# The vigour of glasshouse roses

## *Scion-rootstock relationships*
## *Effects of phenotypic and genotypic variation*

Promotor:

Dr. J.Tromp, Hoogleraar in de Tuinbouwplantenteelt, in het bijzonder de overblijvende gewassen.

D.P. de Vries

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**Stellingen behorende bij het proefschrift:**

# The vigour of glasshouse roses

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*door D.P. de Vries.*

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1. Bij het beschrijven van de effecten van onderstammen op de groei van snijrooscultivars verdient de term 'basale dominantie' de voorkeur boven 'apicale dominantie'.
   *( Dit proefschrift )*

2. Door onderstammen geïnduceerde groeikracht bij rozencultivars berust primair op de mate van vertakking.
   *( Dit proefschrift )*

3. Het gebruik van zaailing en/of klonale Edelcanina als onderstam voor de kasrozenteelt op substraat is achterhaald.
   *( Dit proefschrift )*

4. Het kweken van snijroos-genotypen voor de teelt op eigen wortel is een ongewenst compromis tussen de verschillende functies van cultivar en onderstam.
   *( Dit proefschrift )*

5. Stabiele of mogelijk dalende bloemproductie van nieuwe snijrooscultivars is mede het gevolg van onbekendheid bij veredelaars met de negatieve correlatie tussen scheutlengte en bloemproductie van zaailingen.
   *( L.A.M. Dubois & D.P.de Vries, 1987. Prophyta 2: 45-47. )*

6. Na realisatie van de verplichte keuring van rozencultivars en -onderstammen door de NAKS/NAKB heeft het virusvrij maken van onderstammen prioriteit boven dat van cultivars.

7. Alle axillaire knoppen aan de tak van een snijroos zijn onderhevig aan correlatieve remming. Het onderscheid tussen sylleptische en proleptische rozenknoppen door Zamski et al. berust mogelijk op te kortstondige waarneming betreffende de ontwikkeling van de bloeiwijze.
   *( E.Zamski, S.Oshri & N.Zieslin, 1985. Bot.Gaz.146: 208-212. )*

8. De veronderstelling van Zieslin dat de apicale bloemknop aan de scheut van snijrooscultivars aanvankelijk lateraal zou zijn geplaatst, wordt niet bevestigd door resultaten van onderzoek betreffende de bloemknopontwikkeling van remonterende zaailingen.

*(N.Zieslin, 1992. Scientia Hort.49: 305-310.)*

9. Dagneutraliteit van rozencultivars is een handicap voor de systeemontwikkeling in de snijroosteelt. Biotechnologisch onderzoek zou zich daarom moeten richten op transformatie met 'daglengte-genen'.

10. Het op voorhand uitsluiten van afgestudeerden aan Hogere Agrarische Scholen (Ing.'s) bij vacatures voor AIO's alsmede voor wetenschappelijk onderzoekers op DLO-instituten, is in strijd met de door de wet geschapen toegang tot de promotie.

11. De opvatting van Dr. D. de Zeeuw (ca. 1980), dat het academici ouder dan 45 jaar ontbreekt aan creativiteit, lijkt te worden bevestigd door de leeftijd waarop onderzoekers zich tot het management voelen aangetrokken.

12. Gesponsored onderzoek, waarbij per definitie het te bereiken doel nauwkeurig is omschreven doet ernstige afbreuk aan de serendipiteit van onderzoekers.

13. Indien de opwekking "geniet, maar drink met mate", gegeven tijdens STER-reclame voor een alcoholische versnapering, bedoeld is om de TV acceptabeler te maken voor Calvinistische kijkers, zou deze beter kunnen luiden: "drink, maar geniet met mate".

14. Het verbieden van het vreugdeschenkende verbranden van planteresten in de open lucht, op grond van de overweging de $CO_2$ uitstoot naar het milieu te verminderen, pleit niet voor de kennis van milieuambtenaren betreffende de koolstofkringloop.

15. Het optrekken van de leeftijd waarop het rijvaardigheidsexamen mag worden afgelegd tot die waarop het recht op een O.V.-jaarkaart vervalt, zal een significante bijdrage leveren aan de verkeersveiligheid alsmede aan het terugdringen van het autogebruik.

16. Het vermelden van de straatwaarde van in beslag genomen harddrugs via de pers, krijgt pas waarde wanneer deze drugs door de politie daadwerkelijk op straat worden uitgevent.

*Ede, 24 maart 1993.*

# Contents

# Summary

Glasshouse roses commonly are combination plants, consisting of a scion variety and a rootstock of different genotypes. In this study, various environmental and genotypic factors have been investigated that influence the vigour of rootstocks and scion varieties, separately and in graft combination.

In a field crop of Edelcanina (selections of *R.canina* L.) rootstock plants, significant phenotypic variation occurred for all plant characters investigated. Nurserymen partly disguise variation by grading the rootstock plants by standard classes for the diameter of the root collar. Even amongst plants of the same diameter (8-12 mm), both between and within batches of 'Inermis' of different provenance, significant variation occurred in branching of the roots, in the number of shoots, in the number of bottom-breaks and in the root collar diameter.

The effect of the plant density, as a possible source of variation, was investigated by growing 'Inermis' rootstock seedlings at nine plant densities between 30 and 190 plants per m². As density increased, the root collar diameter of one-season-old stocks decreased; the distribution of plants over diameter classes shifted from a majority of thick (>10 mm) to one of thin (≤6 mm) stocks; interplant variation for root collar diameter increased; biomass increased to a maximum at a density of 170 plants per m². Density significantly affected the expression of plant characters. Hence, as density increased, shoot number per plant decreased, shoots became longer and lighter, the root system became lighter and less well-branched, and the shoot/root (fresh) weight ratio decreased. Density did not affect the percentage of plants with crooked root collars. Phenotypic variation of plant characters of 'Inermis' is mainly attributed to variation in plant age and in plant-to-plant distance in the seedling field.

The diameter of the root collar of stocks at grafting had significant influence on the subsequent growth of 'Sonia' combination plants in the glasshouse. As the root collar diameter of the Edelcaninas 'Inermis', 'Brögs Stachellose' and 'Pollmers' increased from 3 to about 15 mm, the primary shoots of 'Sonia'

were longer, bottom-breaks emerged earlier and yield measured in terms of the number, weight and length of shoots, increased. After 12 months, the absolute fresh weight of the roots of thick stocks was greatest, but the increase in weight of thin stocks was much larger (20 fold) than of thick ones (2-5 fold). The shoot/root (fresh) weight ratio in 12-month-old plants was not affected by the original stock diameter, but 'Brögs Stachellose' induced higher ratios than 'Inermis' or 'Pollmers'.

Scion-rootstock relationships were studied by comparing the growth and development of own-rooted Hybrid Tea rose seedlings in the first year, with those of their clones grafted on 'Inermis' in the second year. Allowing for differences in level, the growth and development of Hybrid Tea seedlings generally agreed with those of their clones. The numbers of bottom-breaks and of harvested shoots of seedlings and clones were not affected by scion-rootstock interaction. As the vigour of scion genotypes increased, the quiescent axillary buds of scions sprouted sooner after grafting, while more bottom-breaks emerged in an earlier stage; over a 12-month period shoot yield was higher, and root weight of the stocks increased. The value set in practice on a high number of bottom-breaks as a basis for high flower production was confirmed. Breeders are recommended to use the number of bottom-breaks and the shoot yield in own-rooted seedlings as a predictor of the shoot yield of future cultivars.

In clones of weak Hybrid Tea cut rose seedlings, the rootstock 'Inermis' promoted the vigour of combination plants but, as the original seedling had been more vigorous, increase of the vigour of combination plants on 'Inermis' was smaller. In combination plants of various scion varieties grafted on one type of stock, the vigour is controlled by the scion variety rather than by the stock. The high cultural value attached to *R.canina* 'Inermis' as a rootstock, does not seem justified. A major component of the vigour of scion varieties is their branching capacity. Since branching capacity depends on degree of correlative inhibition, the ratio of auxins synthesized in the shoot and cytokinins produced in the root, is supposed to be the controlling mechanism of axillary bud-break. The lead in growth of vigorous over weak scion genotypes, is likely owing to a larger leaf area per plant as a result of earlier sprouting of more axillary buds after grafting or shoot harvest.

