpeedVac). Thereafter, 1 ml of  $\text{H}_2\text{O}$  was added to the dried contents and kept in an ultrasonic bath for 10 minutes. After centrifuging (15 minutes, 5000 rpm) and dilution (5 times), sugar concentration in the extract was determined with a HPLC (Dionex CarboPac PA1 column, Dionex PED detector).

#### *Starch*

Starch was quantified by measuring the amount of glucose after the starch had been hydrolysed. Following the first extraction and centrifugation of the sample, the remaining supernatant was discarded (if the supernatant had already successfully been used for measuring the soluble sugars as described). The sediment was washed twice with 3 ml 80% ethanol to remove any remaining glucose and dried in the vacuum concentrator. The pellet was then added to 2 ml thermostable alpha-amylase (SERVA, 13452) solution (1 mg/ml  $\text{H}_2\text{O}$ ) and kept in a shaking waterbath at  $90^{\circ}\text{C}$  for 30 minutes. After this 1 ml amyloglucosidase (1 mg/ml citrate buffer, 50 mM pH=4.6) was added to the pellet and it was kept in a shaking waterbath at  $60^{\circ}\text{C}$  for 15 minutes. Thereafter, the sample was centrifuged (5000 rpm) for 15 minutes and glucose in the supernatant was determined. Starch content was expressed in amount of glucose per unit of dry matter ( $\mu\text{g}/\text{mg DM}$ ).

### 3.3 Results

#### 3.3.1 Vegetative growth and development

The rootstock had, as expected, a significant effect on growth of the primary shoot. Average fresh shoot weight per plant was highest on 12—06 and lowest on 18—23. A similar result was found for the average fresh root weight per plant except in *Natal Briar*, which was the lowest in this parameter (Table 3.1).

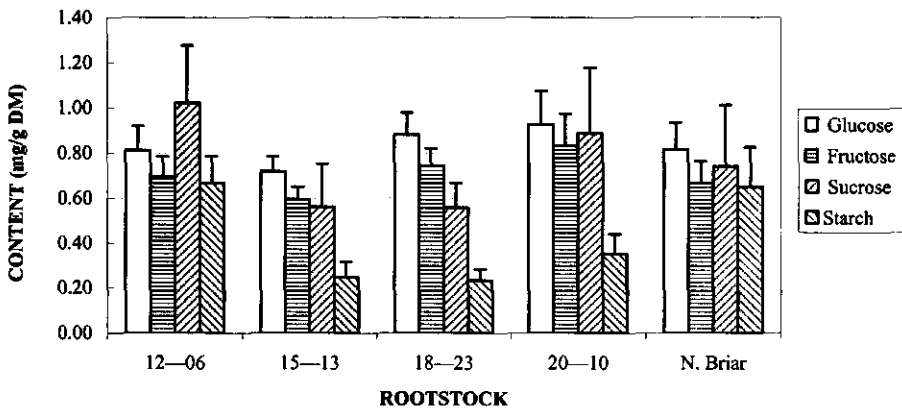
**Table 3.1** Average fresh shoot weight per plant, average fresh root weight per plant and S/R ratio as affected by the rootstocks on the moment of shoot pruning. Numbers followed by different letters in the same row are significantly different at 5% level according to Student's *t*-test.

Rootstock	12—06	15—13	18—23	20—10	N. Briar
Fresh shoot weight (g)	26.25a	17.48c	14.95c	17.35c	21.15b
Fresh root weight (g)	7.51a	4.98bc	4.61bc	5.70b	4.06c
S/R ratio	3.5	3.51	3.24	3.04	5.21

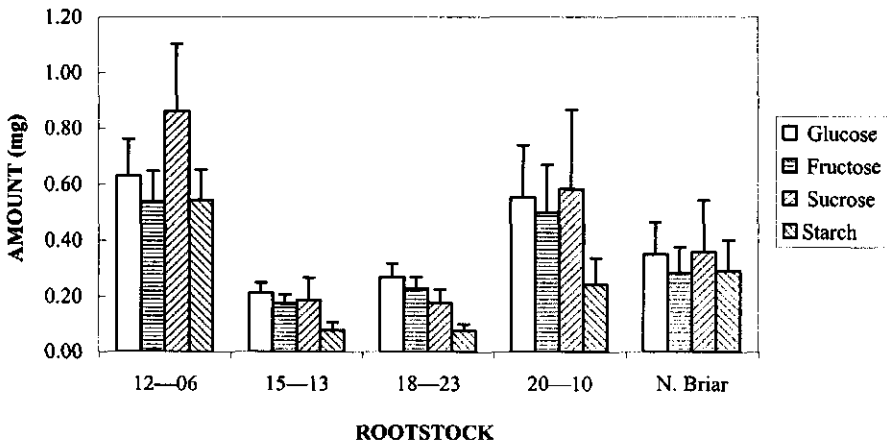
#### 3.3.2 Root carbohydrates

The content of non-structural carbohydrates in the roots was generally very low. The three most common sugars *i.e.* glucose, fructose and sucrose, were lower than 1mg/g DM in almost all the rootstocks on the moment of and after the shoot removal (Figure 3.1a, 3.1b). The content of total non-structural carbohydrates tended to be higher in the vigorous rootstocks than in the weak ones at the moment of shoot removal. However, just a few days later the differences disappeared, except in *Natal Briar* where the level seemed to be higher than in the other rootstocks (Figure 3.2a). Sucrose accounted for a major part for the variation in soluble sugar, while the contents of glucose and fructose were not significantly altered by the rootstocks.

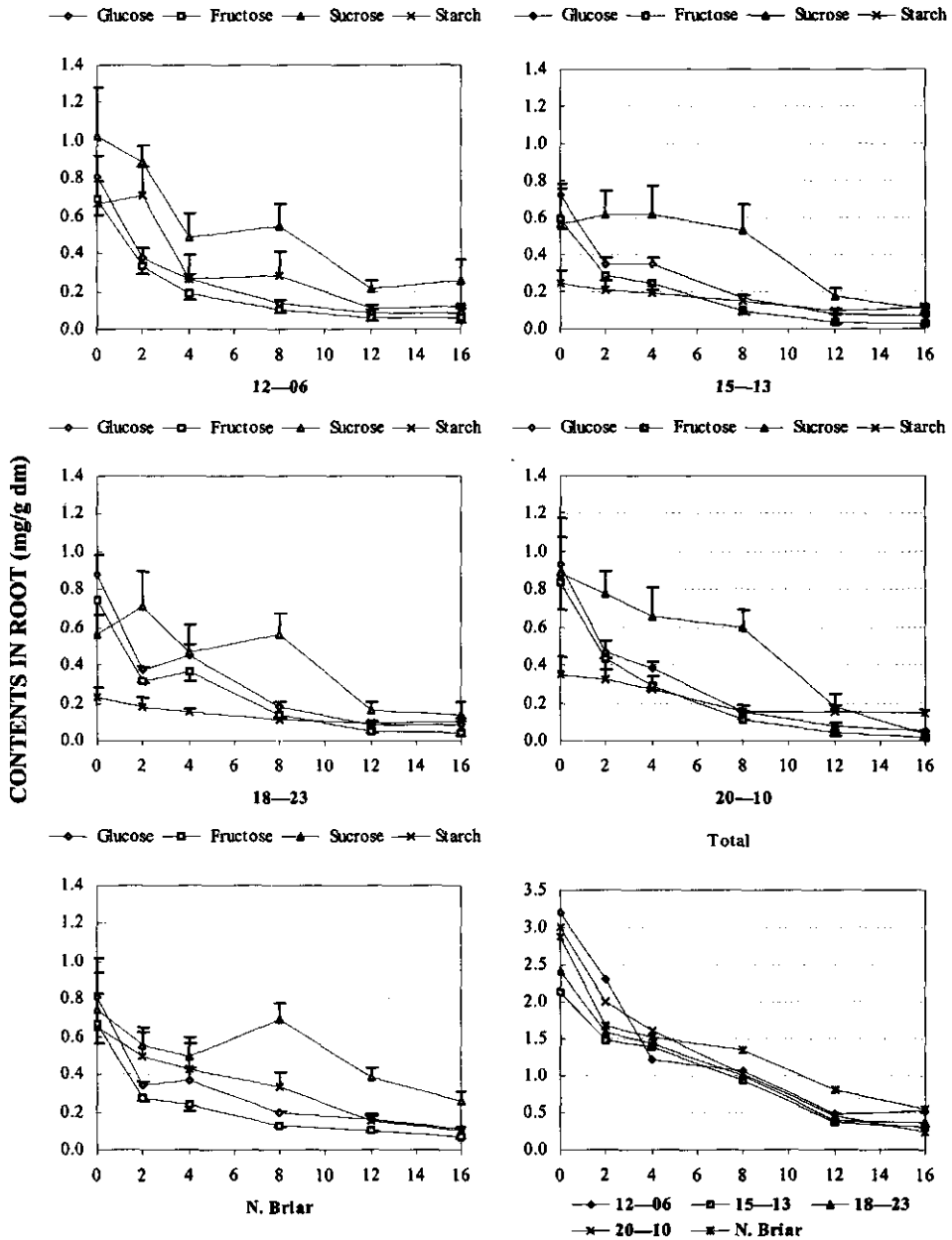
The contents of all investigated soluble sugars decreased substantially during the investigated period (Figure 3.2a, 3.2b). Within 12 days, the soluble sugars were almost depleted in most rootstocks. Glucose and fructose were depleted a few days earlier than sucrose. Both glucose and fructose dropped immediately after shoot removal. In just 2 days the concentration fell to approximately half of their original levels. Thereafter, the decrease went on at a slower pace. There was a very high correlation ( $r > 0.99$ ) between



**Figure 3.1a** The concentration of glucose, fructose, sucrose and starch in the roots on the moment of shoot pruning. Data are the mean of 6 replicates. Vertical bars indicate standard error of the means.

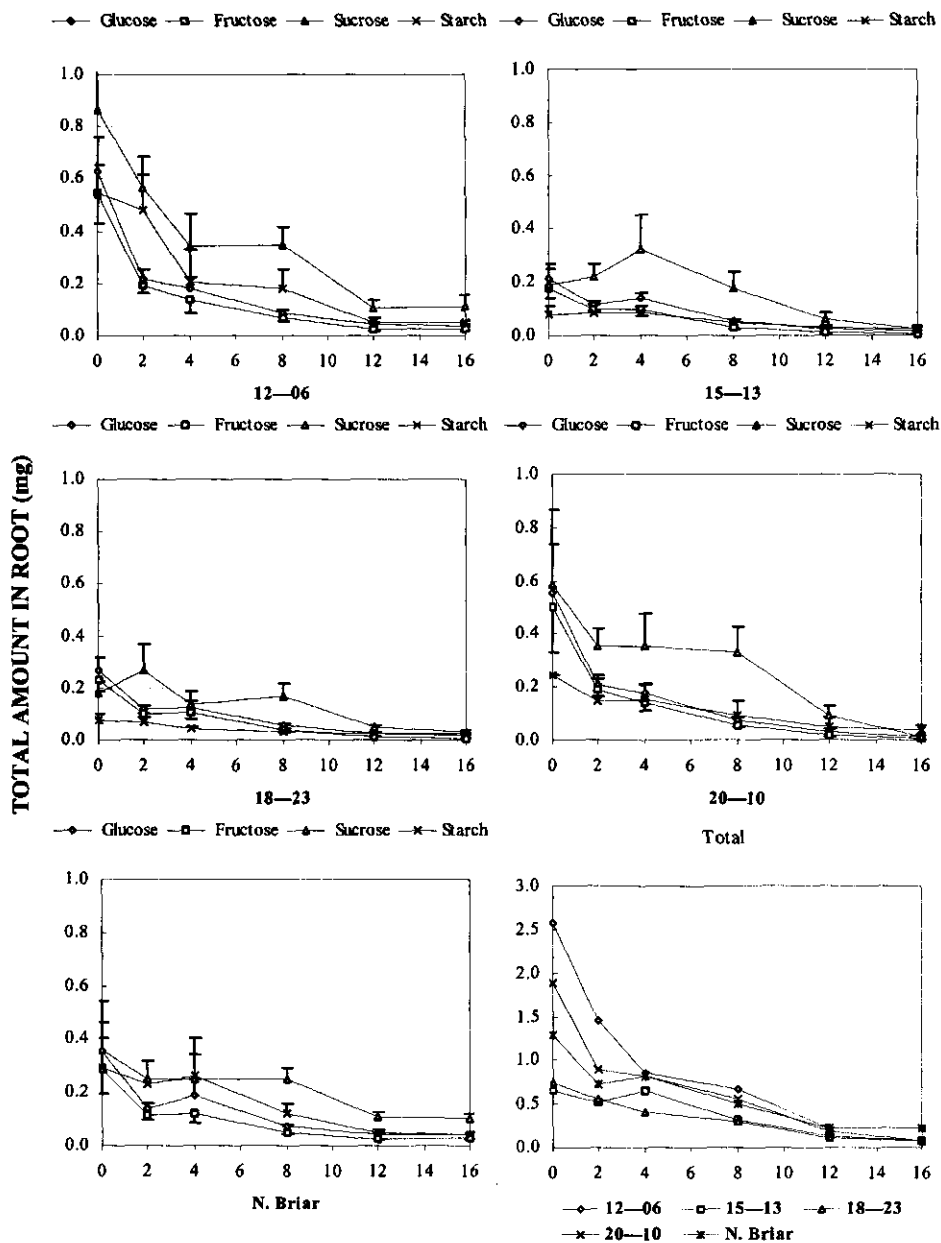


**Figure 3.1b** The total amount of glucose, fructose, sucrose and starch in the roots on the moment of shoot pruning. Data are the mean of 6 replicates. Vertical bars indicate standard error of the means.



### DAYS AFTER CUTBACK OF PRIMARY SHOOTS

**Figure 3.2a** The concentration of glucose, fructose, sucrose and starch in the roots at 0, 2, 4, 8, 12 and 16 days after shoot pruning. Data are the mean of 6 replicates. Vertical bars indicate standard error of the means when larger than symbols.



### DAYS AFTER CUTBACK OF PRIMARY SHOOTS

**Figure 3.2b** The total amount of glucose, fructose, sucrose and starch in the roots at 0, 2, 4, 8, 12 and 16 days after shoot pruning. Data are the mean of 6 replicates. Vertical bars indicate standard error of the means when larger than symbols.



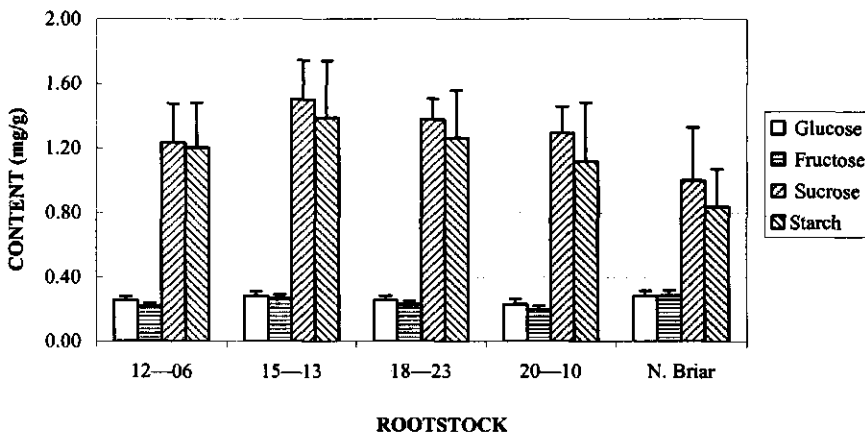
glucose and fructose in all the rootstocks. Sucrose, however, behaved differently. It remained at more or less the same level until a substantial decrease occurred at day 8 except for 12—06.

Compared to sugars, starch accumulation was more significantly affected by the rootstocks. There was hardly any starch in the roots of 15—13 and 18—23. The starch levels of *Natal Briar* and 12—06 were also low, although they were higher than those of 15—13 and 18—23 (Figure 3.1a, 3.1b).

Starch content in 20—10 seemed higher than in 15—13 and 18—23 but considerably lower than that in *Natal Briar* and 12—06. The content of starch was, however, less than sugar content most of the times.

### 3.3.3 Carbohydrates in basal stem

Glucose and fructose levels were very low in the basal stems as compared to that in the roots, but sucrose was higher. Unlike in roots, the content of sucrose in the basal stem tended to be lower in the vigorous rootstocks than in the weak ones (Figure 3.3). There is, however, a positive correlation between the content of sucrose and the plant size within each scion/rootstock combination (the correlation coefficients of shoot weight with the content of sucrose varied from 0.39 to 0.87, depending on the rootstocks).



**Figure 3.3** The concentration of glucose, fructose, sucrose and starch in the basal stem on the moment of shoot pruning. Data are the mean of 6 replicates. Vertical bars indicate standard error of the means.

The rootstock effect on starch was comparable to that of sucrose in the basal stem. The starch and the sucrose contents, in fact, were closely correlated ( $r=0.96$ ).

### 3.4 Discussion

A rootstock will affect the growth and development of a scion as soon as they combine to create a combination plant. The scion will in turn affect the growth and development of the rootstock. Therefore, the root carbohydrate reserve at the time of observation was a result of the growth and development of the whole plant during the entire period prior to that time. The accumulation of carbohydrates in roots could be affected directly by the rootstock (direct effect, which is related to the ability to store carbohydrates) or indirectly by the rootstock via its effect on shoot development (indirect effect, which is not related to the ability to store carbohydrates). Indeed, correlation analysis showed that the carbohydrate content varied with both the plant size and the rootstock. Relatively, the size effect is more significant as it shows a strong correlation with the carbohydrate contents both within and between the rootstocks. This means that different shoot growth and development could substantially change the level of root carbohydrate reserves. It was, therefore, very likely that the observed variation in carbohydrates was mainly a result of the indirect effect rather than the direct effect.

In all the rootstocks, glucose and fructose followed almost the same line of decline during the observed period. Sucrose and starch followed different lines than that of glucose and fructose, but again there were no significant differences in pattern among the rootstocks. This is probably suggesting that there were no significant differences in the carbohydrate-related physiological processes in the roots (*e.g.* root respiration) among the rootstocks. What seemed different was the original content, not the behaviour, of the carbohydrates. It is worth noting that the rootstock showed greater effects on the contents of sucrose and starch than on those of glucose and fructose. Sucrose and starch are therefore more indicative parameters of the rootstock effect than glucose and fructose. This is in agreement with the finding of Caruso *et al.*, (1997) in peach trees and also in line with the physiological functions of these carbohydrates. It is well known that sucrose is the preferential form of substance of transport of photosynthates from leaves to roots in plants (Mohr and Schopfer, 1994), while starch is the main form of substance of storage. Both of them are closely related to state of growth and development. However, sucrose reflects the carbohydrate supply on the moment of observation, while starch reflects the cumulative effect of excessive carbohydrate supply.

In agreement with the finding that dwarfing citrus (Mendel and Cohen, 1967) and apple stocks (Colby, 1935) contain more starch than vigorous ones, the weakest rootstock

(15—13) had the highest sugar and starch contents in basal stems and the lowest sugar and starch contents in roots at the same time. This means that, while the content of carbohydrate reserves in roots seemed to be positively correlated with the vigour of the plants ( $r = 0.88$ ), the correlation between the content of sugar (predominantly sucrose) and starch in the basal stem and the plant vigour appeared to be negative ( $r = -0.92$  with sugar, and  $r = -0.75$  with starch). Since the piece of basal stem above the graft union was not included in the measurement (only the piece below the graft union, *i.e.* the part that was of the rootstock origin, was used), a blocking effect by graft union, if it exists, is not involved here. This is suggesting that there existed a sort of 'barrier' in the roots of 15—13 that prevented the roots from utilising the carbohydrates from shoots. It is not known, however, whether this 'barrier' was a result of a greater mechanical resistance in the transport pathway between the basal stem and the newly formed roots that prevents sucrose from being freely transported from the basal stem to the roots, or due to a "block" in the utilisation of sugar in the rootstock, as suggested for fruit rootstocks (Messer and Lavec, 1969). Since there is little reason to assume any physical barrier in the transport pathway, a "block" in the utilisation of sugar in the rootstock seems a reasonable explanation. The low carbohydrate content in the roots was therefore at least partly related to the root property—an indication of a direct effect. This conclusion is also in line with the hypothesis that it is not the amount of carbohydrates available to the roots that limit the root growth but the ability of roots to utilise carbohydrates (Wardlaw, 1968; Lambers, 1983; Gaudillère *et al.*, 1992), as indicated by the contrast of a higher sugar content in basal stem and a lower sugar content in roots in the same rootstock.

It is worth noting that carbohydrate reserves in young and small roots are likely to be different from those in old and big roots. As a rose crop lasts for several years, the regular harvest of flower stems during such a long period would likely increase rather than decrease the difference in carbohydrate reserves among the rootstocks. It is, however, difficult to judge whether such a difference has a significant effect on the recovery of plants in terms of speed or number of budbreaks on the basis of current results. In the aboveground stem parts, Kool *et al.* (1996) found that the starch concentration increased and sugar concentration decreased from upper to lower stem parts. Total carbohydrate storage was, however, too low to argue a clear role for the possible use of carbohydrate reserves towards new growth (Kool, 1996; Kool *et al.* 1997). The chance is that the differences in carbohydrate reserves, either in roots or in stem parts, among different rootstocks are of little significance as a supply of assimilates for new growth, but they might be of great importance if they work as a signal for budbreak and/or flower initiation.

## Acknowledgement

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## Chapter 4

### Effect of the rootstock on shoot regeneration of cut rose in darkness

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Ximing Hu and Peter A. van de Pol

#### *Abstract*

Shoot regeneration in darkness after complete shoot pruning of *Rosa hybrida Madelon*<sup>®</sup> (cv. 'Ruimeva') grafted on seven rootstocks was examined with respect to the amount and 'life time' of the regenerated shoots. Two pruning treatments, i.e., pruning at the same date (time pruning) and pruning at the same stage (stage pruning), were applied. There were clear rootstock effects on both the amount of regeneration and the 'life time' of the regenerated shoots. But there was no significant correlation between these effects and the rootstock vigour. The plant size at the moment of pruning influenced new shoot regeneration due to the presence (or a higher rate) of outgrowing shoots in bigger (therefore more developed) plants. Although different pruning treatments resulted in differences in plant size at the moment of pruning, it had only a small effect on shoot regeneration.

*Keywords:* Rosa, rose, pruning, rootstock, shoot regeneration

#### 4.1 Introduction

An important aspect of cut rose cultivation is the regular harvesting of flower shoots while they are actively growing. These flowering shoots make up a major portion of total leaf area and are the main source of photosynthates (Aikin, 1974, Mor and Halevy, 1979). As a result of harvesting, the equilibrium between different parts, particularly between the aboveground and the belowground parts, of a rose bush is disturbed, and a new equilibrium needs to be established by regeneration and growth of the shoot and/or by dying off of the roots.

The number of budbreaks after shoot harvest is known to be the main reason for differences in flower productivity on various rootstocks (Chapter 2; De Vries, 1993). Rootstock productivity (vigour) is probably a complex of different characteristics. Besides cytokinin production, which is widely assumed to be responsible for differences in rootstock vigour (Dieleman, 1998), the ability to supply assimilates to the shoot after pruning and the resistance of the root system to pruning are considered to be important aspects of rootstock vigour.

The effects of shoot (foliage) pruning on root growth have been studied in a number of crops such as apple (Head, 1966, 1967; Haas and Hein, 1973, Saure, 1987), grass (Ennik, 1966; Davidson and Milthorpe, 1966; Kleinendorst and Brouwer, 1969), tea (Visser, 1969), sour cherry (Maurer, 1972) and Citrus (Eissenstat and Duncan, 1992). It is a general rule that removing part of shoots will reduce root growth and vice versa. For greenhouse roses, it was reported that removing part of or entire shoots resulted in dying of roots (Zieslin *et al*, 1976; Fuchs, 1986, 1994). Dying of roots depends not only on the severity of pruning, but also on the root genotype (Fuchs, 1994). It is hypothesised that root resistance to shoot pruning, characterised by low root mortality (especially after shoot harvesting) and fast and easy root regeneration, is a component of rootstock vigour. Under this hypothesis, shoot regeneration, which is expected to be affected by the root resistance to shoot pruning, would be positively correlated with rootstock vigour. The objective of this chapter was to examine the rootstock effect on shoot regeneration, and the correlation between the effect on shoot regeneration and rootstock productivity (vigour). In order to differentiate rootstocks of similar vigour, severe stress was imposed by complete shoot pruning followed by dark treatment to eliminate photosynthates and shoot-derived carbohydrates as well as hormones. Hence, regeneration of the shoot after cutback depended solely on the remaining stocks.

## 4.2 Materials and methods

The present research consisted of two experiments: one in a greenhouse and the other under controlled conditions. The rootstock effects on shoot regeneration, measured in terms of budbreak speed and/or (maximal) amount of regeneration after complete shoot removal, were investigated in these two experiments. A major difference between the two experiments was the pruning treatment. In the first experiment (greenhouse), all plants were pruned at the same date (for convenience, it is termed 'time pruning' or TP). In the second experiment (phytotron), plants were pruned at the same (marketable flower) stage (for convenience, it is termed 'stage pruning' or SP), which means all plants had to be treated individually.

In Experiment I, *Madelon*<sup>®</sup> (*Rosa hybrida* cv. 'Ruimeva') was propagated on February 14, 1996, either by stenting on a rootstock (Van de Pol and Breukelaar 1982) or by cutting. Seven rootstocks were used: 12-06, 15-13, 18-23, 20-10, *Helena*, *Moneyway* and *Natal Briar*. New stentlings and cuttings were firstly incubated at saturated humidity in a heated propagation bench at 21°C. After three weeks, the humidity was gradually reduced by controlling ventilation through the cover. One week later, the rooted stentlings and cuttings were transplanted in pots and moved to a bench in a greenhouse. The growing conditions in the greenhouse were maintained more or less the same as in a commercial greenhouse. On May 14, when most plants of the weakest rootstock, i.e., 15-13, had reached the flowering stage, all plants, regardless of the rootstocks and the plant size, were cutback to just 1 cm above the lowest axillary buds of the primary shoots. Bottom-breaks (basal shoots) that were longer than 1 cm were removed at the same time. The fresh weight of bottom-breaks and that of the primary shoots (including flowers) were recorded separately. The pruned plants were kept in darkness under a black screen until the end of the experiment. Regenerated shoots were collected when they had reached maximum size (indicated by changes in colour from greenish white to yellow – a symptom of wilting) and the dry weight was recorded. The layout of the experiment was a random block design (4 blocks × 5 replications).

In Experiment II, the plant materials were prepared as in Experiment I, but the potted plants were grown in a phytotron instead of in a greenhouse. The temperature was 21°C/19°C (day/night) and the relative humidity was 76%. PAR (photosynthetic active radiation) provided by a mixture of metal halide and high-pressure sodium lamps (HPI-T 400W and SON-T 400W) was about 20Wm<sup>-2</sup> at plant height at the beginning. Those plants of which the primary shoots reached the marketable flower stage were cut back to 1 cm above the lowest axillary buds of the primary shoots. The plants were then moved to a dark room with the same temperature and humidity as in the phytotron. This procedure was followed until all plants were pruned. For each individual plant, the pruning date was recorded and the growing time (from propagation until pruning) was calculated. The regenerated shoots in the dark were collected when they became yellow (wilting) like in Experiment I. Dry weight (mg) of the new shoots and the wilting date were recorded. The duration from shoot pruning until regenerated shoots (or buds) started to wilt was calculated, for convenience, it is termed 'Post-pruning Lifespan' or LS. The layout of the experiment was also a random block design. The plants were arranged in 12 blocks (12 blocks, no repetitions).

The following growing parameters of the rose plants were measured during pruning. In Experiment I, fresh weight of entire bush (thus including bottom-breaks and side shoots), fresh weight of bottom-breaks and incidence of bottom-breaks; In Experiment II, growing time, length and fresh weight of primary shoots.



## 4.3 Results

### 4.3.1 Experiment I – Time pruning

#### *State of growth and development*

There were, in general, large differences in growth and development before pruning between plants with different rootstocks. The weak (*i.e.*, less productive) rootstocks of 18–23 and 15–13 (particularly the latter) performed significantly lower in all of the three examined parameters than the vigorous (*i.e.*, more productive) rootstocks (Table 4.1). The differences among the vigorous rootstocks were small in terms of bush fresh weight but significant in the other two parameters. *Natal Briar* had both the highest amount of fresh weight of bottom-breaks and the highest incidence of bottom-breaks.

**Table 4.1** The state of growth and development as affected by the seven rootstocks before pruning. Means within the same row followed by different letters are significantly different at 5% level according to Student's *t*-test.

Rootstock	12–06	15–13	18–23	20–10	Helena	M'way	N. Briar	Madelon® *
Bush fresh weight (g)	65.1 <i>b</i>	12.9 <i>d</i>	45.3 <i>c</i>	85.1 <i>a</i>	85.9 <i>a</i>	81.7 <i>a</i>	84.6 <i>a</i>	68.7 <i>b</i>
Fresh weight of BB** (g)	13.7 <i>bc</i>	1.3 <i>d</i>	11.8 <i>bcd</i>	30.8 <i>a</i>	6.4 <i>bcd</i>	15.9 <i>b</i>	32.9 <i>a</i>	3.9 <i>cd</i>
Incidence of BB	55%	25%	55%	75%	45%	55%	90%	30%

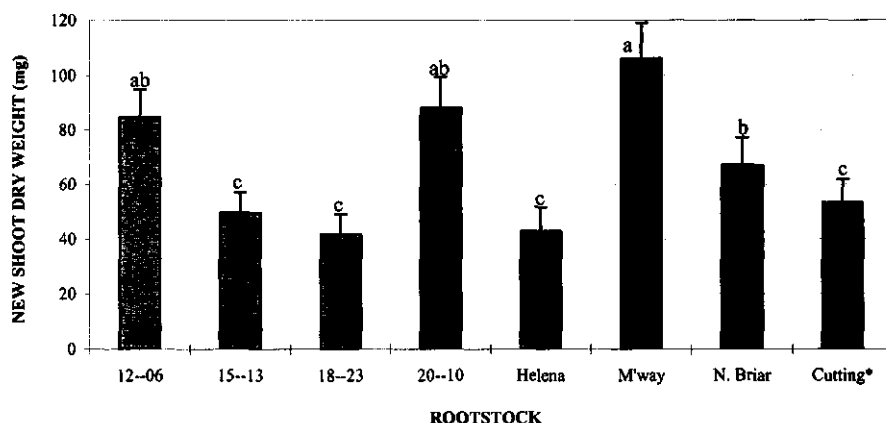
\* Madelon® on its own roots (propagated by cutting).

\*\* BB=bottom-breaks. Average based on all plants of the rootstock.

#### *Shoot regeneration in darkness*

Shoot regeneration varied significantly among the rootstocks. Regeneration with the weak rootstocks, *i.e.*, 15–13 and 18–23 was low. The vigorous rootstocks, however, gave rise to both high and low regeneration (Figure 4.1).

The differences in regeneration cannot fully been explained by different growth and development before pruning. Comparing the rootstocks of a similar bush fresh weight (*i.e.* 20–10, *Helena*, *Moneyway* and *Natal Briar*), it can be seen that the rootstocks had a direct and significant effect on shoot regeneration. The differences in development (indicated by the fresh weight of bottom-breaks and the incidence of bottom-breaks) was not closely correlated with the amount of regeneration ( $r = 0.48, 0.37$  respectively).



**Figure 4.1** Dry weight of shoots regenerated in darkness on seven rootstocks after time-pruning. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

#### 4.3.2 Experiment II – Stage pruning

##### *State of growth and development*

Except for 15-13, there were almost no significant differences before pruning between the rootstocks with respect to both the length and the fresh weight of primary shoot (Table 4.2). 15-13 gave rise to significantly lighter primary shoots than the other rootstocks, although the growing time of it was not. The shoot length on 15-13 was also generally shorter than those on the other rootstocks except for Moneyway.

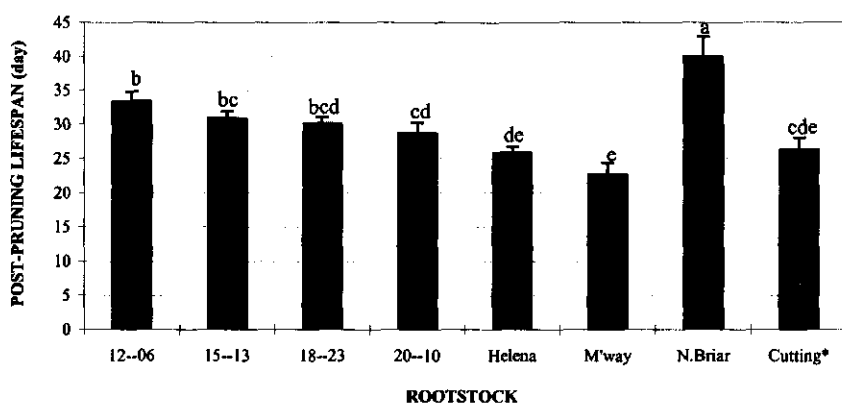
**Table 4.2** The state of growth and development as affected by the seven rootstocks before pruning. Means within the same row followed by different letters are significantly different at 5% level according to Student's *t*-test.

Rootstock	12-06	15-13	18-23	20-10	Helena	M'way	N. Briar	Madelon® *
Fresh shoot weight (g)	31.4 a	26.7 b	34.3 a	34.5 a	31.9 a	31.3 a	32.3 a	32.7 a
Shoot length (cm)	65.9 ab	62.1 b	69.9 a	69.7 a	65.3 ab	60.4 b	68.5 a	65.7 ab
Growing time (days)	71.0 c	73.5 abc	75.0 a	73.6 abc	73.1 abc	70.7 c	71.2 bc	74.7 ab

\* Madelon® on its own roots (propagated by cutting).

*Shoot regeneration in darkness*

There were significant differences between the rootstocks with respect to the post-pruning lifespan (LS) of the regenerated shoots (or buds) in darkness (Figure 4.2). The average LS varied from 23 days (*Moneyway*) to up to 40 days (*Natal Briar*). It is obvious that this parameter did not give a good indication of the productivity (vigour) of the rootstocks since *Moneyway* and *Natal Briar* are considered to be on the same level of productivity (vigour).



**Figure 4.2** Post-pruning lifespan (LS) of shoots regenerated in darkness on seven rootstocks after primary shoots were cut back at the flowering stage (stage-pruning). Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

Like in Experiment I, shoot regeneration varied significantly among the rootstocks and the less productive rootstocks (*i.e.*, 15-13 and 18-23) generally generated shoots with less dry weight than the more productive rootstocks like 12-06 and 20-10, but not all the productive rootstocks gave rise to high regeneration, such as *e.g.* *Helena* (Figure 4.3). Also in this experiment, this parameter was not closely correlated with the productivity (vigour) of the rootstocks ( $r = 0.49$ ).

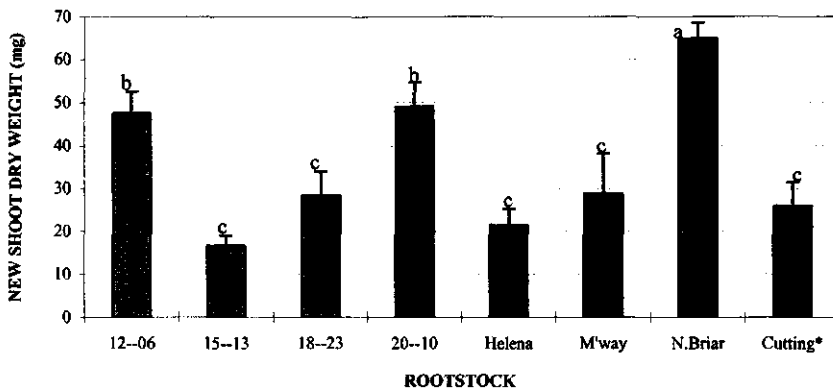


Figure 4.3 Dry weight of shoots regenerated in darkness on seven rootstocks after stage-pruning. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

#### 4.4 Discussion

The rootstock effect on the shoot regeneration after cutting was composed of a primary effect (genotype effect) and a secondary effect (size effect). The magnitude of the secondary effect depended on the type of pruning treatment. Obviously, when all plants were pruned at the same time (TP), the secondary effect should be much more significant than when all plants were pruned at the same development stage (SP). However, as indicated by the similarities of the results in the two experiments, the huge difference in plant size as well as in development stage between the rootstocks in Experiment I did not lead to a dominating size effect on shoot regeneration, as indicated by the similarity of shoot regeneration in the two experiments. There was no significant correlation between the bush fresh weight and the dry weight of regenerated shoots within the rootstocks (correlation coefficients vary from -0.20 to 0.13), indicating that the size effect was either insignificant or counteracted by other effects. It is noticed that in Experiment I, the variation of plant size was much smaller within the rootstocks than between rootstocks. The fact that the size effect was insignificant within the rootstocks does not necessarily mean that the size effect was insignificant between the rootstocks. The differences within and especially between the rootstocks were not only in size but also in stage of development. The analysis of the correlation between the shoot regeneration (dry weight) and the growing parameters revealed that the within-rootstock variation in regeneration was highly and negatively correlated with both the fresh weight

and the incidence (%) of the bottom-breaks, which were removed together with the primary shoots (data not shown). The differences in growth and development before pruning resulted in a complex effect on shoot regeneration.