To investigate the possibility of (undesired) hybridization in Edelcanina rootstocks, first the genotypic variation of 'Inermis' was studied as to characters and adventitious root formation of individual rootstock plants. After 6 months in the glasshouse, originally uniform (8-12 mm) 'Inermis' stocks appeared to differ in internode length, number of leaflets per leaf and the leaf area. In 23-day-old softwood cuttings of different genotypes, significant genotypic variation occurred for the time of axillary bud-break, axillary sprout length and weight of adventitious roots. Between rootstock clones, the root weight of cuttings was correlated with: number of leaflets per leaf, leaf area, and days to axillary bud-break.

Subsequently, genotypic variation in *R.canina* 'Inermis' and 'Brögs Stachellose' was studied as variation in the growth and development of 'Sonia', grafted on clones of these stocks. Owing to different induction of vigour, 'Sonia' combination plants varied for: the date of emergence of the first and second bottom-break, the number of bottom-breaks, and the number of 'Sonia' shoots harvested after 12 months. Correlations between the root weight and the diameter of the graft union were significant for both 'Inermis' and 'Brögs Stachellose' clones. Graft unions of 'Brögs Stachellose' were always thicker than 'Inermis' of equivalent root weight. Genotypic variation of Edelcanina selections is attributed to hybridization with other Edelcaninas or other species. Finally, the effect of root clones of Hybrid Tea rose seedlings, pre-selected for vigour, was studied in 'Sonia' combination plants. For that purpose a complete Hybrid Tea rose seedling population was studied. In that population, the shoot yield of 8-month-old, own-rooted seedlings was negatively correlated with the time from seed germination to first flowering (juvenile period). The shoot yield of 12-month-old 'Sonia', grafted on root clones of low or high yielding Hybrid Tea seedlings, was positively correlated with both the yield of the original Hybrid Tea seedlings, and with the root weight of the clonal Hybrid Tea stocks.

In all experiments the shoot yield of 'Sonia' combination plants was positively correlated with the number of bottom-breaks per plant per rootstock. It was generally found that as rootstock clones induced a first bottom-break earlier, the second bottom-break emerged earlier as well. Furthermore, 'early' rootstock clones induced more bottom-breaks and more shoots per 'Sonia' plant than 'late' clones. The diameter of bottom-breaks at pinching, was not-significantly correlated with the number of harvested shoots of a clone. The vigour of rose genotypes appears to be an inherent character, that is expressed in both the aerial and subsoil parts. In combination plants, the vigour of the rootstock genotype is transmitted to the scion variety.

A major effect of vigorous rose rootstocks is an increased branching capacity of the scion variety, visible as earlier and more profuse axillary bud-break in all stages of plant development. Owing to induction of a larger branching capacity, scion varieties on vigorous stocks have a larger photosynthetically active area than those on weak stocks at an early stage of plant development. This results in a lead in growth. Main differences in the vigour of rootstocks are attributed to endogenous hormone action, a concept in which rootstocks are supposed to differ for cytokinin synthesis. A model of the vigour of combination plants, based on additive vigour of scion variety and the rootstock, derived from endogenous hormone action, is tentatively proposed.

Edelcaninas generally induce mediocre vigour, show genotypic variation for yield and are too large plants for most artificial substrates. Because Edelcaninas generally are recalcitrant to vegetative propagation, they are unsuitable as clonal stocks. Also, because healthy Edelcanina stocks can only be produced in fields that are chemically disinfected, the important role of these stocks for the glasshouse culture seems to be finished. If, despite these disadvantages Edelcaninas are yet to be improved by breeding, at short notice genotypic variation may be stabilized by selecting good-looking mother bushes, to be planted in monoclonal seed gardens. At long term, such seed gardens may be established with mother bushes of which the (seedling) offspring has been thoroughly tested for a range of characters.

For the modern cut rose culture in artificial substrates, clonal stocks should be given preference over seedlings. Populations for the selection of clonal stocks may arise from cross-breeding or genetic modification. Preliminary selection for rootstock vigour may be carried out on the basis of number of shoots and/or shoot length of individual genotypes. Vigorous genotypes are likely to occur among individuals with a short juvenile phase. Selection for rootstock genotypes that induce a high shoot/root (fresh) weight ratio at the same vigour of combination plants, should be an aim. The management of

combination plants on vigorous stocks is discussed. In weighing pros and cons of the use of self-rooted cultivars and those on a vigorous rootstock, preference is given to the latter.

# Basis of Research

**The present study is for the greater part based on the following scientific articles published between 1983 and 1990.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1983. Relations between basal bottom-breaks and harvested shoots in own-rooted Hybrid Tea-rose seedlings and their clones. Gartenbauwissenschaft 48: 189-192.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1983. Relations between time of sprouting of the scion in the nursery, the time of formation and number of basal bottom-breaks, and the number of harvested shoots of glasshouse rose clones on *R.canina* 'Inermis'. Scientia Hort.21: 375-379.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1984. Scion-rootstock relationships in Hybrid Tea-cut roses on *Rosa canina* 'Inermis'. Neth.J.Agric.Sci.32: 3-7.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1987. Variation for plant characters and for performance of softwood cuttings of *Rosa canina* 'Inermis' seedlings. Euphytica 36: 407-412.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1988. Shoot and root characters of one-season-old *Rosa canina* 'Inermis' rootstock seedlings in relation to the root collar diameter. Gartenbauwissenschaft 53: 30-33.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1988. Effects of plant density on root and shoot characters of one-season-old *Rosa canina* 'Inermis' seedlings. Gartenbauwissenschaft 53: 117-121.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1989. Variation for the shoot production of Rosa Hybrida 'Sonia', as induced by different Edelcanina rootstock clones. Gartenbauwissenschaft 54: 211-215.**

**DE VRIES, D.P. & Lidwien A.M. DUBOIS, 1990. The shoot production of 'Sonia' on Hybrid Tea rootstock clones of different vigour. Gartenbauwissenschaft 55: 268-271.**

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# Chapter 1

# General introduction

*'What's in a name ? A rose by*
*any name would smell as sweet'.*

*William Shakespeare (1564-1616).*

# Chapter 1. General Introduction

## 1.1. State of affairs

## 1.2. Objectives of this study

## 1.3. Outline of this study

## 1.1. State of affairs

This introductory chapter deals briefly with the culture of glasshouse rose cultivars, the rootstocks used for their propagation and the problems arising in the use of rootstocks in the glasshouse.

In The Netherlands the rose is the leading cut flower. About 900 ha cut roses under glass produced a value of more than Hfl. 750 million in 1991 (ANON., 1992). Estimations are that 25-30% of the area was on artificial substrate in 1990 (PEELEN, 1991), all being equipped with supplementary lighting.

Being highly heterozygous for most characters, rose cultivars must be propagated vegetatively to conserve the genotype. Methods of propagation include various kind of cuttings, layering or micropropagation to obtain self-rooted plants, and budding, bench grafting or cutting-grafting onto suitable rootstocks for combination plants.

Contrary to current views on the function of stocks, "originally roses were grafted for the purpose of getting them on their own roots" (BUCK, 1951), with the underlying idea that self-rooted plants were more true to type than those on roots of a strange kind. In spite of good rooting capacity of most cultivars, nowadays self-rooted plants form a minority, as they commonly lack vigour (yield) (DUBOIS et al., 1990a) and hardiness (HAENCHEN, 1982).

Commercial rose plants commonly are *combination plants* consisting of a scion variety (cultivar) which forms the aerial part, and a rootstock which is subsoil. Formerly, stocks were only used to obtain more plants of a cultivar with relatively little effort at a low price. Today, the primary objectives of stocks are to influence scion vigour and obtain adaptation to various cultivation media. In addition, stocks are used for their longevity and superior anchoring.

From the earliest reported use of rootstocks onwards, both clones and seedlings have been involved. In course of time clonal rose stocks have become popular around the Mediterranean, in the United States of America and in Australia, while seedling stocks mainly flourished in Middle- and NorthEurope and in Japan. For both categories of stocks, widely diverging species and cultivars of the various sections of the subgenus *Eurosa* Focke (REHDER, 1960) have been appraised (FERGUSON, 1933; BUCK, 1951; EDWARDS, 1955;

KRÜSSMANN, 1962; 1986). Today, scion variety and rootstock commonly belong to different species. Only a very restricted number of rootstocks are suitable to the greenhouse culture, upon which the present thesis is focussed.

In The Netherlands, current glasshouse cultivation in soil is almost 100% on Edelcanina *seedling* stocks, but in artificial substrates mainly *clonal* stocks of various origin, or self-rooted cultivars are used. For establishing new plantations and replacing old ones, more than 10 million rootstocks are used annually.

However advantageous the use of Edelcanina stocks may be, the plants of one scion-rootstock combination vary considerably in growth and development (KOOL et al., 1991). In cut roses this is manifest as an unacceptable variation in *individual* shoot yield per bush which, because the scion variety is considered a more or less unchangeable unit, is attributed to the stock (DE VRIES & DUBOIS, 1990).

During the seventies, when financial returns in the Dutch cut rose industry stabilized or even decreased, while prices of fuel and labour rose, also the moderate *overall production level* of cultivars on Edelcanina stocks was rightly questioned by growers. Parallel with these events, analysis of the yield level of new cut rose cultivars showed decreasing trends for large-, middle-, or small flowered cultivars over a seventeen year period (DE VRIES & DUBOIS, 1987). This indicates that in spite of other major improvements, yield of cultivars (all grown on Edelcanina stocks) is likely to have reached maximum level. It is expected, therefore, that further progress in yield may result from improved stocks and cultural measures, rather than from new cultivars.

Even without further research, variation of rootstocks is credible, because a field crop of Edelcanina is so variable for plant size, that externally uniform batches can only be produced by grading for root collar diameter. This situation suggests both strong environmental effects and/or genotypic variation for vigour.

Surprisingly, until about 1980 rootstock research had been mainly confined to testing the shoot yield of new cultivars on stocks that had already received local or nation-wide attention. Experiments have nonetheless resulted in discarding several unsuitable or low yielding stocks and in promoting Edelcaninas. It is notable, however, that in experiments involving both clonal and Edelcanina stocks, the former category usually gave highest yields (DUBOIS et al., 1990a). Within the limited choice of rootstocks for the greenhouse, empirical knowledge is that a high yielding stock would not be optimal for all cultivars, thus suggesting scion-rootstock interaction for yield.

In spite of the demand for better yielding stocks, for various reasons rootstock breeding is not undertaken. The relative ease, however, by which current high yielding clonal stocks for artificial substrates were selected, may show great promise for future breeding.

It is concluded that current combination plants for the glasshouse consist of highly specialized scion varieties and relatively underdeveloped stocks. This means that performance of combination plants has hitherto been sub-optimal mainly owing to stocks that do not meet requirements of modern culture. This state of affairs, which is irreconcilable with the important position of the cut rose industry in Dutch horticulture, has stimulated both research workers and growers organizations to substitute a practical for a more fundamental approach of rootstock research.

## 1.2. Objectives of this study

It is characteristic of rose rootstock research, that it has always been carried out on an empirical basis and on combination plants. Therefore, todays scientific approach is seriously hampered by lack of information about the individual vigour of scion varieties and rootstocks. Moreover, the underlying mechanisms of variation in the vigour of both scion varieties and rootstocks have been left unstudied. A scarcity of parallels with other woody crops aggravates this situation. As a preliminary to essential improvement of stocks by breeding, the present study investigates aspects of the variation in vigour of individual rootstocks, of scion varieties and of their combination plants.

It is proposed to express the 'vigour' of cut rose plants, either self-rooted or on a rootstock, by mainly the parameter 'shoot yield'. Thus a horticultural rather than a physiological approach (POORTER, 1991) has been chosen.

Because of their importance for the Dutch cut rose industry on the one hand, and major problems arising in their use on the other hand, experiments were mainly carried out with Edelcanina rootstocks. In experiments with one scion variety only, the well-known cultivar 'Sonia' ('Sweet Promise') was used.

## 1.3. Outline of this study

Horticultural terminology as used in this study, the propagation of cultivars, glasshouse conditions, growth and development of cut rose combination plants, and the probable hormonal basis of yield are reviewed in Chapter 2.

Aspects of the phenotypic variation of Edelcanina rootstocks, variation owing to plant density in the field, and after-effects of this variation as to stock diameter on the growth and development of 'Sonia' combination plants, are studied in Chapter 3.

Scion-rootstock relationships, with emphasis on the growth and development of scion genotypes, own-rooted and grafted on *R.canina* 'Inermis' rootstocks, are investigated in Chapter 4.

The genotypic variation in Edelcanina and Hybrid Tea rootstocks and the effects of variation in rootstock vigour on the growth and development of 'Sonia' combination plants, are studied in Chapter 5. A model of scion and rootstock vigour in combination plants is proposed.

Possibilities of improvement of the uniformity of seedling Edelcaninas and the vigour of clonal rose rootstocks by breeding, as a result of the present study, are considered against the background of breeding clonal fruit rootstocks in Chapter 6.

The impact of vigorous rootstocks on plant management, and the pros and cons of the use of self-rooted scion varieties in cut rose culture, are the subjects of the Practical Consequences considered in Chapter 7.

# Chapter 2

# Production and growth of combination plants

## synopsis

*'Ik heb je nooit een rozentuin beloofd*
*Ik heb alleen gezegd dat er een tuin zou komen*
*Maar jij, jij had alleen maar rozen in je hoofd*
*En daar bleef je over malen en van dromen......'*

*Paul van Vliet, Westbroekpark, 1984.*

# Chapter 2. Production and growth of combination plants

*synopsis*

2.1. Introduction

2.2. Production of cut rose combination plants

2.3. Glasshouse conditions

2.4. Growth and development of cut rose combination plants

2.5. Enhancement of the number of bottom-breaks

2.6. Correlative inhibition and shoot yield in the rose

## 2.1. Introduction

This chapter introduces the terminology, methods of propagation and glasshouse conditions of cut rose culture. The growth and development of glasshouse-grown rose cultivars in the *first* year, as studied in this thesis are described. Enhancement of the emergence of bottom-breaks, which form the physical basis of shoots to be harvested, is reviewed.

Within the scope of the present study, analysis of phytohormones has not been carried out. Nevertheless, endogenous hormone action is supposed to be the underlying mechanism of inhibition and sprouting of axillary buds in the rose. Therefore, the literature concerning this subject in the rose is considered in some detail.

## 2.2. Production of cut rose combination plants

In The Netherlands, cut rose plants on seedling stocks are raised by bench grafting or by budding. Combination plants on clonal rootstocks for the culture in artificial substrates, are cutting-grafted or root grafted, both methods yielding the required easy-manageable small plants.

*Bench grafting* is usually carried out between December and April. Scions of the cultivar, consisting of a piece of internode with a shortened leaf and a quiescent axillary bud, are 'rind grafted' (GARNER, 1958) onto one-season-old 8-12 mm thick stocks. Subsequently, young combination plants are raised at high temperature (20-25°C) and high air humidity in the nursery glasshouse. In this system plants are ready for planting 3-4 weeks after grafting. By selecting for uniformity of young plants, propagators disguise initial differences in sprout length of the scion springing from (i) variation in graft-take, (ii) the original position of the scion on the shoot (DE VRIES & DUBOIS, 1992) or (iii) variation of the rootstock (see Chapter 5).

*Budding* may be subdivided into 'early' or 'late'. *Early budding* is carried out in the field in May-June, onto 6<8 or 8-12 mm stocks planted in late winter. After cut-back of the stock in June-July, the bud of the cultivar will sprout so that combination plants with 1-2 light shoots may be planted in the glasshouse from November onwards. These field-grown plants are graded by length of the shoot and diameter of the root collar (LOUVENBERG, 1989). Traditionally, *late budding* is carried out in July-August. Unlike outdoor roses, few plants for the glasshouse are still being raised in this way. If so, plants may be either planted in the glasshouse with a 'dormant eye' in November of the same year or, as is now considered old-fashioned, as a bush in November of the next year.

The process of *cutting-grafting* (McFADDEN, 1963; OHKAWA, 1980; 1984a), also named 'slant grafting' (HANAN & GRUEBER, 1984), is referred to as *stenting* in The Netherlands (VAN DE POL & VAN DER VLIET, 1979; VAN DE POL & BREUKELAAR, 1982). Internodes, or 5-7 cm long pieces of shoots of the rootstock plant are 'splice grafted' (GARNER, 1958) with scions of the cultivar, consisting of a piece of internode with a complete subtending leaf and a quiescent axillary bud. Both plant parts are temporarily held together with a clothes-peg. Before striking, the proximal end of the stock internode is treated with a synthetic auxin (usually indole-3-butyric acid, IBA) to promote adventitious rooting. Newly-made cutting-grafts are grown at high temperature (25-30°C), at a light intensity of 10-15 $Wm^{-2}$ and at high air humidity, in blocks or cylinders of rockwool. In most new clonal stocks, union of scion and stock, adventitious root formation of the stock and sprouting of the scion, in this order, occur in 3-4 weeks time. Cutting-grafting clonal Edelcanina, however, has limited success only (BAKKER, 1987).