Three aspects that are important to the regeneration in darkness could be affected by the presence of bottom-breaks before pruning: Firstly, bottom-breaks originate from the most developed axillary buds at the bottom of the primary shoots (*i.e.*, basal buds). If they break out before pruning, they are removed. Otherwise, they break out after pruning and become the regenerated shoots; Secondly, growth of bottom-breaks results in new and strong apical dominance which enhances the correlative inhibition of the rest of the buds; Thirdly, carbohydrate reserves, the only source for regeneration after shoot pruning, are likely reduced due to the break-out and growth of bottom breaks and side shoots and therefore less reserves are left in the roots or stems. In Experiment I, the incidence of bottom-breaks varied from 90% (*Natal Briar*) to 20% (15—13). The more advanced the growth and development, the more basal buds as well as other axillary buds, broke out into new shoots. As a consequence, the effect of advanced vegetative growth (size effect) was partly or totally overruled by the break of bottom-breaks and side shoots (stage effect). This is probably why the relative effect of *Natal Briar* and that of *Moneyway* were inconsistent between the two experiments. In Chapter 3, we found *Natal Briar* has high root carbohydrate reserves. Its exceptionally high regeneration and long LS that were found in Experiment II are possibly a result of high root carbohydrate reserves. It should also be noted that the temperature under the cover screen in Experiment I was neither controlled nor checked. The likely high temperature might have an impact on the shoot regeneration and thereby affect the results.

In none of the experiments, the amount of shoot regeneration in darkness was closely correlated with the productivity (vigour) of the rootstocks (both less than 0.5). This does not necessarily mean, however, that it is unimportant because, firstly, the dark assessment is probably not a good estimate of the pruning resistance of the rootstocks and, secondly, the behaviour of these young (few-month-old) plants may be different from that of older ones (many months to many years). For the first reason, the regeneration in darkness is totally dependent on the reserves and, therefore, it reflects only the amount of reserves that have been translocated to and used in the shoot regeneration. It is not clear whether the regeneration in darkness is a good estimate of the regenerating ability in light. Recovery of plants after shoot removal depends not only on the reserves, but also on the speed of regeneration. For the same amount of regeneration, the speed of regeneration may make a significant difference in the rootstock's ability to stand and recover from severe pruning when plants are exposed to light since fast regeneration results in an early establishment of new source of carbohydrates. In this experiment, it was noticed that the buds on rootstock 15—13

remained 'dormant' (visual judgement) for a long time after the shoot was pruned. As a result, the post-pruning lifespan (LS) was considerably prolonged. By contrast, buds on *Moneyway* were easy to break out. It took less time for *Moneyway* to generate more dry weight in darkness than 15—13, 18—23, *Helena* and *Madelon*<sup>®</sup>. The amount of regeneration should therefore be considered in relation to the speed of regeneration. For the second reason, the results may not be applicable to older plants. In young plants like in the experiments, there are hardly any suberized thick roots and the carbohydrate reserves in the white roots are very limited (Chapter 3). Rose crops usually last for several years and the primary shoots are never cut. Because of the big difference in starch content between the rootstocks, the difference in total carbohydrate reserves and hence the pruning resistance between the rootstocks are expected to be greater in older plants than in young plants.

It is unexpected that the primary shoots on 18—23 were longer as well as heavier compared to those on the other rootstocks except for 20—10 (Table 4.2). It is probably due to the fact that 18—23 enjoyed longer growing time than the other rootstocks and that the late pruned plants enjoyed more growing space as a result of diminishing number of plants that were left in the phytotron. It is also worth noting that primary shoots develop from the buds that are originally grown on mother plants and therefore the bud stage of the primary shoot has not been affected by the rootstocks.

## Acknowledgement

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## Chapter 5

### **The effect of rootstock on photosynthesis, dark respiration and root respiration of greenhouse rose 'First Red®'**

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Ximing Hu and Peter A. Van de Pol

#### ***Abstract***

The photosynthesis and the shoot and root respiration of 'First Red®' (cv. 'Pekcoujenny') grafted on six rootstocks were examined and compared. The rootstocks affected the capacity of photoassimilation predominantly by their effect on leaf area (*i.e.* size effect). The same was true for root and shoot respiration. The size effect accounted for most of the variation in photosynthesis and in respiration of the plants both between and within the rootstocks. When the size effect was eliminated, neither the rate of photosynthesis nor that of respiration could consistently distinguish the weak rootstocks from the vigorous ones. However, the rootstocks did show significant effects on these parameters but these effects were not in close correlation with the rootstock vigour. The significance of the results was discussed on the background of possible disturbing factors in the experiment.

**Keywords:** Photosynthesis, respiration, CO<sub>2</sub>, rootstock, rose, rosa

#### **5.1 Introduction**

Photosynthesis and respiration are the two most important, opposite physiological processes in plants. Plant growth is dependent upon the balance between carbon gain during photosynthesis and carbon loss through respiration (McCree, 1986; Dutton *et al.*, 1988). The effects of rootstocks, which modify growth and development, must be therefore reflected directly or indirectly in the photosynthesis and/or the respiration of the plants that are grown on the rootstocks.



The effects of rootstock on photosynthesis were indeed reported in a number of fruit crops such as mandarin (Morinaga and Ikeda, 1990), grapefruit (Van der Walt and Davie, 1995), cherry (Perez, *et al.*, 1997), grape (During, 1994; Koblet, *et al.*, 1997; Iacono, *et al.*, 1998), peach (Almaliotis, *et al.*, 1997; Cappellini and Antonelli, 1997) and apple (Schechter, *et al.*, 1991; Sharma and Chauhan, 1992). The rootstock effects on respiration, though less investigated, were also reported. Werner and Young (1982) found significant effects of rootstock on stem tissue respiration in peach, while Wutscher, *et al.* (1993) showed significant differences in respiration of various citrus rootstocks. For greenhouse roses, the rootstock effects on photosynthesis and respiration, particularly root respiration, have hardly been investigated. Traditionally, flower production has been thought to be proportional to the size of the root system. This premise, however, essentially ignores the tremendous investment of photoassimilate energy by plants for the production and maintenance of an extensive root system. In most crops, between one-quarter and two-thirds of all the photosynthates produced per day are respired in the same period, and root respiration accounts for a major portion of this respiration (Poorter *et al.*, 1990; Van der Werf *et al.*, 1994). A major part of the energy derived from respiration is used for growth and maintenance processes and, in roots, also for uptake and transport of ions (Veen, 1981). Hence, the question arises whether a weak rootstock is less efficient with respect to root respiration. In grasses it was found, however, that the rate of root respiration of fast-growing species, when grown at a high nitrogen supply, is generally higher than that of the slow-growing ones (Van der Werf, 1996). This result, although it appears contrary to the intuition, suggests nevertheless that there might be a connection between the rate of root respiration and the vigour of a rootstock.

The aim of the present experiments in this chapter is to investigate the rootstock effect on photosynthesis and respiration, particularly root respiration, and their relationship with rootstock vigour.

## 5.2 Materials and methods

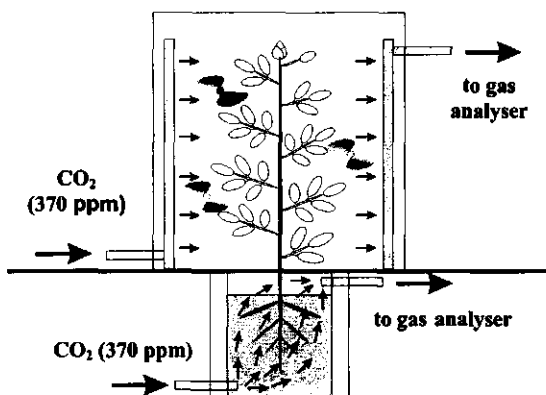
### 5.2.1 Material preparation

Experiments started on August 3, 1996. *First Red*<sup>®</sup> (cv. 'Pekcoujenny') was stented (Van de Pol and Breukelaar, 1982) on six rootstocks, *i.e.* *Moneyway*, *Natal Briar*, 12—06, 15—13, 18—23 and 20—10. Stentlings were initially propagated in a mixture of peat and sand (1:1 v/v) in a propagation bench in a compartment of a multispans Venlo-type greenhouse at Wageningen University. In the propagation benches, humidity was saturated and soil temperature was set at 22°C. After 10 days (August 13), when root primordia appeared, the plants were lifted from the propagation benches, washed with

tap water and then transferred to a hydroculture system in a climate room (phytotron). The hydroculture system was composed of two vertically arranged water containers. Plants were grown in the upper container. Solution was pumped from the lower into the upper container and fell back to the lower one through an overflow pipe, and was thus aerated. Temperature set point was 21/19°C (day/night). Humidity was 70%-75%. Light intensity (PAR) at plant level was approximately 40W/m<sup>2</sup> supplied by fluorescent lamps (TLD 50W 84HF, Philips). The nutrient solution used was standard for roses (Kreij and Kreuzer, 1989). The pH and EC were adjusted to approximately 5.8 and 1.6 respectively. After transferring to hydroculture, plants were kept under saturated humidity by using a transparent plastic cover and a light screen. After two weeks, the light screen was removed. In the third week, humidity of the air was gradually lowered down through controlling the ventilation. One week later, the plastic cover was removed. Plants remained under the specified climate conditions until the end of the experiment. Each rootstock was assayed in six replications.

### 5.2.2 Photoassimilation and respiration determination

Measurements were carried out during September 11–16, 1996 (39–44 days after stenting). Grafted plants were transferred from the phytotron to a measurement room where the temperature was set at 20°C. There were four measurement units in the room. Therefore, four plants could be measured at the same time. The sequence of the measurements was arranged in such a way that the rootstocks were allocated in 'time' blocks to minimise the time effects. To counteract possible systematic error of the measuring units, the plants were assigned on a random basis.



**Figure 5.1** A schematic drawing of a measurement unit.

A measurement unit consisted of an upper glass chamber for the shoot and an under cuvette for the root system (Figure 5.1). The root cuvette was filled with a fresh culture solution, which had the same composition as used for cultivation. There was a hole between the upper chamber and the root cuvette. The plant was held in that hole with a cloth peg. Both the upper chamber and the under cuvette were connected through two air pipes with a measuring system: one for

incoming air (bottom); one for outgoing air (top). CO<sub>2</sub> exchange was measured in a gas analyser. In each chamber, mini-fans ensured sufficient mix of air. The flow speed of incoming air was set at approx. 0.213 l/s to the chamber and 0.089 l/s to the cuvette. CO<sub>2</sub> concentration in the incoming air was 370ppm. The CO<sub>2</sub> concentration in the outgoing air was determined through an infrared gas analyser that connected to the outgoing pipe. The chamber and the cuvette were sealed from each other during the measurement. The air temperature in the chambers was approx. 19.3°C. The light intensity in the measurement room was approximately the same as in the phytotron.

Root respiration rate ( $R_r$ ) was determined on basis of CO<sub>2</sub> efflux from root during the light period. Net photoassimilation rate ( $P_n$ ) was determined on the basis of CO<sub>2</sub> consumption by shoot during the light period. Dark shoot respiration rate ( $R_d$ ) was determined on basis of CO<sub>2</sub> efflux from shoot after the light was switched off for about 10 minutes.

Leaf area, leaf fresh weight and shoot fresh weight were recorded at the end of the experiment. Root dry weight was also recorded after drying at 70°C for 24 hours.

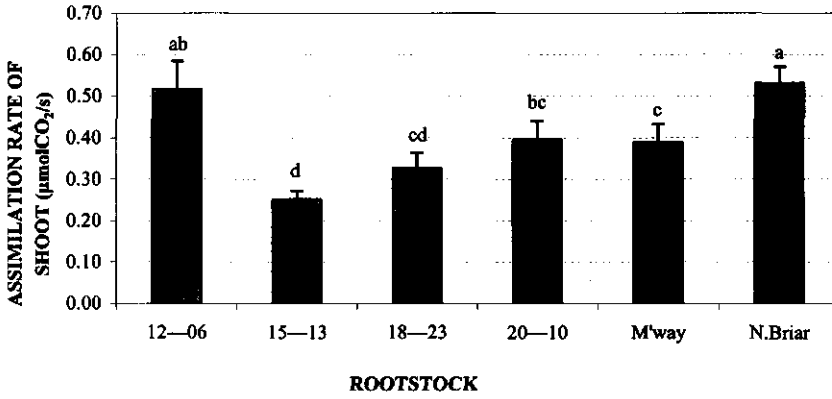
## 5.3 Results

### 5.3.1 Growth and development

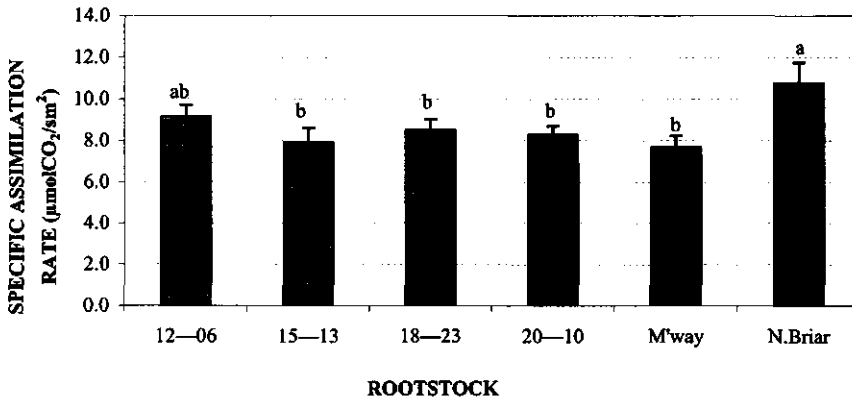
There was no significant difference among the four vigorous rootstocks with respect to the growing parameters under investigation (Table 5.1). The two weak rootstocks were, as expected, significantly different from the vigorous ones. *15—13* was significantly lower in all parameters than the other rootstocks except for *18—23*. *18—23* was significantly lower in all parameters than *12—06* and *Natal Briar*. It was also lower than *20—10* and *Moneyway*, but not all the differences reached statistical significance.

**Table 5.1** Growth parameters on the moment of measuring photosynthesis and respiration as affected by the six rootstocks. Values followed by different letters on the same row differ significantly at the 5% level according to Student's *t*-test.

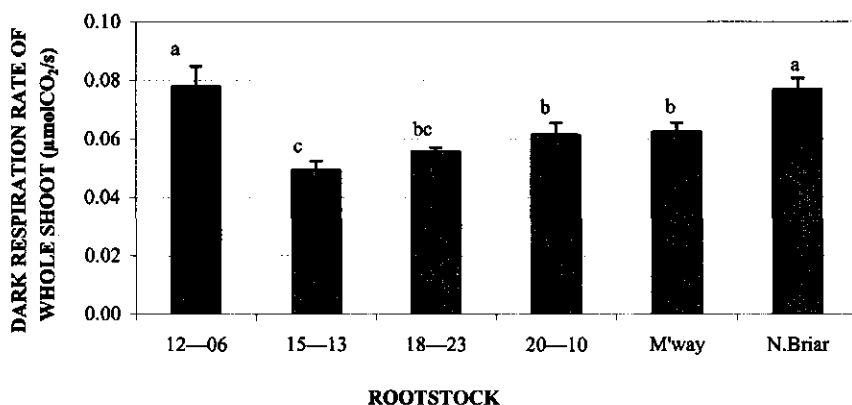
Rootstock	12—06	15—13	18—23	20—10	M'way	N. Briar
Root dry weight (g)	0.288 <i>a</i>	0.120 <i>c</i>	0.176 <i>bc</i>	0.281 <i>a</i>	0.250 <i>ab</i>	0.280 <i>a</i>
Leaf area (cm <sup>2</sup> )	554 <i>a</i>	324 <i>c</i>	380 <i>bc</i>	477 <i>ab</i>	503 <i>a</i>	505 <i>a</i>
Shoot fresh weight (g)	13.1 <i>a</i>	7.9 <i>b</i>	8.9 <i>b</i>	11.3 <i>a</i>	11.4 <i>a</i>	11.9 <i>a</i>
Shoot length (cm)	43.0 <i>a</i>	33.7 <i>c</i>	35.3 <i>bc</i>	42.0 <i>a</i>	41.0 <i>ab</i>	41.8 <i>a</i>



**Figure 5.2** Assimilation rate of the primary shoot on different rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.



**Figure 5.3** Specific assimilation rate on the basis of per  $\text{m}^2$  of leaf area as affected by the rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.



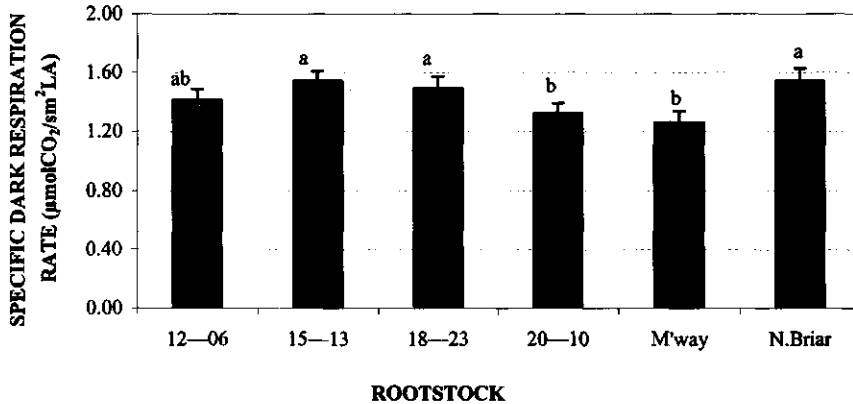
**Figure 5.4** Dark respiration rate of the primary shoot on different rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

### 5.3.2 Photoassimilation

There were large differences, as expected, in the photoassimilation rate ( $P_n$ ) among the rootstocks (Figure 5.2). However, there were no significant differences in the leaf-area-specific photoassimilation rate ( $P_{ns}$ ) (i.e., the photoassimilation rate per unit leaf area) among the rootstocks except for *Natal Briar*, suggesting that the variation in  $P_n$  can be primarily attributed to the variation in leaf area. *Natal Briar* seemed to have a significant higher  $P_{ns}$  than most of the other rootstocks. There was, however, no clear difference between the weak and the vigorous rootstocks regarding this parameter (Figure 5.3).

### 5.3.3 Shoot dark respiration

The rootstock effect on dark respiration rate of the primary shoot ( $R_d$ ) showed a similar pattern as the assimilation rate ( $P_n$ ) (Figure 5.4). Again, the difference in size accounted for most of the variation in the parameter. However, the specific rate of dark respiration ( $R_{ds}$ ) showed a different pattern than that of the specific assimilation rate ( $P_{ns}$ ) (Figure 5.5). The weak rootstocks (i.e., 15-13 and 18-23) appeared to have a slightly higher  $R_{ds}$  than most of the vigorous rootstocks except for *Natal Briar*, suggesting the rootstock effects on these two parameters were not parallel in the rootstocks.