The method of *root grafting* follows a similar course as cutting-grafting, but instead of internodes of the clonal rootstock, about 5 cm long pieces of root of rootstock seedlings or of well-rooted clonal rootstock plants are used (VAN DE POL, 1986). Root grafting might be considered a highly successful method, if only conveyance of soil-borne diseases to artificial substrates (HUIS IN HET VELD et al., 1988) could be prevented.

In view of present change of cut rose culture from soil to artificial substrates, the rather large-sized bench grafted or budded plants are expected to give way to cutting-grafted, root grafted or self-rooted plants before the turn of the century (C.A.M. Groenewegen, Nursery Advisory Service, Personal Communication).

## 2.3. Glasshouse conditions

The yield and quality of cut roses are determined by (i) the cultivar, and (ii) the environment in which the crop is grown. Flower production in roses following the "solar energy curve" (POST & HOWLAND, 1946), light is doubtless the major factor determining rose production in glasshouses where year-round culture is pursued. For that reason, in the temperate zone, natural daylight in glasshouses is supplemented with various sources of photosynthetic active radiation in winter.

Roses of the perpetual flowering category, to which all cut roses belong, are genetically programmed to initiate an apical flower bud on each shoot (SEMENIUK, 1971a; DE VRIES & DUBOIS, 1978) when, depending on the genotype, a more or less constant number of leaves has segregated (LINDSTROM, 1956; HORRIDGE & COCKSHULL, 1974; DE VRIES et al., 1981). Cut roses, being day-neutral (WAREING & PHILLIPS, 1981; HALEVY, 1984), plants will continuously initiate flowers and produce marketable flowering shoots in the glasshouse, unless that process is seriously intervened by external factors (MASTALERZ, 1987). The most serious intervention is by low light intensity, as occurring in winter. This causes early abortion of flower buds (MOE & KRISTOFFERSEN, 1969; DE VRIES, 1977; DE VRIES & SMEETS, 1978), leading to the formation of 'blind shoots'.

Temperatures of 15-20°C during the night and 18-25°C during day-time are considered optimal for most cultivars (VAN DEN BERG, 1987), but many significant deviations from that generalization are practised depending on the time of year, the scion variety and individual aims of the grower.

Until about 1980, soil was the only root substrate used in glasshouse culture. However, since that time an increasing percentage of the acreage is occupied by artificial substrates, mainly consisting of rockwool. It is estimated that about 30% of a total of 900 ha under glass in The Netherlands was on artificial substrate in 1991 with supplementary lighting (PEELEN, 1991).

## 2.4. Growth and development of cut rose combination plants

Under the same glasshouse conditions, the growth and development of combination plants of various cultivars follow a similar course. As this conduct is, in principle, the same for bench grafted, cutting-grafted or budded combination plants (VAN DE POL et al., 1988b), the growth of the first plant type which has been mainly used in this study, is described. Taking 'time of grafting of the scion' as a starting point (Fig.2.1.1.), in most cultivars the axillary bud of the scion breaks after 10-20 days, developing into the 'primary shoot' that flowers in 8-12 weeks from grafting (DE VRIES, 1976b) (Fig.2.1.2.). When apical dominance of one or more distal axillary buds of the primary shoot has released, which usually occurs before anthesis (DE VRIES et al., 1986), these buds will sprout and grow out into lateral shoots that are longer than the primary shoot itself (Fig.2.1.2.). Consequently, unsupported primary shoots will become top-heavy and topple over (Fig.2.1.3.). Bending or natural toppling over of the primary shoot promotes breaking of its lowest quiescent buds about 15 weeks after grafting (see Chapter 4). In principle, two buds at the base of the primary shoot, initially incorporated in the axillary bud of the scion, are ready for that event (MOR & ZIESLIN, 1987). Exceptionally vigorous shoots growing from these buds (Fig.2.1.3.) are termed 'basal bottom-breaks'. In later stages of growth, other low positioned axillary buds may sprout as well. Equally vigorous laterals of basal bottom-breaks, originating from axillary buds situated 10-30 cm above the base of the plant (Fig.2.1.3.), are termed 'renewal canes', 'axillary bottom-breaks', or 'secondary bottom-breaks' (ZIESLIN et al., 1972).

Bottom-breaks are thicker, much longer and bear about 50-80% more leaves than their lateral shoots (D.P. de Vries, unpublished results). They form the frame of a rose bush and may as such last its lifetime. Neither the physiological or morphological basis, nor the probable presence of genes from non-perpetual flowering species that have contributed to the Hybrid Tea class, have been studied in relation to the extraordinary vigour of bottom-breaks.

In order to obtain marketable shoots, bottom-breaks are pinched, viz. pruned-down to a length of 25-40 cm. Depending on the stage of development in which pinching is practised, it is named 'soft', viz. when the flower bud is

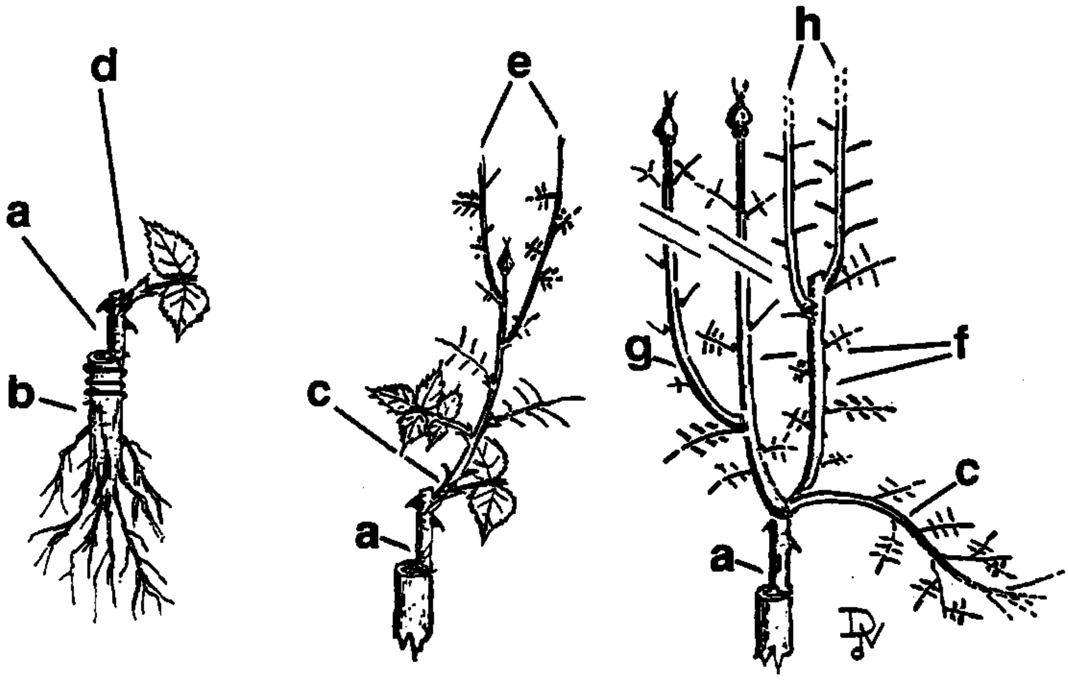

*Fig.2.1.1* *Fig.2.1.2* *Fig.2.1.3*

*Fig. 2.1. Stages of initial growth and development of a bench grafted rose plant.*
*2.1.1. Day 0: scion (a) grafted onto a seedling rootstock (b); 2.1.2. 10 Weeks old: primary shoot (c) grown from quiescent bud (d); two upper axillary buds grown out into laterals (e); 2.1.3. 18 Weeks old: primary shoot (c) toppled, basal bottom-breaks (f) grown from lowest axillary buds; axillary bottom-break (g); basal bottom-break hard pinched, two (saleable) laterals (h).*

'pea-sized' and the shoot still herbaceous, or 'hard' when the flower bud is well-developed and the shoot is partly lignified (MASTALERZ & LANGHANS, 1969). Harvesting of a bottom-break with a marketable flower may considered a form of hard pinching. Both soft- and hard pinching, in most cultivars result in the sprouting of the 1-3 distal axillary buds of a bottom-break (Fig.2.1.3.). About 6-8 weeks after pinching, the first marketable product of a young plant is obtained by harvesting the lateral shoots that have developed from these sprouts. From that moment on, combination plants may continuously produce saleable (lateral) shoots from lateral shoots.