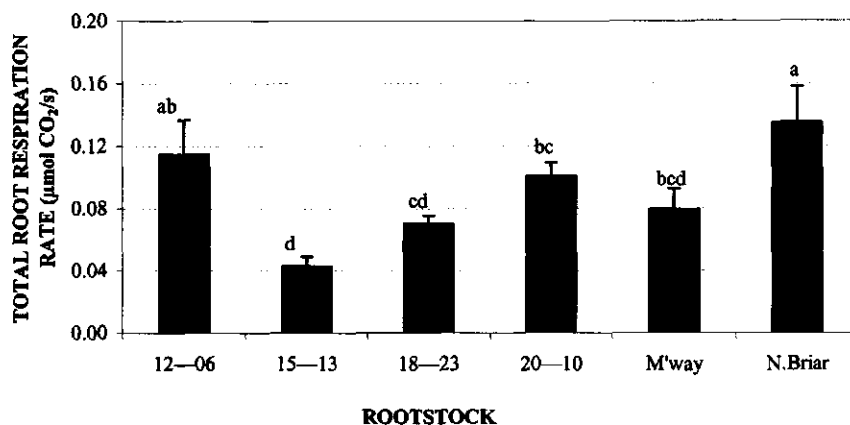


**Figure 5.5** Specific dark respiration rate of the shoot on the basis of per m<sup>2</sup> of leaf area as affected by the rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

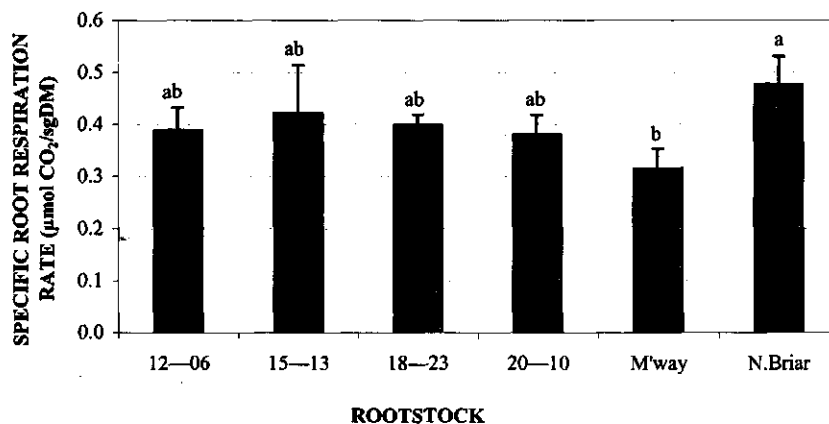
#### 5.3.4 Root respiration

There were significant differences among the rootstocks with respect to the respiration rate of the root system ( $R_r$ ) (Figure 5.6). Like in shoot, the size effect accounted for most of the variation in this parameter. There were little differences in the specific respiration rate based on root dry weight ( $R_{rs}$ ) (Figure 5.7). Significant difference was found only between *Moneyway* and *Natal Briar* (both of them were previously shown to be at the same level of vigour), suggesting that there was no correlation between the rootstock vigour and  $R_{rs}$ .

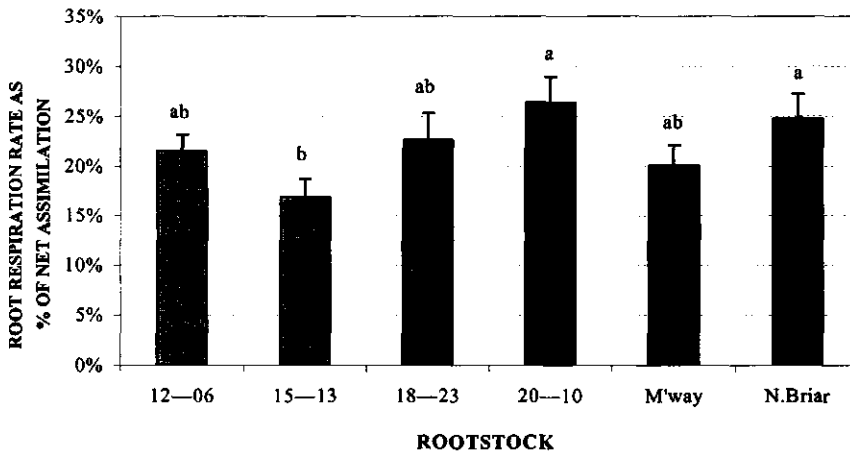
The root respiration as percentage of net assimilation varied dramatically within as well as between the rootstocks. A great part of this variation could be attributed for the variation in S/R ratio. On average, about 22% of the net gain of CO<sub>2</sub> in photosynthesis was consumed in the same time in the root respiration. Again, there was no clear difference between the weak and the vigorous rootstocks in this parameter. Although 15-13 was significantly lower than 20-10 and *Natal Briar*, the differences with other rootstocks did not reach statistical significance (Figure 5.8).



**Figure 5.6** Respiration rate of different root systems. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.



**Figure 5.7** Specific root respiration rate on the basis of per gram of dry root weight as affected by the rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.



**Figure 5.8** Root respiration rate as % of net photoassimilation on different rootstocks. Vertical bars indicate standard error of the mean. Bars with different letters are significantly different at 5% level according to Student's *t*-test.

## 5.4 Discussion

The net photoassimilation rate of a plant ( $P_n$ ) can be factored into the photoassimilation rate per unit leaf area and the total leaf area of the plant. The results of the study suggested that the rootstocks affected the capacity of photoassimilation predominantly by their effect on leaf area (*i.e.* size effect). The variation in the net photoassimilation rate ( $P_n$ ) could be almost fully accounted for by the variation in the leaf area. This was also the case with the rootstock effect on the respiration of the root system. In fact, when the size effect was eliminated, none of the examined parameters could consistently distinguish the weak rootstocks from the vigorous ones. Thus, the differences between the weak and the vigorous rootstocks represented only a casual relationship. Nevertheless, the results indicated that the rootstocks could affect the process of photoassimilation, but not necessarily corresponding to their vigour. *Natal Briar*, for instance, had a significant higher photoassimilation rate per unit leaf area than the other rootstocks except for 12-06, although this effect contributed little to the variation in the net photoassimilation rate ( $P_n$ ) when compared with the leaf area. There was also some difference in the dark respiration rate per unit leaf area between the rootstocks. However, the relatively high rate found in the weak rootstocks could be a result of size effect since their leaves were less expanded and the specific respiration rate generally



decreases as leaf ages (Azcon-Bieto *et al.*, 1983; Amthor and Cumming, 1988; Amthor, 1989). Moreover, the variation in the dark respiration had also a small effect on the variation of the photoassimilation since the first parameter was only a small fraction of the latter.

The smaller (total) leaf area of the weak rootstocks was primarily a result of delayed growth and development of the primary shoot and this delay was caused mainly by a late breakout of the axillary bud, rather than a low growth rate of the shoot. This effect was essentially equivalent to a difference in the time of propagation for the same rootstock. Since it is the number of shoots that accounts for most of the difference of leaf area between and within various rootstocks except for the primary shoot stage, the observed differences in this study, therefore, could not directly explain the rootstock effect on flower production of an entire producing period. An important point is that the number of shoots is related to the number of budbreaks, which might be affected by the level of carbohydrate supply.

Assuming the same assimilation rate in shoots ( $P_n$ ), differences in growth could only be caused by different partitioning of assimilates to roots. This portioning of assimilates would either be added up to root dry matter or be respired there. The differences in specific respiration rate ( $R_{rs}$ ) were, however, not significant between the rootstocks. Moreover, the cause of these small differences could be the same as for dark respiration rate, *i.e.*, the size effect. As can be drawn from Figure 5.4 and Figure 5.6, the specific root respiration rate ( $R_{rs}$ ) was, in relative terms between the rootstocks, quite similar to the specific dark respiration rate ( $R_{ds}$ ). There was a close correlation between the two parameters ( $r=0.88$ ), suggesting that both shoot and root respiration were to certain extent controlled by the same factor(s) and that the difference was probably an indirect effect of rootstock (*i.e.* not an inherent character of the genotype). Since root activity is ultimately dependent on the supply of substrate from the shoot, root respiration may be, as suggested by Hatrick and Bowling (1973), closely linked with the rate of translation of carbon substrate to the root. Many experiments showed that the respiration rate was indeed positively correlated with the level of carbon substrate by crop plants under many conditions (Breeze and Elston 1978; Penning de Vries *et al.*, 1979; Coggeshall and Hodge, 1980; Moser *et al.*, 1982; Hrubec *et al.*, 1985; Baysdorfer *et al.*, 1987). It was also reported that the dependence of root respiration rate on recent and current  $CO_2$  assimilation by the shoot is sometimes strong as with leaves, and whole plants (Amthor, 1989). In previous experiment, we found that the concentration of root soluble sugars in the weak rootstocks were only slightly lower than in the vigorous rootstocks. Since only one scion cultivar was involved and the specific assimilation rates were similar between the rootstocks (except for *Natal Briar*), the similar specific root respiration rate found in this experiment suggests that there was no inherent difference in this parameter between

the weak and the vigorous rootstocks. As to *Natal Briar*, the significant higher respiration rate could be explained by the high assimilation rate, rather than an inherent high respiration rate.

The last and perhaps the most important leverage for root respiration is the S/R ratio. Lambers (1979) stated that, in regulation of plant growth, the growth rate itself and the shoot/root ratio might be more important than the regulation of efficiency of energy metabolism. Fuchs (1994) found that rootstocks have a significant effect on S/R ratio of rose plants grown in hydroponics. At comparable development stage, S/R ratio may be more important than the specific respiration rate with respect to the contribution to the variation in total root respiration rate. In the current experiment, root respiration as percentage of net assimilation appeared to be lower in 15—13 due to a higher S/R ratio. This is, however, not necessarily also the case in late developmental stage and especially in production stage as we found in our preliminary experiments that S/R ratio decreases more sharply in the weak rootstocks than in the vigorous rootstocks during the primary shoot stage. Although a high efficiency (*i.e.*, a low root respiration as percentage of net assimilation) does not necessarily imply a high growth rate, we cannot rule out the possibility that the variation of root respiration is a component of rootstock vigour.

Unlike in a greenhouse where different plants are exposed to the same air conditions, the air conditions in a measuring chamber depend on the plant in that chamber because of small air volume and therefore low buffer. A higher assimilation rate ( $P_n$ ) would lead to a lower CO<sub>2</sub> concentration in the chamber, while a lower assimilation rate ( $P_n$ ) would lead to a relatively higher CO<sub>2</sub> concentration in the chamber. This effect could result in a negative feedback and the differences in the assimilation rate ( $P_n$ ) between the plants could therefore be reduced. Similarly, the air humidity in a chamber could also be affected by the plant in that chamber because of different transpiration, and the differences in air humidity and transpiration would affect the assimilation of the plants. In this experiment the flow speed was set at 0.213 l/s. At this rate the CO<sub>2</sub> concentration in the measuring chambers was within the range from 315ppm to 345ppm, depending on the plant size. The above-mentioned disturbing factors, however, probably did not play a significant role in the experiment.

## **Acknowledgement**

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## Chapter 6

### Water status of greenhouse roses as affected by rootstocks

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Ximing Hu and Peter. A. van de Pol

#### *Abstract*

The water content and the water potential (general termed as 'water status') of flower shoots of *Rosa hybrida Frisco*<sup>®</sup> (cv. 'Korflapei') and *First Red*<sup>®</sup> (cv. 'Pekcoujenny') grown on seven rootstocks were examined. It was found that shoot water content and leaf water potential were significantly affected by the rootstock on rockwool under greenhouse conditions and in hydroculture in controlled environment (phytotron). Flower shoots on vigorous rootstocks had a higher water content and a higher water potential than those on weak rootstocks irrespective of the variety of the scion. The rootstock effect was consistent in different parts of shoots (*i.e.* stems, leaves and flowers), indicating that it was not a result of alteration of the composition of the shoots. The scion variety did affect shoot water content, but had no significant effect on water potential. The water conductivity of the root system was significantly different among the rootstocks. The water conductivity of the graft-union, though significantly different across the scion-rootstock combinations, seemed not a major constraint for water transport and, therefore, was not responsible for the difference in the leaf water status. The results were compared with and discussed against the background of important horticultural characteristics of the rootstocks. The high correlation between the rootstock effect on the water status of shoots and the rootstock effects on flower productivity and quality suggests that rootstocks affect growth and development, at least partly, via the water supply.

*Keywords:* Rose, rosa, rootstock, vigour, water content, water potential, water stress

#### 6.1 Introduction

It has repeatedly been shown that the water supply in dwarfing fruit rootstocks is

reduced compared with that of invigorating ones (Syvertsen, 1981; Olien and Lakso, 1984, Ranney *et al.*, 1991, Glenn and Scorza, 1992). However, the topic hasn't been dealt with in relation to rootstocks for greenhouse roses. There are various reasons for the lack of attention from researchers for a similar effect in rootstocks for cut roses. One of those is perhaps the misconception that the water supply in modern greenhouses is only a question of the irrigation system rather than the roots. In The Netherlands, all cut roses are nowadays grown in greenhouses. The water supply to roots is guaranteed, especially on artificial substrates. Access to water is obviously not a problem for any rootstock. Root distribution, an important character that closely relates to the water absorbing potential for rootstocks in (dry) soil, will probably not affect the water uptake in artificial substrates where the scheme of irrigation is usually well-formulated and guaranteed with modern equipment. It seemed, therefore, that the water supply was no longer a problem of significance for rose rootstocks. However, there are strong indications that suggest the contrary. Firstly, information from the literature of fruit rootstocks indicates that the most likely components of root resistance to be involved are water absorption at the root surface and radii and number of xylem vessels for water transport (Olien and Lakso, 1984). These intrinsic rootstock characters are not likely to change significantly in different growing systems. If they do, it may increase rather than decrease the difference. Thus, ample water supply to roots is not a guarantee for ample water supply to shoots. Secondly, it has been observed that transpiration of rose grown on rockwool in greenhouses was affected by rootstocks (Agbaria *et al.*, 1995). Whatever is the underlying mechanism, it means the water balance could be affected by rootstocks. Thirdly, it was found that dry matter content of rose shoots was significantly affected by rootstocks throughout the year (personal communication of Ir. W. Berentzen). Since the dry matter content is the complement of the water content, it is possible that the water balance, rather than the dry matter, of the rose shoots is affected by the rootstock. It is well known that water content is closely related to water potential, which has a profound effect on growth (Hsiao, 1973, 1993). All this evidence suggests that, no matter how well the growing conditions in modern greenhouses may be, the water supply to the above-ground part in cut roses is affected by rootstocks, perhaps to a great extent.

The aim of this study is to examine whether the water relations of greenhouse roses, particularly the leaf water potential, is affected by the rootstock, whether this effect, if true, is caused by the root system or the graft-union, and what is the relationship of this effect with the important horticultural characteristics of the rootstocks.

## **6.2 Materials and methods**

The investigation of the rootstock effects on water content and water potential in flower shoots was carried out both in the greenhouse and in the phytotron at the Wageningen

University. The investigation on the water conductivity of the rootstock and that of the graft union were conducted in a phytotron. In the greenhouse experiment seven rootstocks, three commercial types (*Moneyway*, *Helena*, *Natal Briar*) and four new hybrids (12—06, 20—10, 18—23, 15—13), were used in two trials in separate compartments with different scion cultivars: *Frisco*<sup>®</sup> (cv. 'Korflapei') and *First Red*<sup>®</sup> (cv. 'Pekcoujenny').

### 6.2.1 Material preparation

At the end of September 1995, scions of *Frisco*<sup>®</sup> were stented on the rootstocks (Van de Pol and Breukelaar, 1982). Marketable flower shoots of *Frisco*<sup>®</sup>, which had been taken from a commercial nursery, were used as scion material. Only 3-5 nodes below the upper-most five-leaflet leaf were selected for making the combination plants. Stock material was taken from the greenhouse of the University. Stented plants were propagated on rockwool cubes (7×7×6cm, Grodan) under 100% humidity. Rockwool cubes were isolated by plastic from the bottom of the beds of the propagation benches, which were heated to 21°C. After three weeks, most stentlings formed roots. When roots were visible, plants were hardened. On November 1, stentlings were transplanted on rockwool slabs in a greenhouse compartment of 12m×12m.

The growing system was a knot system with growing benches positioned from north to south. There were nine benches in total. Each had two parallel lines of eight rockwool slabs (133×15×9cm) at a height of approximately 65cm from the ground except those in the east and the west where there was only one line of rockwool slabs. The layout of the experiment was a randomised Latin-square. The middle bench and two side benches in the east and the west were used as guard plants. On slabs at both ends of the remaining six benches, the outside half were occupied by border plants and the other half by stentlings of *Moneyway* rootstock. Each rootstock had six sub-plots (except *Moneyway* which had 12 half sub-plots) and each sub-plot consisted of two parallel rockwool slabs. On each rockwool slab, there were eight plants. There were 96 plants of each rootstock. Supplementary light, provided by high-pressure sodium lamps (SON-T, 400W, 36.5µmol m<sup>-2</sup>s<sup>-1</sup> PAR) during the daytime (18hd<sup>-1</sup>), was used until mid March when global radiation outside the greenhouse dropped below 100Wm<sup>-2</sup>. On March 15, 1996, the lamps were removed. Bending of the primary shoots started in the middle of December with all rootstocks except 15—13, because development was delayed. The primary shoots were bent when the primary shoots and the secondary shoots reached approximately the same length. The first and the second, and sometimes the third, bottom-breaks were also bent regardless of the time so that every individual plant of all rootstocks had more or less the same leaf area before any flowers were to be harvested. Flowers were harvested three times a week from February 2 onwards. Other growing



practices were the same as in commercial practice. The number, fresh weight and the stem length of flower shoots produced by each rootstock were recorded.

The relative productivity of these rootstocks was quantified based on the fresh weight of flowers produced within a period of 15 months. Three levels of productivity were distinguished, i.e., *Moneyway*, *Helena*, 20—10, *Natal Briar*, 12—06 > 18—23 > 15—13.

In the experiment with *First Red*<sup>®</sup>, stentlings and cuttings were made on February 6, 1996, and transferred into the greenhouse on March 18. The preparations of material were the same as in the *Frisco*<sup>®</sup> trial. However, in *First Red*<sup>®</sup> own-rooted cuttings were included and the growing benches were conventional, which were low and movable. Nevertheless, the plants were treated as in the knot system described for *Frisco*<sup>®</sup>.

### 6.2.2 Water content and water potential measurement

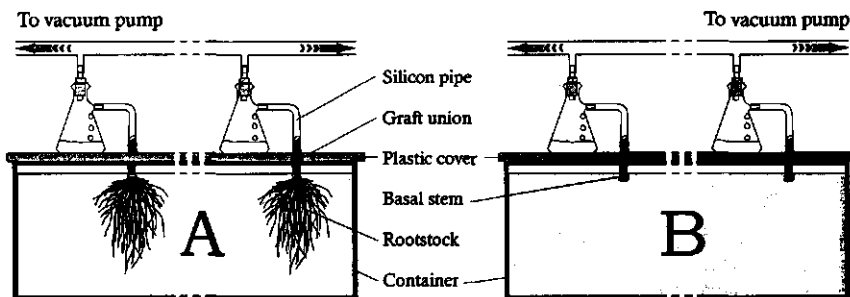
Flower shoots for measuring water content were taken in the normal marketable stage of ripeness. Sample shoots, at least two pieces per plot, were taken on October 21, 1996 in the *Frisco*<sup>®</sup> experiment and November 3, 1996 in the *First Red*<sup>®</sup> experiment respectively. Fresh shoot weight of each plot was recorded correspondingly. The measurement was carried out immediately after cutting. The dry weight was determined after drying at 105°C for 32 hours. The water content at different stages of shoot development was followed for a period of two months with *Frisco*<sup>®</sup>.