Marketable shoots are harvested by cutting just above their first or second five-leaf from below. After harvest (decapitation of the shoot), one or more axillary buds that would remain quiescent in non-harvested plants, are now in an apical position and will commonly sprout within 1-3 weeks (VAN DEN BERG, 1987). Because a piece of shoot of about 10-15 cm is left after each harvest, plants gradually increase in height. Owing to the fact that after pinching the bottom-breaks or after harvest of the lateral shoots, usually more than one axillary bud will break, cut rose plants become progressively broader as they grow higher.

It is notable, that owing to various factors (ZIESLIN et al., 1973; 1976a), both environmental and physiological, the above described growth and development is not identical for the same combination plants, even when grown under similar conditions.

In practice, the shoot yield of a cultivar is expressed as the number of saleable flowers per $m^2$ glasshouse per calendar year. Because the number of plants per $m^2$ is dependent upon the habit of the cultivar and the (highly variable) plant-to-plant distance, in this study the ***number of shoots per plant per annum*** is used. Both among growers and in practical research the shoot yield attained in the second year is considered representative for 'the yield level' of a certain cultivar-rootstock combination. However, the significant correlations between the first and the second year's yields of numerous cultivars as found by DE VRIES & DUBOIS (1987), indicate the first year's yield to be an accurate parameter. For that reason most of our experiments were continued for about 12 months only.

Dozens of experiments have demonstrated that, given a certain environment, rootstocks are capable of significantly modifying the yield level of the scion variety (DUBOIS et al., 1990a). It is notable that in all major rootstock experiments published, 'shoot yield' (number of harvested shoots) of the cultivar has been used as a parameter of the 'vigour' of the stocks used. In such experiments accuracy of results is enhanced by the maintenance of an even harvesting level among the plants of an experiment. In all experiments in this study we have followed the above approach, in which the vigour of either different scion varieties on one rootstock, or of one scion variety on different stocks, is expressed by the parameter 'shoot yield'. It is realized that 'fresh weight' of the harvested shoots might have been a much better, but rather unpractical parameter of vigour.

## 2.5. Enhancement of the number of bottom-breaks

Between cultivars, genotypic variation of the number of bottom-breaks occurs (BACHRACH, 1971; ZIESLIN et al., 1976a; ANON., 1988; Section 4.5.1.). Furthermore, within cultivars competition and difference in the time of emergence lead to variation in the number of bottom-breaks per plant (KOOL et al., 1991; Section 4.5.3.). As bottom-breaks form the physical basis of future shoots to be harvested (KOFRANEK & FISCHER, 1949), various experiments were carried out to promote their emergence in combination plants (ASEN & HAMNER, 1953; BREG, 1980; KHAYAT & ZIESLIN, 1982). Although cleverly disbudding enhanced the number of bottom-breaks of young rose plants (ZIESLIN et al., 1976b), the majority of experiments were carried out with established rose bushes rather than, as should be preferred, with young ones. To my best knowledge, in The Netherlands disbudding has only been applied for experimental purposes.

Based on accelerated release from apical dominance of normally quiescent axillary buds in the lower part of the plant, effective but laborious methods have been developed to apply various synthetic hormones. Either after pruning or scarification, synthetic cytokinins in aqueous sprays or dissolved in agricultural foam, successfully broke quiescence of axillary buds in established bushes (CARPENTER & RODRIGUEZ, 1971; PARUPS, 1971; CARPENTER, 1975; OHKAWA, 1984b), resulting in the desired development of bottom-breaks. Benzylamino-tetrahydropyranyl (PBA) or gibberellic acid, applied in lanolin paste (FABER & WHITE, 1977), induced a larger number of bottom-breaks. PBA, applied via flower tubes to cut-surfaces of shoots (VAN DE POL & MARCELIS, 1988), released numerous axillary buds from inhibition but did not enhance bottom-break emergence. Contrary to that, aqueous solutions of benzylaminopurine (BAP), applied in a similar way to young 'Madelon' and 'Vivaldi' plants grown in nutrient solution, did enhance bottom-break emergence (F.W.A.Verstappen, CABO-DLO, Wageningen, Personal Communication). In addition to cytokinins, the ethylene-producing substance ethephon, employed to plants without leaves, effected release from inhibition as well (ZIESLIN et al., 1972; MOR & ZIESLIN, 1987).

In spite of the above results, neither cytokinins nor ethephon have found practical application for this aim in The Netherlands.

## 2.6. Correlative inhibition and shoot yield in the rose

**Since the cut flower trade requires long, straight, unbranched rose shoots, breeders select upright-growing, long-stemmed genotypes in seedling populations (see Chapter 4). Deliberate choice of this plant type results in cultivars of which the axillary buds on shoots display strong correlative inhibition . This means that going downwards from the apex of a rose shoot, successive axillary buds are increasingly inhibited (quiescent) (ZIESLIN & HALEVY, 1976). It should be noted that variation for correlative inhibition has been observed. Correlative inhibition in the rose has two known effects on shoot yield. It influences (i) the number of quiescent buds that break after each harvest (ZIESLIN et al., 1973), viz. the 'degree of branching', and (ii) the lapse of time between the previous harvest and actual bud-break (VAN DEN BERG, 1987).**

**The general role of auxins, mainly indole acetic acid (IAA), in correlative inhibition of plants is well-established, but interpretations of its mode of action have changed in course of time (PHILLIPS, 1969; WAREING & PHILLIPS, 1981; HILLMAN, 1984; TAMAS, 1987; RUSSELL & THIMANN, 1988; CLINE, 1991; TAMAS et al., 1991). In search of an acceptable model for hormonal action in correlative inhibition in the rose, several authors have studied bud-break in relation to endogenous hormones. It is remarkable that in these rose studies only IAA, cytokinins, and rarely abscisic acid (ABA) have been considered. Major results are reviewed in this paragraph.**

**As in other crops, axillary bud inhibition (quiescence) in the rose is mainly attributed to IAA, synthesized in the shoot apex (ZIESLIN et al., 1976a). In 'Baccara', besides IAA other inhibitors including ABA, would be involved (ZIESLIN et al., 1976b; 1978; ZIESLIN & HALEVY, 1978).**

**Assuming cytokinins to play an active role in release from inhibition by antagonizing IAA, VAN STADEN et al. (1981) and VAN STADEN (1982) investigated cytokinin levels in axillary rose buds. Initially, buds lower on the shoot (which are more inhibited than more apically positioned ones), contained higher instead of lower cytokinin levels. In using labelled $^{14}$C-zeatin, the same authors demonstrated upward cytokinin transport from subtending leaves (which do contain natural cytokinins) towards axillary buds sprouting**

after harvest, thus hinting a positive role of cytokinins in bud-break.

After complete decapitation of established rose bushes by sawing them off a few centimeters above the graft-union, prior to outgrowth of basal shoots, high levels of both bud inhibiting ABA (cis-configuration) and of cytokinins were detected in root collar tissues. Only when owing to high light intensity cis-ABA had changed into trans-ABA (which would be much less inhibitive), plants would sprout again (ZIESLIN & KHAYAT, 1983). In spite of its presence (and inhibitive properties) in old rose buds, there is no indication of a general function of ABA as *the* correlative signal from dominant organs like the apex (TAMAS, 1987), thus suggesting a major role of IAA. VAN DEN BERG (1987) rightly distinguished between the lateral bud-break in complete and harvested rose plants, and attributed great sense to the sink of the top meristem in maintaining correlative inhibition. MOR & ZIESLIN (1987) proposed a balance between cytokinins and 'inhibitory complex' in the regulation of axillary bud-break after harvest. Despite the above studies, a consistent working-hypothesis about the effects of single- or interactive endogenous hormones on the growth and development of rose combination plants has not been put forward. It is clear, however, that correlative inhibition, or rather release from inhibition after harvest plays a central role in the yield capacity of cut rose combination plants. As correlative inhibition is hormone controlled, it is proposed to discuss the variation in vigour of scion varieties and of rootstocks against the background of probable endogenous hormone action in this study (Sections 4.6.3., 5.6.4., 5.6.5.).