Leaf water potential was determined by the Pressure Chamber Technique (Scholander *et al.*, 1965). Sample leaves were taken from the first five-leaflet leaf from the top of the shoots that had a flower bud of approximately 1.5cm in *Frisco*<sup>®</sup> and 2.5cm in *First Red*<sup>®</sup> respectively. Measurements were carried out on September 25-26, 1997, when the weather was clear and sunny. To minimise the time and weather effect during measurements, which took approximately 4 hours, they were carried out in four time blocks. In each time block one sample from each plot was taken and measured. Each rootstock was represented in six plots that were distributed in six spatial blocks.

### 6.2.3 Hydraulic properties of whole root systems and graft unions

In the phytotron experiment, investigation was focused on the water conductivity of different root systems and graft unions. The water content and potential were also measured. The plants were grown in hydroponics. The scion cultivar was *First Red*<sup>®</sup>, which was stented (Van de Pol and Breukelaar, 1982) on six rootstocks, i.e. *Helena*, *Natal Briar*, 12—06, 15—13, 18—23 and 20—10. Experiments started on September 3-5, 1997. Stentlings were initially propagated in a mixture of peat and sand (1:1 v/v) in a

propagation bench in a compartment of a multispan Venlo-type greenhouse of Wageningen University. In the propagation benches, saturated humidity was maintained and the soil was heated when the temperature dropped below 22°C. After three weeks rooting in propagation benches, the plants were lifted and washed with tap water and then transferred to a hydroculture system in the phytotron. Temperature and humidity were computer-controlled. The temperature was set at 21°C during the daytime (16 hours) and 19°C during the night. Humidity was within the range of 70%-75%. Light intensity at the height of the origin of primary shoots was approximately 80Wm<sup>-2</sup> (high-pressure sodium lamps SON-T 400W and HPI-T 400W). The culture solution was standard for roses (De Kreij and Kreuzer, 1989). The pH and EC were adjusted to approximately 5.8 and 1.6 respectively. The hydroculture system was composed of two vertically arranged water containers. Plants were growing in the upper one. Water was circulated by pumping the water from the lower into the upper container, where the water level was controlled by an overflow pipe through which the water fell back to the container beneath and was thus aerated. After they were transferred to the hydroponic growing system, the plants were still kept under saturated humidity by using a transparent plastic cover and a light screen. After two weeks, the light screen was removed. In the third week, the humidity was gradually lowered and one week later the plastic cover was removed. The plants were kept growing under the specified climate conditions until they were pruned. When most primary shoots reached the marketable stage, they were all cut back to just 1 cm above the basal bud crown. The layout of the experiment was a randomised block design. Each of the three hydroculture units served as a block with 12 plants for each rootstock combination.



**Figure 6.1** Schematic representation of the device for measuring the flow rate through the root system (A) and the basal stem that contained a graft union (B).

The evaluation of the hydraulic conductivity of the rootstocks was based on the flow rate of exudate through the root systems ( $K_r$ ), with an external pressure difference of 0kPa, 35kPa or 70kPa. The pressure difference was created by placing a vacuum pump on the

cut surface of the decapitated root systems. For that purpose, the plants were pruned below the base of the primary shoots, the cut was made smooth and round by a blade about 1 cm above the graft union, then, a silicone tube was mounted onto the stump. The other end of the tube was connected through a filtering flask and then a large rubber tube to a vacuum pump (Figure 6.1). There were six silicone tubes allowing all six different rootstocks to be measured at the same time (not shown in Figure 6.1). Firstly, the flow rate without external force, the exudate due to root pressure was measured. After 15 hours, the amount of root exudate was recorded. Thereafter, two levels of differential air pressure, firstly 35kPa (P1) and then 70kPa (P2), were applied, each for 1 hour. The forced exudate (mainly nutrient solution) was separately collected and the volume was determined for each plant at each pressure. The hydraulic conductivity of the graft union was estimated by measuring the conductivity of a piece of stem that contained the graft union. Firstly, the root system was removed 2cm below the graft union. The lower end of the basal stems was then submerged in fresh nutrient solution. The previously applied pressure differences were used again, each for 10 minutes. The procedure was continued as before. Water content and water potential were measured as described for the experiments in the greenhouses.

Since the rate of water flow was size-dependent, it needs to be properly normalised before being used for comparing intrinsic water conductivity of the rootstocks. In literature, conductivity is usually normalised: (a) stem—by using the cross-section as a reference or (b) root—by using root surface or root length. These methods are particularly appropriate for investigating water conductivity on the structural or tissue levels. But for our research questions, such normalisation is unnecessary because then we have to take these normalising factors (cross-section, root length, or root surface) back into account since we want to compare the ratio of water-absorbing capacity of the entire root system to the capacity of transpiration of entire shoot and since. For this reason, we tentatively use the ratio of the water flow rate ( $K_{rt}$ ) to the leaf dry weight (LDW) or the root dry weight (RDW) to reduce the size effect and, by comparing the ratios ( $K_{rt}/LDW$ ), to examine whether the leaf water status is related to the ratio of the functional capacity between rootstock and scion, *i.e.* the water uptake capacity to the transpiration capacity, which is closely related to the leaf area. Here, we use LDW, instead of the leaf area, as an indicator of the transpiration capacity because there is a very high correlation between these parameters.

### *Statistics*

The presented results of water content and water flow rate were weighted means by fresh weight. LSD (least significant difference) was calculated on the basis of Student's *t*-test ( $P=0.05$ ).

## 6.3 Results

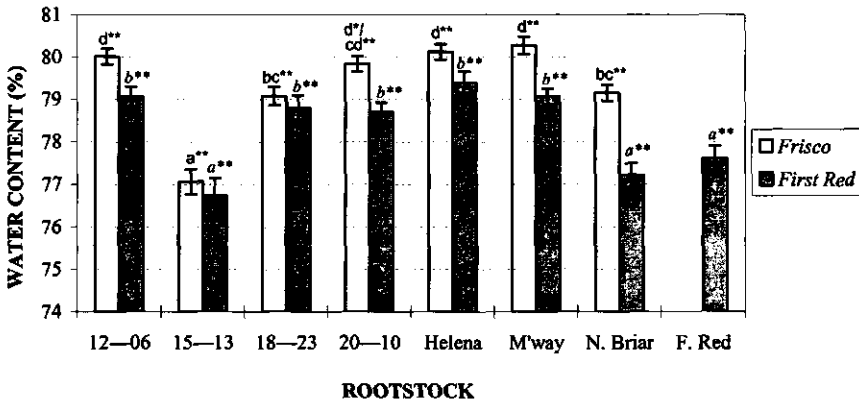
### 6.3.1 Water content

Both the rootstocks and the scion cultivars had a significant effect on the water content of the flower shoot (Figure 6.2 and 6.3). The shoot of *Frisco*<sup>®</sup> had consistently higher water content than that of *First Red*<sup>®</sup> irrespective of the rootstock. However, the difference between the two cultivars depended on the rootstock. It was statistically significant on the vigorous rootstocks, but not on the weak (15—13) and the medium weak (18—23) ones. On average, the difference was approximately 1%.

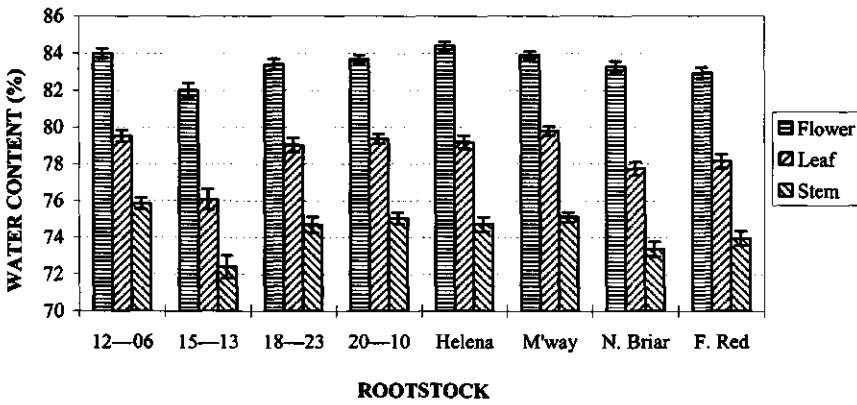
The rootstock effect on the water content of shoot fell into three distinct levels when *Frisco*<sup>®</sup> was used as the scion, but only two levels could be distinguished with *First Red*<sup>®</sup>. In both cultivars, the shoot on 15—13 had the lowest water content. The maximum difference exceeded 3%. The scion effects for 15—13 and for 18—23 are small, but they seem large for the other rootstocks (especially *Natal Briar*), an indication of scion-rootstock interaction. It seems that the water content of shoot tended to be higher on vigorous rootstocks than on the weak ones. This is more obvious with *Frisco*<sup>®</sup> than with *First Red*<sup>®</sup>. Nevertheless, the rootstock effects were generally similar in pattern between *Frisco*<sup>®</sup> and *First Red*<sup>®</sup>.

The rootstock-induced changes in the water content of the shoot were not a result of alteration of the composition of different parts, i.e., the leaf, the flower and the stem. The rootstocks did not only affect a particular organ but the entire shoot, as is shown in Figure 6.3. Despite the consistent differences in water content between different parts, the pattern of the rootstock effect was almost the same. The fact that the rootstocks affected the shoot length (data not shown) contributed little, if any, to the differences of water content, since the variation in shoot length was much bigger within the rootstocks than between the rootstocks and there was no significant correlation between the water content and the shoot length within the rootstocks (data not shown).

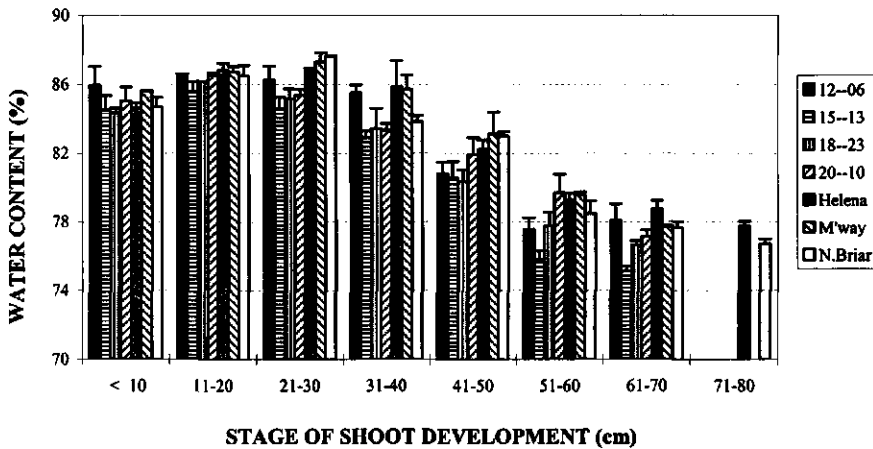
The water content seemed already affected by the rootstocks at an early stage of shoot development, but the differences were getting bigger at a later stage (Figure 6.4). The water content was also dependent on the stage of development: it increased for a short period after budbreak, and then gradually declined to the lowest levels at flowering stage, irrespective of the rootstock.



**Figure 6.2** Water content in flower shoots of *Frisco*<sup>®</sup> and *First Red*<sup>®</sup> as affected by the rootstocks. Vertical bars indicate standard error of the mean. Bars with no common letters are significantly different at 1% level with \*\* and 5% level with \* respectively according to Student's *t*-test.



**Figure 6.3** Water content in flowers, leaves and stems of *First Red*<sup>®</sup> flower shoots as affected by the rootstocks. Vertical bars indicate standard error of the mean.

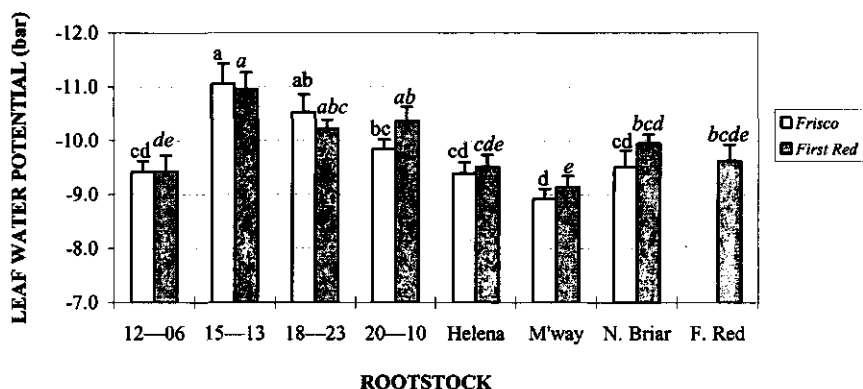


**Figure 6.4** Water content in flower shoots of *Frisco*<sup>®</sup> as affected by the rootstocks at different stages of shoot development. Vertical bars indicate standard error of the mean.

### 6.3.2 Water potential

In general, the rootstock effect on the leaf water potential showed a similar pattern as the rootstock effect on water content, and was as significant (Figure 6.5). The leaf water potential tended to be lower in the weak and the medium weak rootstocks than on the vigorous ones. The correlation coefficient between the two effects across the rootstocks was 0.88 in *Frisco*<sup>®</sup> and 0.70 in *First Red*<sup>®</sup> respectively. However, the two effects were not consistent when only the vigorous rootstocks were considered. There seemed to be more variation in water potential than in water content among the vigorous rootstocks.

Unlike water content, water potential was not affected by the scion cultivars. Although the water content between *Frisco*<sup>®</sup> and *First Red*<sup>®</sup> was significantly different, the difference in leaf water potential between the two cultivars was relatively small and insignificant, regardless of the rootstock.



**Figure 6.5** Water potential in flower shoots of *Frisco*<sup>®</sup> and *First Red*<sup>®</sup> as affected by the rootstocks. Vertical bars indicate standard error of the mean. Bars with no common letters are significantly different at 5% level according to Student's *t*-test.

### 6.3.3 Hydraulic conductivity of the root system and of the graft union

As expected, the flow rate through the whole root system ( $K_r$ ), either without or with external pressure, varied considerably between as well as within the rootstocks (Table 6.2). The high variation can be attributed for a great part to differences in plant size, which depended on the rootstock (Table 6.1). Nevertheless, factors other than size did contribute to this variation since the normalised conductivity, both  $K_r/LDW$  and  $K_r/RDW$ , were significantly affected by the rootstock (Table 6.2).

The flow rate through a piece of basal stem that contained a graft-union showed the same pattern of variation as that of the flow rate through the whole root system ( $K_r$ ). However, the former ( $K_{bs}$ ) was much greater than the latter ( $K_r$ ) on the same plant. The ratio of the two flow rates ranged from 10 up to 93, depending on the rootstock and the difference of air pressure. In general, it increased when the rootstocks became more vigorous and also when the differential pressure became greater. On average, the flow rate through the basal stem was as high as nearly 50 times the rate through the whole root systems, indicating that the hydraulic resistance of graft union was much smaller than that of the root.

**Table 6.1** The vegetative growth as affected by the rootstocks. LSD was calculated based on Student's *t*-test ( $P=0.05$ ).

Rootstock	12—06	15—13	18—23	20—10	Helena	N. Briar	Average	LSD
Leaf fresh weight (g)	33.67	35.02	29.29	48.71	55.67	45.35	41.29	18.54
Stem fresh weight (g)	19.36	18.89	15.16	25.75	37.19	35.64	25.33	15.10
Shoot fresh weight (g)	52.99	53.93	44.15	74.32	92.85	81.01	66.54	32.85
Root fresh weight (g)	18.45	15.61	11.80	27.59	25.18	15.43	19.01	11.93
Leaf dry weight (g)	8.42	9.06	7.14	11.72	14.90	11.46	10.45	5.03
Stem dry weight (g)	5.06	5.13	3.68	6.07	9.51	8.62	6.35	3.70
Shoot dry weight (g)	13.49	14.20	10.80	17.80	24.42	20.07	16.80	8.58
Root dry weight (g)	2.48	1.61	1.42	3.28	3.74	2.39	2.49	1.50
Dry weight S/R ratio	5.44	8.80	7.63	5.43	6.53	8.39	6.76	1.83

**Table 6.2** The water flow rate of the root system and that of basal stem as affected by the rootstocks under different differential air pressure. LSD was calculated based on Student's *t*-test ( $P=0.05$ ).

Rootstock	12—06	15—13	18—23	20—10	Helena	N. Briar	Average	LSD
K <sub>rt</sub> -P0 (ml/hr)	0.24	0.13	0.26	0.41	0.51	0.35	0.32	0.20
K <sub>rt</sub> -P1 (ml/hr)	0.70	0.43	0.75	1.65	1.07	0.63	0.87	0.64
K <sub>rt</sub> -P2 (ml/hr)	0.91	0.56	0.90	2.32	1.41	0.81	1.15	0.72
K <sub>bs</sub> -P1 (ml/hr)	28.45	11.13	7.88	56.59	53.87	38.86	32.80	35.60
K <sub>bs</sub> -P2 (ml/hr)	61.02	15.01	16.82	95.25	74.63	75.45	56.36	52.20
K <sub>rt</sub> -P0/LDW	0.028	0.014	0.037	0.035	0.034	0.030	0.030	0.019
K <sub>rt</sub> -P1/LDW	0.083	0.047	0.105	0.141	0.072	0.055	0.083	0.056
K <sub>rt</sub> -P2/LDW	0.108	0.062	0.126	0.198	0.094	0.070	0.110	0.065
K <sub>rt</sub> -P0/RDW	0.10	0.08	0.19	0.13	0.14	0.15	0.13	0.11
K <sub>rt</sub> -P1/RDW	0.28	0.26	0.53	0.50	0.29	0.26	0.35	0.28
K <sub>rt</sub> -P2/RDW	0.37	0.35	0.63	0.71	0.38	0.34	0.46	0.33
K <sub>bs</sub> -P1/K <sub>rt</sub> -P1	40.89	26.13	10.51	34.24	50.41	61.97	37.70	40.50
K <sub>bs</sub> -P2/K <sub>rt</sub> -P2	67.23	26.88	18.75	41.13	53.10	93.58	49.08	53.80
K <sub>rt</sub> -P2/K <sub>rt</sub> -P1	1.30	1.31	1.20	1.40	1.32	1.29	1.32	0.56
K <sub>bs</sub> -P2/K <sub>bs</sub> -P1	2.14	1.35	2.14	1.68	1.39	1.94	1.72	0.99

\* K<sub>rt</sub>-P0, K<sub>rt</sub>-P1 and K<sub>rt</sub>-P2 stand for the flow rate through the root system under the differential air pressure of zero, 35kPa and 70kPa respectively. K<sub>bs</sub>-P1 and K<sub>bs</sub>-P2 stand for the flow rate through the basal stem under the differential air pressure of 35kPa and 70kPa respectively. LDW for leaf dry weight. RDW for root dry weight.



### 6.3.4 Effects of rootstock on water content and leaf water potential in phytotron

Unlike those in the greenhouse, the plants in the phytotron were not affected by the rootstocks with respect to shoot water content (Table 6.3). The values of leaf water potential were quite different from those obtained in the greenhouse both in absolute values and in relative magnitude between the rootstocks, although 15—13 was still the lowest.

**Table 6.3** Shoot water content and leaf water potential of *First Red*<sup>®</sup> as affected by the rootstocks grown in hydroponics. Values followed by different letters on the same row differ significantly at the 5% level according to Student's *t*-test.

Rootstock	12—06	15—13	18—23	20—10	Helena	N. Briar
Leaf water content (%)	75.0 <i>a</i>	74.1 <i>a</i>	75.6 <i>a</i>	75.9 <i>a</i>	73.2 <i>a</i>	74.7 <i>a</i>
Stem water content (%)	73.8 <i>ab</i>	72.8 <i>a</i>	75.8 <i>bc</i>	76.4 <i>c</i>	74.4 <i>abc</i>	75.8 <i>bc</i>
Shoot water content (%)	74.5 <i>a</i>	73.7 <i>a</i>	75.5 <i>a</i>	76.0 <i>a</i>	73.7 <i>a</i>	75.2 <i>a</i>
Leaf water potential (bar)	-5.8 <i>ab</i>	-6.6 <i>a</i>	-5.2 <i>b</i>	-5.0 <i>b</i>	-5.9 <i>ab</i>	-5.7 <i>ab</i>

### 6.3.5 Correlation of the rootstock effects with those on productivity and quality

The rootstocks' effect on water relations was well correlated with the effect on plant productivity (see Appendix 1). The lower the water content induced by a rootstock, the less productive the rootstock. The same was true for water potential. Similar correlation can also be found with quality parameters. The closeness of correlation, however, depended on the cultivar and perhaps the experimental conditions. Both water content and water potential had a closer correlation with flower productivity in the *Frisco*<sup>®</sup> experiment than in the *First Red*<sup>®</sup> experiment.

Generally, high and positive correlation was also found between the parameters of water relations in the same experiments, but not through different experiments. The rootstock effect on water content and water potential in the phytotron was quite different from that in the greenhouse.  $K_{tr}/LDW$  was more closely correlated with the water status observed in the phytotron (same experiment) than in the greenhouses (different experiments).

## 6.4 Discussion

A plant will develop a water deficit at high light, such as at a sunny midday, because the absorbing surface or the vascular architecture of the root system is inadequate to supply the water needs of the leaves even though there is enough water in the substrate (Urban

*et al.*, 1994). Under growing conditions that induce a high transpiration, different rootstocks, which differ in vascular architecture and root surface, may give rise to differences in water status in the shoot. This rootstock-induced change of water status then would lead to other rootstock effects. Numerous references, as cited by Davies and Zhang (1991) and Hsiao (1993), show that a change of water potential has profound effect on a number of growth aspects in many plants. If rootstock-related variations of water status are significant and have an impact on photosynthesis, then they must be a component of rootstock vigour. Flower shoots grown on weak (*i.e.* less productive) rootstocks were significantly low in water content and water potential compared with those on vigorous (productive) rootstocks, and they took a longer time to reach a closed canopy and produced flower shoots with a shorter stem and smaller leaves (data not shown). These effects resemble the symptoms caused by water deficit (Hsiao, 1973), suggesting that plants with weak rootstocks suffered from an inadequate supply of water. Water supply, therefore, accounts at least partly for rootstock vigour. This conclusion is in line with the findings of Agbaria *et al.* (1995), who showed that rose rootstocks could reduce the transpiration and stomatal conductivity of the scion cultivar grafted on them.

Agbaria *et al.* (1995) proposed that the grafting-imposed alteration in vascular connection between rootstock and scion (Marcelis-van Acker, *et al.*, 1993) may be responsible for the reduced rates of transpiration since they found that the rate of transpiration was reduced even in auto-grafted plants. However, the present research has shown that the graft union is not a primary constraint for water transport since the hydraulic resistance of graft union was only a fraction of that of the root system. Although significant differences were indeed observed among different scion-rootstock combinations, it was probably a result rather than the cause of differences in growth. The work of Gur and Blum (1975) also showed that water transport through a graft union is usually not a major problem. Besides, in bench grafting or traditional T-budding, the grafting procedure will alter the vascular connection and consequently change the pathway (sometimes dramatically) as the stock has already formed roots before grafting, it seems, however, unlikely that the vascular connection of an auto-grafted seedling will significantly differ from that of a cutting because in both cases the root system is formed afterwards. In case of low compatibility, the graft-union could indeed become a major obstacle for water transport due to poor vascular connection (not the alteration in vascular connection), which is then more likely to happen to hetero-grafted plants because of a higher chance of incompatibility (Hasek, 1968; Schmid and Feucht, 1985; Andrews and Marquez, 1993). However, the rootstock effect on water content seems irrelevant to the type of scion cultivars and there is generally no interaction between rootstock and scion cultivar regarding rootstock vigour (De Vries, 1993). It is, therefore, probably an exception rather than a rule that a graft union would represent a major constraint for water transport.

Under given environmental conditions, the conductivity of the root system as a whole in relation to the water loss through transpiration by entire shoots determines the water status in leaves and stems. Since the size of a root system depends on the rootstock, the specific conductivity of the roots is not a reliable parameter for the comparison of the conductivity of the whole root system since a lower specific conductivity could be compensated by a higher root volume and vice versa. Also, when shoot/root ratio is arbitrarily changed by e.g. shoot or root pruning, the water relations between roots and shoots will be changed. It should be emphasised that rose is different from most other crops in the way in which it is cultivated and managed. Its growth is frequently disturbed and the S/R ratio is drastically and regularly reduced by routine harvests. As a result, the water status and its relations with S/R ratio is more complicated than when growth is not disturbed and it is generally difficult to describe under these growing practices. Any factor that affects the S/R ratio will affect the water balance. For instance, root mortality and regeneration ability are expected to have impacts on S/R ratio in functional terms, especially during the period of shoot regeneration after harvesting (Fuchs, 1994). *Natal Briar* has been shown to be the most pruning resistant rootstock (Chapter 3, 4). It is probably the reason why *Natal Briar* did not affect the final production so much as it would be expected from its effect on the water potential. Similarly, 18–23, which was found to be very difficult to regenerate (data not presented), might have a low ratio of  $K_{rt}/LDW$  under regular harvesting.

The ability to keep the balance between water uptake and transpiration at a high level of leaf water status depends on the ratio of the capacity of water absorption to the capacity of transpiration. The ratio of water flow rate to dry leaf weight ( $K_{rt}/LDW$ ) as an indicator of this ability is a tentative method to quantify this aspect (on the other hand, it also is difficult to directly measure the capacity of transpiration because of the rootstock effect). The apparent water flow rate observed under the experimental conditions could be different from the real situation. LDW may also not be in direct proportion to the capacity of transpiration because of differences in leaf age. Nevertheless, similar experiments with other crops show that such a method is generally valid in reflecting the water conducting property. Another problem with the parameter of  $K_{rt}/LDW$  is that it is (still) biased by plant size. It is, however, worth noting that the size effect tended to reduce rather than increase the difference since the correlation between this parameter and the plant size was negative within the rootstocks (data not shown). This means that the difference in the ratio would increase rather than decrease if the size effect is completely eliminated.

The discrepancy in the rootstock effect on water status between the experiment in the greenhouse and that in the phytotron is probably caused by the fact that the plants in the greenhouse had been treated differently from those in the phytotron. In the greenhouses,

all the plants were subject to regular shoot pruning (harvesting) just like in commercial greenhouses. This was, however, not the case in the phytotron. Since  $K_n/LDW$  depends on the S/R ratio, which is significantly affected by harvest and further complicated by root dying and root regeneration, the result from the phytotron experiment is not comparable with those in the greenhouse. In fact, we found in a previous experiment that root segments of 18–23 were much more difficult to regenerate than those of the other rootstocks (data not shown). Moreover, the differences in microclimate and in growing medium (in the phytotron plants were grown in nutrient solution while in the greenhouses they were in rockwool) might have also contributed to the disagreement. The different results between the experiments, therefore, do not necessarily suggest that they are inconsistent; instead, this could be a sign of interaction between rootstock and growing practice or between rootstock and environmental conditions.

Since water content and water potential were measured only on a limited number of times, the results were dependent on the moment in the growing cycle and the weather conditions during the measurements. The data on flower production and quality, however, represent the result of rootstock effects in a long period. Therefore, it was not to be expected that the two sets of parameters would be fully parallel, even if the rootstocks' effect on water potential accounts for a great part of vigour. It is not surprising if the correlation coefficients between the rootstock effect on water potential and the effect on productivity are not very high. Another reason is that the relationship between the parameters is almost certainly not linear, therefore the correlation coefficients, which reflect the linear relationship between two variables, are not able to show the true relations between the parameters, unless the parameters were properly transformed beforehand.

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## Chapter 7

### General discussion

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#### 7.1 Rootstock effects and rootstock vigour

It has been shown in this research that rootstocks affect the scion in many ways, including flower productivity. In the present research the rootstock effects on length and diameter of the flower stem (Chapter 2), flower productivity (Chapter 2), photosynthesis/respiration (Chapter 5), regeneration after pruning (Chapter 4), storage of starch (Chapter 3) and leaf water content as well as water potential (Chapter 6) have been examined. It is clear that not all of these effects are of equal importance to flower productivity in all rootstocks. In other words, these rootstock effects do not contribute equally to rootstock vigour.

As shown in Chapter 2 the rootstock effect on total flower (fresh weight) production could be attributed mainly to the effect on total number of flower stems and to a smaller extent to the effect on the average flower fresh weight. In accordance with the findings of Zieslin *et al.* (1973) and De Vries (1993), the rootstock affected the flower production (in number of flowers) mainly by affecting the number of budbreaks after harvest rather than the duration of the flush cycle. In other words, the number of budbreaks in a flush cycle is directly and closely related to rootstock vigour as defined here (the number of budbreaks in a flush cycle is, in fact, the same parameter as the number of flower shoots that are produced in the period of the flush cycle, providing that no blind shoots are formed). Knowing this it is still difficult to identify which root property affects this parameter, because it is difficult to separate effects of different root properties. The analysis of rootstock effects on other growth parameters (stem length, average weight, growth rate, etc.) could provide important information relevant to the rootstock's effect on flower productivity. For instance, although the growth rate has not been examined directly in the present study, it is clear that the growth rate of plants with different rootstocks must be different since the stem length as well as its fresh weight was affected by the rootstocks while the flush cycle (*i.e.* the time for shoot development) was

not. Within a wide range of vigour levels, budbreak and growth rate were consistently related, suggesting that the underlying mechanism of rootstock vigour in rose is the same as that in apple.

There was no clear correlation between the specific photosynthetic rate and the rootstock vigour. The rate did not differ significantly between the weak and the vigorous rootstocks except for *Natal Briar*, on which it was significantly higher than on the other rootstocks (Chapter 5). The lack of correlation suggests that the rootstock effect on the specific photosynthetic rate is not a general reason underlying the differences in productivity of rootstocks. The same was true with the specific respiration rate of the roots. This is in agreement with Barden and Ferree (1979) who found no rootstock effect on net photosynthesis nor on dark respiration in apple leaves. However, Southey and Jooste (1992) reported that the photosynthesis of grape could be affected by rootstocks and they suggested that the rootstock-induced change of stomatal conductance was responsible for the effect.

It should be noted that the experimental plants were young and in an early stage of development and the growth was not disturbed. The results may therefore not be applicable to later stages. As demonstrated by Fuchs (1994), shoot harvesting has a great impact on the activity of roots and there are significant differences in root mortality after shoot pruning between different rootstocks. Therefore photosynthesis may be affected differently by the same rootstocks under regular harvesting, which is usually the case beyond the primary shoot stage. The same could be also true for root respiration. Experiments with detached roots of the apple rootstock M.9 showed that young roots respired faster than secondarily thickened roots (Elbert, 1992).

## 7.2 Significance of carbohydrate contents and of shoot regeneration

Compared to sucrose and starch, the concentration of glucose and sucrose in both, basal stems and roots, is little affected by the rootstock. This is in line with the fact that root respiration did not differ significantly and that these sugars are the most important substrates for respiration.

Fuchs (1994) suggested that the starch content in roots is correlated with the development of shoots (sink) as well as the photosynthetic activity of the leaves (sources). This view is supported by the general observation of seasonal changes of starch content in deciduous woody trees. However, the rootstock-related variation in starch content depends on the season and its possible effect on flower production and flower quality is not clear yet. The contribution of starch reserves towards new growth and development is insignificant in terms of dry weight (Kool, 1996). But the

importance of starch reserves should not be measured only in terms of direct contribution of carbohydrates. As stressed by Loescher *et al.* (1990), the stored carbohydrates may play an important role in the plant's survival under adverse conditions; they possibly prevent plants from dying-off by keeping (parts of) the plants alive or by supporting outgrowing buds to reach the critical self-sustainable stage. Thus, a small reserve might have an impact on the establishment of new shoots (thus also leaf area) far greater than it appears. It is, therefore, also important that the total stored carbohydrate content, not just the concentration, should be taken into account.

As mentioned above, the number of budbreaks is mostly affected by the rootstocks and it is this effect that is mainly responsible for differences in production between the rootstocks. While budbreak may be affected by growth hormones, factors like carbohydrate supply and water status could be also essential. The importance of carbohydrate supply to budbreak was demonstrated by Marcelis-Van Acker (1994). Van den Berg (1987) distinguished between the lateral budbreak in complete and harvested rose plants, and attributed great importance to the sink of the top meristem in maintaining correlative inhibition. In the pruning experiments (Chapter 4), high shoot regeneration in darkness was found only in invigorating rootstocks. The reverse was, however, not true since low shoot regeneration was found both in the weak and some of the invigorating rootstocks. But again, this result may be not representative to later growing stages since the secondarily thickened roots could behave differently than the young and white roots, as is the case with apple rootstocks (Elbert, 1992).

### 7.3 Water relations between shoots and roots

The balance between water uptake and transpiration is one of the most important aspects concerning the shoot-root relationship and this rootstock effect is by far the most consistent one.

At what level of leaf or stem water potential this balance is achieved depends on environmental conditions, rootstock as well as scion varieties (Chapter 6; Southey and Jooste, 1992). In soil cultivation root distribution is often considered the most important rootstock character regarding water uptake. This is quite obvious when the plants are grown in a dry place where ground water level is low and root distribution directly affects their access to water. For roses that are grown in hydroponics, either on artificial substrates or directly in nutrient solution, access to water is, however, no longer affected by the way roots are distributed. Yet the water supply to shoots is still affected (Chapter 6). This means that water supply (to shoots) on soilless culture is not merely a technical issue. The fact that the rootstock-induced variation in water supply to the shoots could not be levelled out by an ample water supply to the growing media suggests that the

hydraulic conductivity of the root system is an important factor and varies significantly with rootstocks. This effect becomes more apparent when access to water is guaranteed and the importance of root distribution is diminished.

Some rootstock effects could be better explained by water relations than by growth hormones. For instance, the shorter shoots with weak rootstocks could be the result of lower water status (Chapter 6) since mild water deficit affects cell elongation more than cell division (Davies and Zhang, 1991). This is in line with the fact that the flush cycle did not change across the rootstocks while the growth rate of shoots was affected (Chapter 2). Van den Berg (1987) also showed that the length of shoots depends in particular on relative humidity and temperature, both of which affect transpiration and hence water status.

Other known rootstock effects may also be related to the water relations: the time till budbreak could be prolonged because of water stress (Larson, 1980); the fact that vigorous rootstocks usually absorb more minerals than weak ones could be partly attributed to water uptake (Jones, 1971; Ohme and Ludders, 1983, Murata, *et al.*, 1983); Water stress affects photosynthesis either directly or indirectly via leaf area (Hsiao, 1993; Iacono, *et al.*, 1998).

## 7.4 General perspective of the nature of rootstock vigour

The productivity of a plant is largely controlled by the aboveground part since plant growth is ultimately dependent on photosynthesis, which is the sole source of carbohydrates from which all other organic compounds are derived. It is reasonable, however, to assume that the growth potential of the aboveground part is usually not realised because there exist many, including root-related, growth-limiting factors even in the best controlled growing conditions. Virtually, all effective growth-enhancing techniques are those that overcome such growth-limiting factors in one way or another. From this perspective, it can be stated that rootstock vigour is a reflection of the roots' functional capability to satisfy the demand of shoot growth. A vigorous rootstock 'promotes' growth by removing the growth-limiting factors owing to the inherent morphological and/or physiological nature of the root system of the grafted variety. However, whether a root system is limiting growth depends not only on its genotype, but also the growing conditions such as plant density, light intensity, air humidity, temperature, CO<sub>2</sub> concentration and the environmental conditions to which the roots are exposed (although rootstocks can overcome to some degree unfavourable soil conditions like low pH, high salinity, etc). Therefore, not all the variation in the roots' functional capacity will be observed since the vigour of a rootstock is judged only by the growth response of scion varieties under *normal* growing practice and greenhouse conditions.

This may explain why in the *Frisco*<sup>®</sup> experiment the five invigorating rootstocks, which had rather different genetic backgrounds as well as very different root morphology, had the same vigour (Chapter 2). It is likely that the conditions did not allow expression of the differences in vigour, rather than a coincidence of the same functional capacity.

## 7.5 Impact of definition, evaluation method and growing practice

Roses are woody shrubs and have a different growth habit than apples. The parameters that are mostly used for evaluating plant vigour in apple trees have hardly been used for roses. In fruit trees the growth rate and the size of the trees are usual indicators of rootstock vigour and, by definition, are positively correlated with the latter. In roses, however, it is the flower yield (either in number or weight) that is usually used as a indicator of rootstock vigour. The difference in definition has an important impact on the evaluation method of rootstock vigour. The conclusion that vigorous rose rootstocks produce flowers with a shorter stem than less vigorous ones, which was drawn by De Dood and Rademaker (1991) and De Vries (1993), does not necessarily mean a different invigorating mechanism of roses. It is more likely a demonstration of such an impact.

Besides, the cultivation method has probably played a very important role. Although there is no evidence that there are fundamental differences between roses and apples regarding the nature of rootstock vigour, the cultivation method can change the limiting factors (both endogenous and exogenous) of growth and development of plants and thereby affect the relative performance of different rootstocks. Some root properties that are unimportant (or hardly important) to apples could be important to roses. For instance, the resistance to regular shoot pruning, reflected in the root mortality after shoot removal, may affect flower productivity in roses by affecting the recovery after shoot harvest (Chapter 4). But it is not to be expected that it will significantly affect the performance of apple rootstocks where shoots are not regularly pruned to that extent. It is therefore important to take those differences into account when the rootstocks of different crops are to be compared.