# Chapter 3

# Phenotypic variation in seedling Edelcanina

*'Science deals with names and shapes, quantities and qualities, patterns and laws; it is all right in its own place. But life is to be lived; there is no time for analysis. The response must be instantaneous - hence the importance of the spontaneous, the timeless. It is in the unknown that we move. The known is in the past'.*

*Sri Nisargadatta Maharaj, 1973. I Am That. Chetana, Bombay, p.261.*

# Chapter 3. Phenotypic variation in seedling Edelcanina

## 3.1. Summary

## 3.2. Introduction

**3.2.1. History of seedling rose stocks. *Review***

**3.2.2. Edelcanina seedling stocks for the glasshouse**

**3.2.3. Production of Edelcanina seedling stock**

## 3.3. Aims of present chapter

## 3.4. Material and methods

**3.4.1. *Experiment 1.* Variation within and between batches of *R.canina* 'Inermis'**

**3.4.2. *Experiment 2.* Effects of plant density in the field on *R.canina* 'Inermis'**

**3.4.3. *Experiment 3.* The growth of 'Sonia' on Edelcanina of different root collar diameter**

## 3.5. Results

**3.5.1. *Experiment 1.* Variation within and between batches of *R.canina* 'Inermis'**

**3.5.2. *Experiment 2.* Effects of plant density in the field on *R.canina* 'Inermis'**

**3.5.3. *Experiment 3.* The growth of 'Sonia' on Edelcanina of different root collar diameter**

## 3.6. Discussion

**3.6.1. Growth and development of seedling stocks**

**3.6.2. Effects of plant density in the field**

**3.6.3. Improvement of external uniformity of Edelcanina**

**3.6.4. Effects of the root collar diameter on the growth of 'Sonia' combination plants**

## 3.1. Summary

One-season-old *R.canina* 'Inermis' plants of various provenance, graded by standard classes of root collar diameter, were studied as to variation of plant characters occurring in (i) a commercial field, (ii) commercial batches, (iii) plots of various plant density. After-effects of variation in root collar diameter were studied in combination plants of the scion variety 'Sonia' with 'Inermis', 'Brögs Stachellose' or 'Pollmers' as a rootstock.

In batches of ungraded rootstock plants, and between and within 28 batches of 'Inermis' graded by 8-12 mm root collar diameter, significant variation for plant characters occurred. The diameter of the root collar was positively correlated with the number of shoots and the branching of the root system.

As plant density increased from 30 to 190 plants $m^{-2}$, the root collar diameter of stocks decreased; the distribution of plants over diameter classes shifted from a majority of thick (>10 mm) to a majority of thin stocks ($\leq$6 mm); interplant variation for root collar diameter increased. The biomass increased until 170 plants $m^{-2}$. In the 6<8 mm class, which was modal at most densities, expression of plant characters was significantly affected by the density. Hence, shoots grew longer as density increased, but shoot number and shoot weight decreased. The roots became lighter and branched less, while plants became relatively 'rootier'. Plant density did not affect the percentage of seedlings with crooked root collars.

A major factor of heterogeneity of Edelcanina stocks is irregular plant distance in the field. Uniformity of stocks, which is a commercially desirable quality, may be enhanced by (i) improved stratification, (ii) sowing more thinly in rows that are closer together in the field, (iii) spaced planting of pre-grown plantlets, or (iv) grading by number of shoots in addition to that for root collar diameter.

The growth and development of 'Sonia' combination plants in the glasshouse was significantly affected by the root collar diameter of 'Inermis', 'Brögs' and 'Pollmers' rootstocks at grafting. As stocks had been thicker, primary shoots of 'Sonia' were longer, 1st, 2nd and 3rd bottom-breaks

emerged earlier, and yield, either as shoot number, shoot weight or shoot length increased. Although absolute (fresh) root weight after 12 months was largest in initially thick stocks, weight-increase was larger in thin (20 fold) than in thick ones (2-5 fold); also the volume of soil held by thin stocks was much larger (about 40 $dm^3$) than of thick ones (about 10 $dm^3$). Shoot/root (fresh) weight ratio of the combination plants was not affected by the initial root collar diameter. However, this ratio was larger for 'Sonia' on 'Brögs' than on 'Inermis' or 'Pollmers'. Of the three stocks, the yield of 'Inermis' in all grades was superior but, particularly in the thicker diameters, 'Brögs' combined quantity and quality of shoots.

A major effect of phenotypic variation for diameter is, that at the cost of scion growth, initially thin stocks appear to make up for arrears in development.

## 3.2. Introduction

### 3.2.1. History of seedling rose stocks. *Review*

In rose growing, earliest use of stocks has been reported in the mid-seventeenth century when, according to a manuscript by J.Rea in 1676, the best stocks were "Damask Rose (*R.damascena* Mill.), White Rose (*R.alba* L.), Franckfort Rose (*R.francofurtana* Muench) and the Wilde Eglantine (*R.rubiginosa* L.)" (FERGUSON, 1933). Seedlings of the Sweet Briar (*R.rubiginosa* L.), a species that is endemic in Europe (REHDER, 1960), have been used until today, the other three have lost significance as a stock. More general appreciation of seedling stocks, particularly of *R.canina* L., dates from the beginning of the 19th century (SAUL, 1850; BUCK, 1951). However, not before 1900 seed gardens for *R.canina* L., *R.multiflora* Thunb. and *R.rubiginosa* L. were established in the Dutch province of Groningen (SMIT, 1974). From about 1920, selections within *R.canina* L., the so-called Edelcaninas, became gradually more important (ASTREGO, 1955; AKKERMAN, 1978a). In general, the Edelcaninas distinguish themselves from unselected *R.canina* L. (which is still used as a stock), in being more homogeneous, and by specific characteristics (LEEMANS, 1964). Particularly in Denmark, N.Germany and The Netherlands, the production of seedling stocks has become an important branch of arboriculture. Estimations are that a total of about 300 ha of seedling stocks are being grown in these countries, producing roughly 250 million plants annually.

The choice of stocks is strongly influenced by the environment in which combination plants will be cultivated. Since about 1930, when Aalsmeer rose culture under glass became a flourishing industry, a relatively sharp division between stocks suitable for 'outdoor' or 'glasshouse' roses has been observed. Nowadays, for the Dutch cut rose culture in soil, exclusively Edelcaninas are used, which form only a small part (5-10%) of the total seedling rootstocks produced in The Netherlands.

### 3.2.2. Edelcanina seedling stocks for the glasshouse

Despite the recent introduction of clonal 'Inermis', it should be noted that Edelcaninas in principle are seedling stocks. Out of about 17 Edelcanina selections available (LEEMANS, 1967), only three have still significance for Dutch glasshouse culture in soil, viz. 'Inermis', 'Brögs Stachellose' and 'Pollmers' (VAN MARSBERGEN, 1983). These stocks were primarily selected for outdoor roses, but for want of better alternatives have also been used for cut roses ever since glasshouse culture started. Like *R.canina* L., the pentaploid ($2n=5x=35$) Edelcaninas have a system of gamete formation that, given the proper conditions for pollination, may guarantee relatively good quality and uniformity of seedlings (FAGERLIND, 1940; Section 5.2.1.). In addition to reliable, be it mediocre glasshouse performance, these Edelcaninas have a reputation for being thornless, which is an advantage in grafting and budding.

*R.canina* 'Inermis' was selected from segregating seedling populations by Gamon in Lyon, France, and introduced around 1905 (KRÜSSMANN, 1954). Of the three Edelcaninas mentioned, 'Inermis' is doubtless the most frequently used and most popular rootstock for both glasshouse and outdoor roses. Estimations are that in The Netherlands about 60-70% of the glasshouse roses are on this stock.

*R.canina* 'Brögs Stachellose' was raised by Robert Brög, Reckenbach bei Lindau, Germany, and commercialized in 1902 (KRÜSSMANN, 1954). Although 'Brögs' was referred to as a high yielding stock (WASSCHER, 1955; PESSALA, 1977), its value has been underrated in The Netherlands, probably owing to its poor fruit set and therefore low production of seedlings.

*R.canina* 'Pollmers' ('Pollmeriana'), classified by KRÜSSMANN (1962) as *R.coriifolia* Fries., would have originated from the cross *R.setigera x R.canina*, carried out by Pollmer, Grossenhein, Germany. The authenticity of this cross is doubtful because *R.setigera* is a diploid. 'Pollmers' was commercialized in 1904 (KRÜSSMANN, 1954). It is noteworthy that morphologically these three stocks are so much alike that their plants may only be distinguished by connaisseurs.