## 7.6 Hypotheses of rootstock vigour

### *Existing theories*

In the early explanations of dwarfing fruit rootstocks, it was assumed that a reduced water or nutrient supply reached the scion from the roots. This concept was, however, dismissed by Lockard and Schneider (1981) based on the fact that scion leaf nutrients differ very little among different rootstocks (Awad and Kenworthy, 1963; Lockard,

1976; Schneider *et al.*, 1978; Chaplin and Westwood, 1980). To deal with what they believed to be an inconsistency between the early theory and the known facts, Lockard and Schneider (1981) proposed a new model in which auxin-cytokinin interactions determine the characteristic of vegetative growth of apple trees. This hypothesis seemed to have dominated the later view on the question as well as the approaches to it. Some experiments were carried out since then in an attempt to clarify the role of hormones in rootstock vigour and generally supportive evidence was obtained (Jones, 1986; Reddy *et al.*, 1990). Soumelidou *et al.* (1994) showed that auxin was transported at a greater velocity in less dwarfing rootstock (MM 111) than in dwarfing rootstock (M9). This result was confirmed by Kamboj *et al.*, (1997)

So far, only few experiments have been carried out with greenhouse roses to increase our understanding of the nature of rose rootstock vigour. Nevertheless, a few hypotheses have been proposed. Winter activity, as suggested firstly by Pollock (1983) and stressed later by Miller (1986) and Fuchs (1994), might be an important aspect of rootstock vigour since the differences in flower production among various rootstocks appeared to be larger in winter than in the other seasons. Most of the winter active rootstocks are of a subtropical origin and show better productivity than the winter hardy ones. However, this kind of comparison is usually empirical. Moreover, it is the light intensity, rather than the daylength or the temperature, that mostly affects rose production in greenhouses in the winter, and there is no evidence that low light intensity affects the roots of a winter hardy species more than those of winter active ones that are grafted with the same type of shoots, which is the receiver of light signals. The possibility of an annual rhythm of rootstock activity is also ruled out since flower production does not change over the seasons as long as the light and the temperature are kept on the same level (the winter hardy rootstock *R. Canina* 'Inermis', which shows stable performance around the year in Ecuador). Like in apple rootstocks, the role of hormones, particularly cytokinins, in rose rootstock vigour received considerable attention (Van Staden *et al.*, 1981; Richards and Wilkinson, 1984; Kuiper *et al.*, 1995; Dieleman *et al.*, 1997<sup>a</sup>, 1997<sup>b</sup>). Based on the model of Lockard and Schneider (1981), De Vries (1993) proposed a model, describing the degree of correlative inhibition. In his model the interaction between auxin synthesised in the shoot apex of scion and cytokinins synthesised in the roots of the stock plants controls the vigour. A high ratio of cytokinins/auxin is thought to favour bud release and hence plant growth.

Although obviously involved in the process of budbreak and subsequent growth, cytokinins from the rootstock are not likely to be the only reason for differences in rootstock vigour. Moreover, differences in hormone production and/or transportation could be a consequence rather than a cause. Indeed, using P<sup>32</sup> Forche (1973) showed that the rate of basipetal transport of P<sup>32</sup> was closely related to the vigour of apple rootstock clones (M7, M9 and M11) – most rapid in vigorous rootstock and slowest in dwarfing

rootstock, just like that of auxins. He suggested that a delayed transport of assimilates to the roots in dwarfing rootstocks not only affected root vigour but also, because of sugar accumulation in the aerial plants, reduced photosynthesis. This could be also the case with rose rootstocks since sucrose content was higher in the basal stems of the weak rootstocks than in those of the invigorating rootstocks (Chapter 3)

There is also counter-evidence that is worth noting. In a comparison between normal and dwarfing tomatoes it was shown that plant vigour was not correlated with the amount of cytokinins in the xylem sap (Van Staden *et al.*, 1987). A similar study with peach rootstocks revealed that cytokinin-like activity and IAA levels in xylem sap were in fact higher in dwarfing than in tall phenotypes (Glenn and Scorza, 1992). In roses, Van Staden *et al.* (1981) found that buds lower down the stem, which were subjected to correlative inhibition, contained in fact higher levels of cytokinin than the upper, less inhibited buds. The activity of endogenous cytokinins in xylem exudate from ungrafted plants was found higher than in exudate from those grafted on Indica Major (Mor and Zieslin, 1992). More budbreaks do not necessarily lead to higher plant vigour. For instance, temporarily high temperature and flush harvesting (Kool, 1996) could enhance budbreak but not plant vigour. Besides, growth hormones could be affected by other factors such as water status. It is well known that water stress will lead to the accumulation of ABA. It was also found that with increasing plant water deficit the activity of IAA oxidase increased (Darbyshire, 1971).

Nevertheless, growth hormones would probably enhance, if not cause, the difference in plant growth via a positive feedback (*i.e.*, more growth  $\rightarrow$  more auxin production and/or fast transport  $\rightarrow$  more growth; or less growth  $\rightarrow$  less auxin production and/or slow transport  $\rightarrow$  less growth). In such a case, hormones that are produced in shoots, like auxin, are expected to be positively correlated with plant vigour. Therefore, differences in hormone production and/or transportation can be correlated with plant vigour without being necessarily the original factor that triggers the initial growth difference. It is worth noting that a limiting factor may appear irrelevant if the response is a negative feedback. For instance, if lower nutrient uptake reduces plant growth, then the leaf nutrient content would tend to be maintained by a reduced growth.

#### *Interpretation of rootstock vigour in water relations*

It is general knowledge that the plant's shoot and root are at least partly complementary in function and interdependent (Brouwer, 1963, 1983; Lambers, 1983). This interdependence can be roughly attributed to three functional aspects of relations between the two parts, namely: (1) material interdependence, *i.e.*, photoassimilates vs. mineral nutrients; (2) interaction of biochemical messages, *i.e.*, hormones (*esp.* auxin)

from the shoot vs. hormones (esp. cytokinins) from the root, and (3) water balance, *i.e.*, transpiration vs. water uptake. Since the theory based on the interaction of hormones seems unable to reconcile many known rootstock effects with rootstock vigour, the importance of other shoot-root relations in the growth regulation need to be re-addressed. Based on this study and literature review, I tentatively propose an explanation based on the water relations to complement rather than to substitute the hormonal theory of growth regulation.

Rootstocks differ in structure and in their ability to absorb water. Under given environmental conditions and with the same scion variety, different rootstocks (also different specific S/R ratios) will lead to differences in leaf/stem water potential at which the water absorption and transpiration of the combination plants are able to balance. This rootstock-induced variation in water potential is permanent and has an impact on plant growth and development.

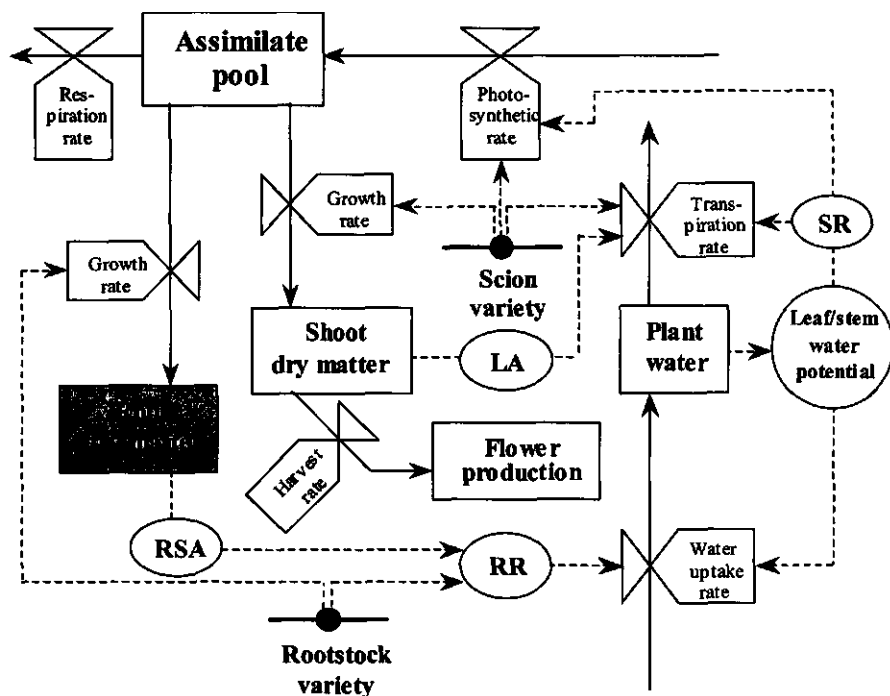
This explanation is consistent with the experimental evidence of rootstock effects on water supply. For instance, it has long been suggested that a greater hydraulic resistance of the stock's root system is a component of the dwarfing mechanism of fruit rootstocks (Tubbs, 1973; Olien and Lakso, 1984). It has been shown in many crops that removing part of the root system would reduce water absorption and create a degree of water stress (Geisler and Ferree, 1984). On the other hand, removing part of the shoots resulted in increased water supply to the remaining shoots. Mika (1986) has reviewed several articles in which winter-pruning increased water content of apple leaves, particularly at the beginning of the growing season. Many experiments indicate that the increased water supply to shoots and leaves of pruned trees is the result of a change in the proportion of foliage area to root system, not of the reduced transpiration per leaf area unit. In fact, shoot pruning increases transpiration from the remaining leaves (Marini and Barden, 1982). Both in apple (Olien and Lakso, 1984) and in citrus (Syvertsen, 1981), dwarfing rootstocks have lower hydraulic conductivity in comparison with the invigorating ones. Regarding the relations between water absorption and transpiration, grafting a scion onto an invigorating rootstock is probably similar to a situation in which part of the plant shoots have been removed, resulting in a higher ratio of the capacity of water uptake to that of transpiration. Similarly, grafting a scion onto a weak rootstock might be similar to a situation in which part of the plant roots have been removed, resulting in a lower ratio of the water uptake capacity to transpiration capacity. An essential difference is that removing part of the plant shoots or roots only results in a temporarily disturbance of the specific S/R ratio. Therefore, the effect on shoot water potential is not lasting since the specific S/R ratio will be gradually restored in the following period of growth. This explains why winter pruning increases water content of apple leaves more significantly at the beginning of the growing season compared to a later time. The specific S/R ratio is



restored at a later stage of the growing season. On the contrary, rootstocks exert a continuous effect on shoot water potential, because both root type and specific S/R ratio are inherently different and cannot be changed. The cumulative effect of the chronic mild water stress caused by rootstocks could be significant (Hsiao, 1973, 1993).

The rootstock effect on water relations is illustrated in Figure 7.1. The rootstock affects the leaf water potential through water uptake. At a given stem and leaf water potential, the same scion variety under the same environmental conditions will transpire at the same rate. On the other hand, different rootstock systems, which differ in water conductivity due to a number of factors (root surface area, hydraulic resistance at root surface, radius and longitudinal hydraulic resistance inside the roots and the average transport distance inside the roots), will not absorb water at the same rate even though the driving force resulting from transpiration is the same. When water uptake lags behind transpiration, leaf and stem water potential will drop and hence the driving force will rise until the water uptake has been increased to such a level that a new equilibrium is reached. In the meantime, transpiration may also be reduced when water stress develops. The mechanism of this regulation is well understood. The process involves a negative feedback induced by the disturbance in water balance. As water potential drops to a critical level, depending on crops (Tan and Buttery, 1982), it will trigger defence responses in the plants to deal with the disturbed water balance (Hsiao, 1973; Jones *et al.*, 1985; Davies and Zhang, 1991; De Graaf, 1995). The most common is to reduce stomatal conductivity to curb further water loss through transpiration (Tan and Buttery, 1982). Agbaria *et al.* (1995) showed that this was also the case with roses. Since stomatal density in rose leaves is not affected by exposing plants to various degrees of water stress (Plaut and Zieslin, 1977), Agbaria *et al.* (1995) suggested that the decreased stomatal conductivity results from a reduced stomatal aperture due to an increased content of ABA. This is considered to happen to many crops under water stress (Zeevaart and Creelman, 1988; Davies and Zhang, 1991).

The immediate effect of a disturbed water balance is the change of stem and leaf water potentials. This change will in the long term result in the alteration of dry matter partitioning and hence the R/S ratio, which tends to reduce the difference in water potential between different rootstocks, but can not eliminate it since the dry matter partitioning is likely to be affected also by other factors such as growth hormones.



**Figure 7.1** Schematic representation of the direct and indirect influence of rootstock and scion variety on growth and flower production through water relations. LA = leaf area, RSA = root surface area, RR = root resistance, SR = stomatal resistance.

## 7.7 Practical consequence and future perspective

In the last decade, there was a lot of controversy among Dutch rose growers about the necessity of using rootstocks for greenhouse roses. The doubts about the rootstock effects on particularly flower productivity were widespread, resulting in a sharp decrease in the use of grafted plants and a corresponding increase of the use of cuttings. Besides the fact that cut rose flower production has a naturally high variation, which often leads to inconsistent results in small-scale rootstock trials, especially when the rootstock effects are relatively small, much of the controversy seems to be due to some misinterpretation of earlier experimental results, which were obtained with only a limited number of genotypes. It is worth noting that usually (and sometimes only) traditional rootstocks were involved in most greenhouse rootstock trials. The notoriously mediocre vigour of traditional rootstocks, particularly the Canina-types, has created a general impression that rootstocks have little value for greenhouse rose production.

Whether or not to use rootstocks instead of own rooted cuttings as such is not a right question. Any root system can be used as a rootstock. Rose roots vary considerably in morphology. The present study has confirmed the experience known from practice that the root system of greenhouse roses can be, but not necessarily is a limiting factor for production. This means that the production of some varieties could be improved by grafting them on a better rootstock. On the other hand, not all varieties need a rootstock because their own roots are not growth-limiting. Since each cultivar has a unique genotype, the own root system of a cultivar can be seen as a unique rootstock. Whether a variety needs an alien rootstock depends on whether the own root system of the variety is growth-limiting under the given growing conditions and whether the rootstock can eliminate or at least relax the limiting effect imposed by the variety's own root system under that conditions. Thus, the variety, the rootstock and the growing conditions all have to be brought into consideration for the assessment of the necessity of using a rootstock.

Of course, rootstocks might still be used for reasons such as the resistance to certain diseases, the uniform root characters when more than one variety is grown in a greenhouse and, the low risk involved in managing a growing environment for a familiar root system, *etc.* For instance, *Natal Briar* is not better than the rootstock clones of *Moneyway* and *Helena* with respect to flower productivity (unpublished results). It is, however, a very pruning-resistant rootstock, as shown in Chapter 4. Some growers in the Netherlands claimed that *Natal Briar* has a better resistance to nematodes. This seems to be in line with the root characteristics of *Natal Briar*, which is noticeably harder and tougher as compared to other common rootstocks used in the Netherlands. Although under well-controlled growing conditions, *Natal Briar* does not necessarily give rise to higher flower production (but usually better quality) than own roots of most varieties, it provides better protection against possible production loss due to adverse growing conditions, particularly with new varieties of which the optimal conditions for roots are usually unknown.

From a commercial point of view, a rootstock is valuable only when its benefits outweigh its costs. Unfortunately, the benefits are often not so obvious as the costs of using a rootstock for greenhouse roses. At the moment, grafting is still manually done and laborious. The high labour cost in the Netherlands makes grafted plants relatively expensive as compared to cuttings. Being unsure about the benefits that a rootstock will bring, the growers understandably choose cuttings. However, the high cost of grafted plants might be partly overcome by carrying out the grafting operation in cheap labour countries like Kenya and Uganda and shipping the grafted materials back to the Netherlands for rooting and distribution. Before that happens, it might be difficult to change the general attitude of favouring cuttings over grafted plants unless a superior

rootstock is found. It is nevertheless important to notice that the potential of a productive rootstock has never been disproved. It is worth noting that modern rose varieties originate from only a fraction (around 5%) of the estimated 200 species that were discovered in the Northern Hemisphere and, as a result of continuous inbreeding and line breeding of hybrid varieties, there has been a decrease in vigour of the modern rose varieties (Edwards, 1955; Hollis, 1974). A better chance to find a rootstock that is much more vigorous than today's rootstocks probably lies in other untouched species (as a matter of fact, the most popular rootstock – *Natal Briar* is a natural breed found wild in South Africa). Ultimately, it is up to the researchers, breeders and growers to exploit the potential value of these species for future development of the rose industry.

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## Summary

Historically in North-western Europe and still in many other parts of the world, rootstocks have been used in large-scale rose production. The introduction in the early 1980's of artificial substrates resulted in significant changes in growing practice. Traditional seedling rootstocks, which have only a mediocre vigour, were immediately found undesirable for rose growing on artificial substrate because of their big size and the risk of carrying soil-borne diseases. Moreover, the growing environment of roots in artificial substrates is very different from that in soil. Most greenhouses are equipped with automatic irrigation systems and soil-borne diseases could be controlled to a large degree. These improvements, together with the use of artificial lighting and heating during the winter period, made most of the seedling rootstock characters that were considered important before unnecessary. The use of seedling rootstocks has therefore lost its significance and the rootstock vigour, which is usually expressed in terms of flower productivity, has become the key attribute for the rootstocks under those conditions.

In the search for adequate rootstocks, a major obstacle is the lack of early selection criteria. In order to find such selection criteria for greenhouse roses it is important to have a better understanding of the relationship between flower productivity and the root attributes that are easily measurable, either directly or indirectly, in an early development stage. In this study, various rootstock effects on growth and production of scion cultivars as well as some root attributes have been examined with a number of rootstocks that differ in flower productivity.

In Chapter 2 the effects of seven rootstocks of contrasting vigour on flower production of *Frisco*<sup>®</sup> on a knot-growing system were examined on a weekly basis during a period of 15 months. The levels of relative vigour of the rootstocks were quantified according to the total fresh flower weight produced. The result served as a reference of vigour of these rootstocks and was used for correlation analysis of various rootstock effects and root attributes. In the meantime the rootstock effects on several growth aspects were also investigated. The rootstocks had significant effects on axillary bud release during the propagation stage and the growth of the primary shoot. The length of primary shoots in the early developmental stage was positively correlated with total flower production in the period. Rootstocks had a significant effect on the number of flowers in each flush cycle, but not on the cycle duration, *i.e.*, the time from harvest till the next harvest. The average fresh weight of the flowers and stem length were affected by the rootstocks. There was in general a positive correlation between rootstock vigour and quality parameters. It was, however, noticed that there was a negative correlation if only



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invigorating rootstocks were compared. It was suggested that this negative correlation was caused by the high stem densities on these invigorating rootstocks rather than the vigour (flower productivity) itself.

Cut rose is different from most other crops in the way in which it is cultivated and managed. Its growth is frequently disturbed and the shoot-root ratio is reduced drastically and regularly by routine harvests. Certain root properties may have a greater impact on crop growth and development in the regular cultivating practice than in our experiments. Carbohydrate reserves, for example, which are considered to be important for budbreak after harvest, could be such a rootstock attribute. In Chapter 3 rootstocks were compared with respect to the concentration and the amount of the non-structural carbohydrates that accumulated in both roots and the basal stem part. The dynamics of root carbohydrates following the removal of the blooming primary shoot was investigated. Carbohydrate reserves were generally low. There were little rootstock effects on the concentrations of the carbohydrates except for the concentration of starch in the roots, though the total amount of each of the four carbohydrates varied significantly among the rootstocks due primarily to the differences in the size of the root system. In the roots, the total amount of carbohydrates and, to a lesser degree, the concentrations of sucrose and starch, were generally higher in the vigorous rootstocks than in the weak ones. In the basal stem parts, however, a reversed relationship between rootstock vigour and the concentration of sucrose and starch was observed, suggesting that the carbohydrate reserves in the roots are mainly affected by the rootstock via its effect on root and shoot development.

To study the effect of the rootstock on budbreak and subsequent growth without a supply of freshly made carbohydrates, shoot regeneration in darkness after complete shoot pruning was examined (Chapter 4). The amount and 'lifespan' of the regenerated shoots were investigated under two pruning treatments, *i.e.*, pruning at the same date and pruning at the same stage. There were clear effects of the rootstock on both the amount of regeneration and the 'lifespan' of the regenerated shoots. However, there was no significant correlation between these effects and the rootstock vigour. The plant size at the moment of pruning had a complex effect on new shoot regeneration due to the presence (or a higher rate of) outgrowing shoots in bigger (therefore more developed) plants. Although different pruning treatments resulted in different plant size at the moment of pruning, especially between the rootstocks, it had only a small effect on shoot regeneration.

Photosynthesis and respiration are important, physiological processes in plants. Plant growth is dependent upon the balance between carbon gain during photosynthesis and carbon loss through respiration, for which roots account for an important part. The

effects of rootstocks, which modify growth and development, must be therefore reflected directly or indirectly in the photosynthesis and/or the respiration of the plants that are grown on the rootstocks. In Chapter 5 plant photosynthesis and respiration of the shoot and the root on different rootstocks were examined and compared. The rootstocks affected the capacity of photo-assimilation predominantly by their effect on leaf area. The size effect accounted for most of the variation in photosynthesis and in respiration of the plants both between and within the rootstocks. When the size effect was eliminated, neither the rate of photosynthesis nor that of respiration was related to rootstock vigour

It has repeatedly been shown that the water supply in dwarfing fruit rootstocks is reduced compared with that of invigorating ones. The early explanations of rootstock dwarfing assumed therefore that a reduced water or nutrient supply reached the scion from the roots. This hypothesis was dismissed by Lockard and Schneider based on the fact that scion leaf nutrients differ very little among different rootstocks. A new hypothesis that was based on hormone interactions was proposed and it received great attention. Nevertheless, a number of facts came to light that suggested that the rootstock effect on the water relations is perhaps of greater importance than it was thought before. In Chapter 6 the water content and the water potential of flower shoots on different rootstocks were examined. Shoot water content and leaf water potential were significantly affected by the rootstock on rockwool under greenhouse conditions and in hydroculture in a controlled environment. Flower shoots on vigorous rootstocks had a higher water content and a higher water potential than those on weak rootstocks, irrespective of the variety of the scion. The rootstock effect was consistent in different parts of shoots (*i.e.* stems, leaves and flowers). The scion variety did affect shoot water content, but had no significant effect on water potential. The water conductivity of the root system was significantly different among the rootstocks. The water conductivity of the graft-union, though significantly different across the scion-rootstock combinations, seemed not a major constraint for water transport and, therefore, was not responsible for the difference in the leaf water status. There was a high correlation between the rootstock effect on the water status of shoots and the rootstock effects on flower productivity and quality, suggesting that rootstocks affect growth and development, at least partly, via the water supply.

The control of plant growth and development is a complex phenomenon which may involve a balance of hormones and other relations between shoot and root. The balance and interaction of hormones may be modified by external factors, such as nutrients and environmental factors, and by internal factors, such as the substrate levels (nutrients and assimilates) and water potential, or external factors associated with it, like EC, humidity and harvesting. In the last chapter of the thesis, various existing theories of vigour-

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controlling mechanisms, especially the one based on hormonal interaction, were reviewed and discussed in relation to the relevant facts that have been reported in recent years. An overall view of the examined rootstock effects (or properties) and their relations to each other, particularly to the flower productivity (*i.e.* vigour), was presented. It could be concluded from the present results that the rootstock effect on water relations is one of the effects that are mostly consistent with the rootstock vigour. The importance of the rootstock effect on water relations was addressed and the mechanism underlying the regulation of leaf/stem water status by different rootstocks and/or by scion varieties was discussed.

## Samenvatting

Snijrozenteelt op onderstammen was in het verleden in N.W. Europa algemeen gebruikelijk. In andere productiegebieden is dit nog steeds het geval. De introductie van kunstmatige substraten in het begin van de jaren 1980 resulteerde in andere teeltwijzen. De traditionele zaailing onderstammen, die slechts een middelmatige groeikracht geven, werden al snel als ongewenst beoordeeld voor kunstmatige substraten door hun grote omvang en het risico van ziektes vanuit de grond. Bovendien zijn de groeiomstandigheden van wortels in kunstmatige substraten zeer verschillend van de volle grond. De meeste kassen zijn nu uitgerust met een automatisch druppelsysteem voor water en voeding en bodemziekten kunnen in belangrijke mate worden vermeden. Deze verbeteringen tezamen met kunstmatige verwarming en belichting maakten vele onderstameigenschappen, die voorheen noodzakelijk waren niet meer nodig. Het gebruik van zaailing onderstammen verloor daardoor zijn betekenis en onderstam groeikracht, uitgedrukt in bloemproductiviteit, werd de hoofdzaak voor onderstammen onder deze omstandigheden.

Bij het zoeken naar onderstammen is het ontbreken van vroege selectiecriteria voor groeikracht een groot probleem. De ontwikkeling van deze criteria vereist een beter begrip van de relatie tussen bloemproductiviteit en worteleigenschappen, die direct of indirect, in een vroeg stadium gemeten kunnen worden. In deze studie werden diverse onderstaminvloeden op de groeiaspecten van geënte cultivars, zowel als enige wortelkarakteristieken onderzocht met een min of meer vaste groep van onderstammen, die variëren in invloed op de bloemproductie.

In hoofdstuk 2 werden de invloeden van zeven onderstammen, die variëren in groeikracht, op de bloemproductie van de roos Frisco<sup>®</sup>, geteeld in een knotroosstelsel, gedurende 15 maanden wekelijks onderzocht. De term relatieve groeikracht werd gebruikt, wanneer slecht naar één of enkele groeikenmerken werd gekeken. De niveaus van relatieve groeikracht werden gekwantificeerd volgens het totaal aan geproduceerd versgewicht van bloemen per periode. Het resultaat diende als maat voor de onderstamgroeikracht en is gebruikt voor correlatie-analyse tussen onderstameffecten en wortelkenmerken. De onderstammen toonden significante effecten op de knopuitloop tijdens de vermeerdering en de groei van de primaire scheut. De lengte van de primaire scheut in het vroege ontwikkelingsstadium bleek sterk gecorreleerd met de totale bloemproductie tijdens de onderzoeksperiode. Gevonden werd, dat de onderstammen significant het aantal bloemen per snee (oogst) beïnvloedden, maar niet de cycluseduur, de tijdsduur van snee tot snee dus. Het gemiddelde versgewicht van de bloemen en de stengellengte werden beïnvloed door de onderstam en over het algemeen was er een

positief correlatie van de onderstam groeikracht op deze kwaliteitsparameters. Er moet echter worden opgemerkt, dat er een negatieve correlatie werd gevonden, wanneer alleen de groeikrachtige onderstammen werden vergeleken. Verondersteld wordt, dat deze omgekeerde relatie veroorzaakt wordt door de hoge stengeldichtheden op deze groeikrachtige onderstammen, meer dan de groeikracht (bloemproductiviteit) als zodanig.

Door de manier van telen zijn snijrozen afwijkend van andere teelten. De groei wordt regelmatig verstoord en de spruit/wortel relatie wordt regelmatig drastisch gereduceerd door de routine oogsthandelingen. Bepaalde worteleigenschappen zullen grotere invloed op de plantengroei en ontwikkeling hebben bij de gebruikelijke teeltwijze dan bij onze experimenten. De koolhydratenreserve, waaraan men betekenis voor de knopuitloop na de oogst toeschrijft zou zo'n factor kunnen zijn. In hoofdstuk 3 werden de concentratie en de hoeveelheid van vier niet structurele koolhydraten in wortels en onderste stengeldeel van de verschillende onderstammen vergeleken. Het patroon van wortelkoolhydraten tijdens de stressperiode na verwijdering van de primaire scheut werd onderzocht. De koolhydratenreserves bleken over het algemeen laag in deze jonge planten. Er waren geringe onderstameffecten op de concentraties van de koolhydraten, met uitzondering van zetmeel in de wortels. Toch bleek de totale hoeveelheid van ieder van de vier onderzochte koolhydraten tussen de onderstammen significant te verschillen, vooral veroorzaakt door verschil in grootte tussen de wortelstelsels. In de wortels bleken de totale hoeveelheid koolhydraten en, in mindere mate, de concentratie van sacharose en zetmeel over het algemeen hoger in de groeikrachtige onderstammen dan bij de zwakke typen. In het onderste stengeldeel werd echter een omgekeerde relatie tussen groeikracht en concentratie van sacharose en zetmeel waargenomen. De resultaten wijzen er op, dat de koolhydraatreserves in wortels vooral beïnvloed worden door de onderstam via de beïnvloeding van de wortel - en scheutontwikkeling.

Om de invloed van de onderstam op de knopuitloop en aansluitende groei te bestuderen zonder de invloed van nieuw gevormde assimilaten, werd in hoofdstuk 4 de scheutregeneratie in het donker na volledige snoei onderzocht. Hierbij werd gekeken naar de hoeveelheid en de levensduur van gevormde scheuten. Bij de twee snoeibehandelingen, snoei op dezelfde dag en snoei in hetzelfde ontwikkelingsstadium, toonden de onderstammen een duidelijke invloed op zowel de hoeveelheid als de levensduur van de gevormde scheuten. Er bleek echter geen significante correlatie tussen deze effecten en de groeikracht van de onderstammen. De plantgrootte op het moment van snoeien had een complexe invloed op de nieuwe scheutvorming door de aanwezige (of sneller) uitgroeïende scheuten in grotere (en daardoor verder ontwikkelde) planten. Hoewel de verschillende snoeibehandelingen resulteerden in wisselende variatie (vooral

tussen onderstammen) in plantgrootte op het moment van snoeien, had dit slechts een beperkte invloed op de scheutregeneratie.

Fotosynthese en ademhaling zijn de twee belangrijkste, tegengestelde fysiologische processen bij planten. Plantengroei is afhankelijk van het evenwicht tussen koolstof toename door de fotosynthese en koolstof verlies door de ademhaling, waarin wortels een belangrijk aandeel hebben. De effecten van onderstammen, die groei en ontwikkeling beïnvloeden moeten daarom direct of indirect te herleiden zijn tot fotosynthese en/of ademhaling van planten op onderstammen. In hoofdstuk 5 werden fotosynthese en de scheut- en wortelademhaling van planten op verschillende onderstammen onderzocht en vergeleken. De onderstammen beïnvloedden de fotoassimilatiecapaciteit voornamelijk door hun invloed op de bladoppervlakte. Het grootte-effect was voor het grootste deel verantwoordelijk voor de variatie in fotosynthese en ademhaling tussen planten, zowel tussen als binnen onderstammen. Wanneer het grootte-effect werd geëlimineerd konden noch voor de fotosynthese en ook niet voor de ademhaling de zwakke onderstammen worden onderscheiden van de sterke. Er bleek dus geen duidelijke relatie tussen deze effecten en de groeikracht van de onderstam.

Herhaaldelijk werd aangetoond, dat de watervoorziening van zwakke fruitonderstammen beperkt was vergeleken met sterke onderstammen. De vroege verklaringen van verzwakkende onderstameffecten waren daarom, dat een beperkte hoeveelheid water of voedingsstoffen de scheuten vanuit de wortels bereikten. Deze hypothese werd verworpen door Lockard en Schneider op grond van de waarneming, dat de voedingsstoffen in bladeren van scheuten op verschillende onderstammen nauwelijks verschillen. Een nieuwe hypothese, gebaseerd op hormoon interacties werd voorgesteld en kreeg grote aandacht. Toch kwamen een aantal feiten aan het licht, die veronderstellen dat de invloed van de onderstam op de waterhuishouding van grotere betekenis is, dan werd aangenomen. In hoofdstuk 6 werden het watergehalte en de waterpotentiaal van bloemscheuten van verschillende onderstammen onderzocht. Gevonden werd, dat zowel het watergehalte als de waterpotentiaal significant beïnvloed werden door de onderstam, zowel in steenwol onder kasomstandigheden als in hydrocultuur in een klimaatcel. De bloemscheuten van groeikrachtige onderstammen hadden een hoger watergehalte en een hogere waterpotentiaal dan degenen van zwakke onderstammen, onafhankelijk van het entas. De onderstameffecten waren consistent in verschillende delen van de bloemscheuten (stengels, bladeren en bloemen). De cultivar had invloed op het watergehalte, maar niet op de waterpotentiaal. De geleidbaarheid voor water van het wortelstelsel was significant verschillend tussen de onderstammen. De watergeleidbaarheid van de entplaats scheen, hoewel significant lager voor de zwakke onderstamcombinaties, geen belangrijke beperking voor het watertransport en

daarom niet verantwoordelijk voor de verschillen in waterstatus van het blad. Er was een hoge correlatie tussen het onderstameffect op de waterstatus van de scheuten en de onderstameffecten op de bloemproductiviteit en -kwaliteit. Hieruit kan geconcludeerd worden, dat onderstammen de groei en ontwikkeling, tenminste gedeeltelijk, beïnvloeden via de watervoorziening.

De beheersing van de groei en ontwikkeling van planten is een gecompliceerd proces waarbij ook een evenwicht tussen hormonen en andere relaties tussen scheuten en wortels betrokken zijn. Het evenwicht en de wisselwerking tussen hormonen wordt beïnvloed door externe factoren zoals voeding en omgeving en door interne factoren zoals het voedingsniveau (voedingsstoffen en koolwaterstoffen) en waterpotentiaal of factoren, die hiermee samenhangen zoals EC, vochtgehalte en oogsthandelingen. In het laatste hoofdstuk van het proefschrift werden verschillende bestaande theorieën over groeikracht bepalende mechanismen, vooral degenen, die gebaseerd zijn op hormoonwisselwerking, samengevat en bediscussieerd met betrekking tot de relevante feiten, die de laatste jaren zijn vermeld. Er werd een overzicht gegeven van de onderstameffecten (of eigenschappen) en hun onderlinge verbanden, vooral ten aanzien van groeikracht. Uit de gepresenteerde resultaten kan geconcludeerd worden, dat het effect van de onderstam op de waterhuishouding een van de meest consistente invloeden op de groeikracht is. Het belang van het onderstameffect op de waterhuishouding werd besproken en het verklarende mechanisme van de sturing van de blad/stengel water status door verschillende onderstammen en/of cultivars werd bediscussieerd.

## Curriculum Vitae

Ximing Hu was born on September 6, 1962, in the coastal Zhejiang Province of the People's Republic of China. He obtained his BSc degree in Horticulture in 1984 from the former Zhejiang Agricultural University and now the Agricultural College of Zhejiang University. He continued his study as an MSc student in the same University and obtained his first MSc degree in 1987. Thereafter, he worked for the government of the former Yuhang County and now Yuhang district of Hangzhou, the capital city of Zhejiang Province. In 1992 he followed an MSc course in Plant Breeding in Wageningen University, the Netherlands. After successful completion, he started a four-year PhD research project in the former Horticultural Department of the same University. This book is the result of this work.



**Appendix 1** The correlation coefficients between water-related parameters and the productive parameters of the flowers produced (quantity and quality). Data of productive parameters represent the first 15 months (5<sup>th</sup> week of 1996 to 18<sup>th</sup> week of 1997) in *Frisco*<sup>®</sup> trial and the first six months (from 19<sup>th</sup> to 48<sup>th</sup> week 1996) in *First Red*<sup>®</sup> trial respectively.

Parameters	TN <sub>r</sub>	TW <sub>r</sub>	AW <sub>r</sub>	AL	WP	WC	PSL	TN <sub>r</sub>	TW <sub>r</sub>	AW <sub>r</sub>	AL	WP	WC	K <sub>r</sub> /L	K <sub>r</sub> /R	WC	WP	Experiment
Total Number	1																	
Total Weight	0.99	1																
Average Weight	0.92	0.96	1															
Average Length	0.95	0.98	0.98	1														
Water Potential	0.74	0.78	0.87	0.77	1													
Water Content	0.57	0.58	0.63	0.50	0.70	1												
P.S. Length	0.94	0.96	0.93	0.94	0.73	0.60	1											
Total Number	0.99	0.98	0.91	0.92	0.75	0.65	0.96	1										
Total Weight	0.97	0.99	0.97	0.96	0.86	0.69	0.94	0.97	1									
Average Weight	0.28	0.36	0.58	0.45	0.71	0.41	0.26	0.23	0.45	1								
Average Length	0.85	0.88	0.92	0.92	0.76	0.50	0.76	0.79	0.89	0.68	1							
Water Potential	0.91	0.95	0.98	0.97	0.89	0.55	0.92	0.89	0.95	0.56	0.88	1						
Water Content	0.90	0.92	0.93	0.88	0.84	0.85	0.89	0.93	0.97	0.48	0.84	0.88	1					
K <sub>r</sub> -P1/LDW	0.38	0.35	0.28	0.28	0.01	0.57	0.33	0.42	0.37	-0.04	0.35	0.12	0.51	1				
K <sub>r</sub> -P1/RDW	0.12	0.05	-0.10	-0.09	-0.24	0.38	-0.01	0.17	0.07	-0.34	0.00	-0.24	0.21	0.87	1			
Water Content	0.15	0.10	0.02	0.07	-0.22	0.08	-0.08	0.09	0.09	0.03	0.32	-0.12	0.14	0.74	0.76	1		
Water Potential	0.80	0.76	0.66	0.70	0.43	0.53	0.61	0.77	0.76	0.22	0.77	0.56	0.76	0.74	0.59	0.70	1	
Experiment	First Red <sup>®</sup> Experiment (greenhouse)						Frisco <sup>®</sup> Experiment (greenhouse)						First Red <sup>®</sup> Experiment (phytotron)					

Abbreviation: T - total; A - average; W - water; W<sub>r</sub> - weight; P.S. - primary shoot; K<sub>r</sub>-P1 - the flow rate under the differential air pressure of 35kPa; LDW - leaf dry weight; RDW - root dry weight.