In spite of their established reputation for glasshouse roses, already in the fifties Edelcanina stocks were found to be much less uniform than initially was assumed by Dutch nurserymen (FLOOR, 1955). However, only from 1980 onwards growers have voiced their discontent with both the plant-to-plant variation for shoot yield of cultivar-rootstock combinations, and with overall yield per area glasshouse. Simultaneously, the current trend to cultivate cut roses in artificial substrates like rockwool instead of in soil, has further discredited the usually too large-sized young plants on Edelcanina rootstocks. Both variation and changed cultivation have turned the grower's attention to clonal rootstocks (DUBOIS et al., 1990b).

### 3.2.3. Production of Edelcanina seedling stock

The production of external (phenotypic) and internal (genotypic) uniform seedling rootstocks is hampered by a number of events occurring before sowing or during growth in the field. Achenes ('seeds') of important Edelcaninas are commonly produced in local seed gardens exploited by individual nurseries. Those of minor stocks are often obtained from the jam industry in e.g. the Balkans. In the seed gardens, mother bushes are seedlings that, upon close examination, show small variation for plant habit, thorniness, flowering capacity or seed production (LEEMANS, 1967). Besides Edelcaninas, seed gardens commonly contain a number of other rose species used as a stock. Because in most years flowering occurs simultaneously (AKKERMAN, 1978b), cross-pollination rather than desired self-pollination of mother plants occurs. Taken into account good possibilities of natural hybridization (KROON & ZEILINGA, 1974), current Edelcaninas are likely to be genetically variable, indicating that genotypic variation for characters, including the diameter of the root collar, may be expected. Effects of hybridization, which are probably enhanced by long-standing nursery tradition to establish new seed gardens with seedlings, are studied in Chapter 5.

An important drawback in seedling production is deep seed dormancy (ROWLEY, 1956; JACKSON & BLUNDELL, 1963), which in *R.canina* takes two, and in most other species one year stratification to break (ANON., 1964). Although sulphuric acid has been successfully used in breaking down the testa, thus reducing the stratification period to one winter only (ANON., 1979; ROBERTS, 1979), the method is considered risky and has not found application in The Netherlands. Initial successes in breaking seed dormancy with hormones like gibberellins or cytokinins (MOREY, 1956; FOSTER & WRIGHT, 1983) have neither found practical application.

In nursery practice, stratified seeds are machine-sown in the field, in beds consisting of 4-5 rows each, in March-April. Depending on the type of stock 600.000 - 1.000.000 plants per ha are aimed at. Economically optimal density for 'Inermis', yielding the highest percentage of 6<8 mm seedlings, would be 7-8 x $10^5$ plants per ha (ASTREGO, 1955). Prior to sowing, nurserymen carefully determine the desired plant density with seed vitality and germination percentage as parameters. In spite of that, due to unpredictable factors (soil conditions, weather, pests, diseases) actual germination is low (30-40%) and erratic (SCHWAMBORN & SCHMADLAK, 1968). This causes plants of different age to be unevenly distributed over the field after emergence. In late summer, fields are thoroughly inspected for the occurrence of 'rogues', which are removed. From the last week of November onwards, about seven-month-old seedlings are mechanically lifted, a process that combines pruning of the roots, cut-back of the shoots and bundling of the plants (SMIT, 1974; VAN DER ZWAAN, 1981).

A field crop of Edelcanina rootstock plants is heterogeneous to such a degree (ASTREGO, 1955; ANON., 1974; AKKERMAN, 1978a), that uniform batches required for the various propagation procedures must be created by (hand) grading for root collar diameter. Common diameter classes for Edelcanina are 2<3, 3<4, 4<6, 6<8, (8<10), and/or 8-12 mm. The latter class includes root collar diameters >12 mm as well. Usually there is a surplus of plants in the 2<3 mm class (DE BRESSER, 1984), which are either discarded or exported to Italy. For the cut rose industry diameter classes 6<8 and 8-12 mm are used for early budding and bench grafting respectively.

Although grading by root collar diameter is assumed to be conducive to even shoot production of cut roses, its effects have not been confirmed by research.

## 3.3. Aims of present chapter

In agreement with nurserymen's practice to grade stocks by root collar diameter and judge their cultural value by that parameter, the diameter of the stocks was the primary observation in this study.

In spite of being graded by root collar diameter, the plants in batches of Edelcanina stocks would still differ for number of shoots, number of bottombreaks and branching of the root system. It is unclear whether these differences, if present at all, are attributable to genetic variation or to environmental effects. Anyhow, environmental factors (Section 3.2.3.), especially the plant density (ASTREGO, 1955; ANON., 1974), are expected to influence the growth and development of seedlings in the field, and hence the expression of their individual characters.

In the present study only phenotypic variation of plant characters is considered. Hence, neither the contribution of genotypic variation nor of environmental effects were distinguished. Genotype x environment interaction was neither investigated.

The *first* aim of this chapter is to investigate variation of the root collar diameter and of shoot and root characters occurring within and between batches of graded and ungraded *R.canina* 'Inermis' rootstock plants of different provenance.

The *second* aim is to investigate the effects of plant density in the seedling field on the variation in root collar diameter, and on shoot and root characters of *R.canina* 'Inermis' plants.

The *third* aim is to investigate the effect of phenotypic variation in root collar diameter of one-season-old *R.canina* 'Inermis', 'Brögs Stachellose' and 'Pollmers' stocks, on the subsequent growth and development of 'Sonia' combination plants in the glasshouse.

## 3.4. Material and methods

### 3.4.1. *Experiment 1.* Variation within and between batches of *R.canina* 'Inermis'

The variation in shoot and root characters of 'Inermis' seedling stocks was studied. An ungraded field crop was compared with batches graded by 8-12 mm, obtained from various nurseries. The experiment was carried out at and in co-operation with, the arboricultural experimental garden at Noordbroek, The Netherlands.

*Plant material*

Plant material consisted of two categories of one-season-old *R.canina* 'Inermis' stocks: (i) an (ungraded) field crop consisting of 177 seedlings grown at a plant density of about 750.000 seedlings per ha, and (ii) 28 different batches of at least 100 stocks each, graded by 8-12 mm, obtained from different nurseries in Denmark, Germany, and The Netherlands. Because the latter plants were the starting material of a selection programme for clonal 'Inermis' (Section 6.1.1.), a broad genetic base was ensured by sampling only batches from nurseries that exploited their own seed garden.

*Observations*

Of individual plants of both categories, the root collar diameter (mm), number of shoots, number of bottom-breaks, and degree of branching of the root system (1 = tap root, ....., 9 = very fibrous; see Fig.3.1.) were recorded; the equidistance of the branching classes was not validated.

In this experiment, the white to reddish-green coloured shoots, varying in

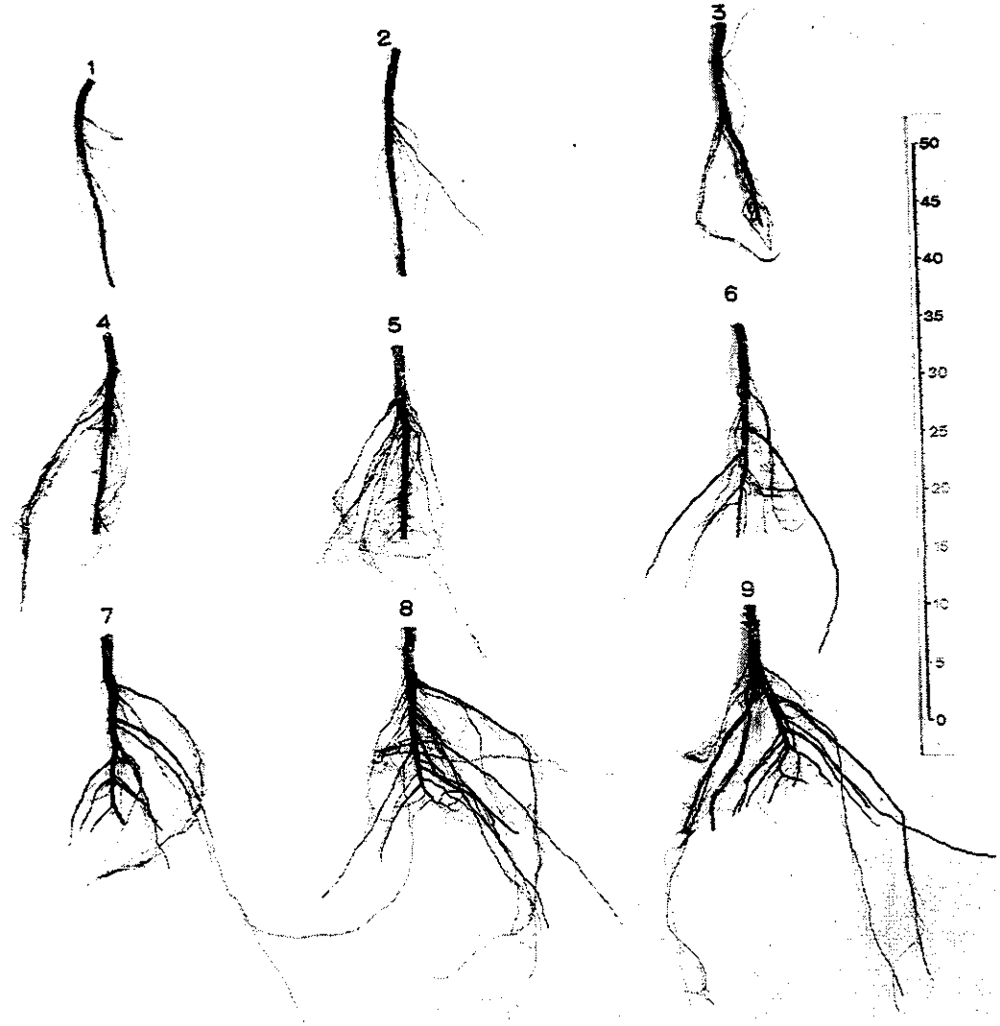

***Fig. 3.1. Classes of branching of the root system of one-season-old R.canina 'Inermis' seedlings (1 = tap root, ....., 9 = very fibrous).***

**length from 0.5 - 50 cm, developing on the root collar mainly just below the first year's shoots, partly emerging from the sub-soil after the canopy has closed in August, are denominated 'bottom-breaks'.**

### *Note*

**The 'bottom-breaks' of rootstock seedlings have been described in German as 'Erstarkungstriebe' (TROLL, 1937); despite similar function for the plant, they should not be confused with those of a scion variety (Section 2.4.).**

### 3.4.2. *Experiment 2.* Effects of plant density in the field on *R.canina* 'Inermis'

The effect of different plant densities in the field on the root collar diameter and shoot and root characters of 'Inermis' seedling stocks was studied. The experiment was carried out at the arboricultural experimental garden at Noordbroek.

#### *Plant material*

Plant material consisted of one-season-old *R.canina* 'Inermis' seedlings. In April, the seeds were sown in plots of 1 x 1 m, each consisting of four rows, 33 cm apart; in all there were 97 plots. As a result of *randomly* occurring differences for seed vitality and percentage of emergence between plots, after light hand-thinning the number of plants per plot varied from about 30 to 190 per $m^2$. This allowed the 97 plots to be distributed over 9 plant density classes: 21-40 (n=10), 41-60 (n=7), 61-80 (n=12), 81-100 (n=16), 101-120 (n=10), 121-140 (n=8), 141-160 (n=15), 161-180 (n=13), 181-200 (n=6) plants per $m^2$. Each density was replicated 6-16 times. In subsequent Tables or Figures, classes are indicated by their means: 30, 50, 70, 90, 110, 130, 150, 170, 190 plants per $m^2$.

Contrary to common nursery practice, neither the shoots nor the roots were cut back when the plants were lifted in November. Lifted seedlings were graded by five standard classes of root collar diameter: <4 mm, 4<6 mm, 6<8 mm, 8<10 mm, and >10 mm (see also Section 3.2.3.).

#### *Observations*

At each density the number of seedlings falling in each grading class was counted. The seedlings having crooked root collars ('bents'), which are discarded in practice, were counted. Of individual seedlings in the 6<8 mm class, which was the modal class at most plant densities, plant height (cm), number and the fresh weight (g) of shoots, number of bottom-breaks (Section 3.4.1.), branching of the root system (see Fig.3.1.) and the fresh weight (g) of the roots were recorded.

*Methods*

The relation between plant density and biomass (g x $10^3$ $m^{-2}$), with the aim to study competition, is expressed by the hyperbola ($Y = N / (b_0 + b_1.N)$), where Y is the (fresh) biomass in g $m^{-2}$, N is the plant density in numbers $m^{-2}$, and $b_0$ and $b_1$ are constants (SPITTERS, 1983).

*Note*

When the number of plants per plot of one $m^2$ as used in this experiment, is to be converted to plants per ha, the conversion factor is 6.666 instead of 10.000 because in commercial nurseries, beds (consisting of four rows) are 50 cm apart, so that 33% more area is used for the same number of plants.

### 3.4.3. *Experiment 3. The growth of 'Sonia' on Edelcanina of different root collar diameter*

The influence of the root collar diameter of 'Inermis', 'Brögs Stachellose' and 'Pollmers' Edelcanina seedling stocks at bench grafting on the subsequent aerial and subsoil growth of 'Sonia' combination plants was studied.

*Plant material*

Plant material consisted of ungraded batches of one-season-old *R.canina* 'Inermis' (n = 150), 'Brögs Stachellose' (n = 175) and 'Pollmers' (n = 185) rootstocks, provenance Messrs Kuiper, Veendam. Within each Edelcanina, stocks were divided into six classes of root collar diameter (Table 3.1.). It should be noted that owing to insufficient number of thin and thick stocks, class diameters were not exactly the same for each Edelcanina. The stocks within a diameter class of each Edelcanina, were bench grafted with 'Sonia' (Section 2.2.) in the first week of January. When about three weeks old, uniform combination plants of each class were planted according to a randomized block design in beds in the glasshouse. Each bed consisted of two rows, 50 cm apart; the plant distance in the row was 20 cm. Each block was replicated five times and contained two plants of each stock/diameter class, that were planted in opposite positions in the rows. The experiment involved: 3 (stocks) x 6 (diameter classes) x 2 (plants) x 5 (blocks) = 180 plants. In the

***Table 3.1. Means and standard deviation of the root collar diameter (Ø) and the fresh weight of the roots of one-season-old R.canina 'Inermis', 'Brögs Stachellose' and 'Pollmers' rootstock plants, each graded by 6 classes of root collar diameter prior to grafting.***

| Class | Inermis | | Brögs | | Pollmers | |
|---|---|---|---|---|---|---|
| | Ø (mm) | weight (g) | Ø (mm) | weight (g) | Ø (mm) | weight (g) |
| *1* | *3.3±0.3* | *1.8±0.7* | *3.9±0.1* | *2.0±0.4* | *3.9±0.2* | *1.3±0.2* |
| *2* | *4.9±0.3* | *4.5±1.1* | *4.5±0.2* | *1.8±0.5* | *5.0±0.3* | *1.7±0.4* |
| *3* | *6.1±0.2* | *7.2±1.1* | *5.5±0.4* | *4.4±2.2* | *7.1±0.2* | *6.1±1.3* |
| *4* | *7.8±0.5* | *12.2±1.4* | *6.6±0.4* | *5.2±1.9* | *9.0±0.4* | *11.7±1.6* |
| *5* | *9.8±0.7* | *15.9±3.0* | *8.1±0.4* | *9.6±1.2* | *11.3±0.3* | *19.7±4.5* |
| *6* | *12.8±1.4* | *32.0±7.9* | *9.8±0.5* | *12.6±2.2* | *13.2±1.0* | *23.2±4.0* |

glasshouse, plants were uniformly treated as described in Section 2.4.; flowering and blind shoots were harvested twice weekly. The plants were uprooted after 12 months.

### *Observations*

Prior to grafting with 'Sonia', in each batch of Edelcanina stocks, the root collar diameter (mm), the number of shoots, and the fresh root weight (g) (Table 3.1.) were recorded per rootstock plant. For each combination plant, the length of the primary shoot was measured 30 days after planting, viz. when in the earliest plants anthesis was about to occur; further, the time of emergence of bottom-breaks, and the number and fresh weight (g) of harvested shoots were recorded. In addition, from November to February, the length (cm) of harvested flowering shoots was determined. After careful uprooting, the fresh weight (g) of the aerial part, the root collar diameter (mm), the root fresh weight (g), and the width and length (cm) of the root system of each combination plant were determined.

### *Methods*

The shape of the uprooted root systems being very similar to an inverse cone with radius (r) and height (h), the volume of soil (V) held by the root system after 12 months (Fig.3.2.) was calculated as: $V = 1/3 \times \pi r^2 h \ \mathrm{dm}^3$. The shoot/root (fresh) weight ratio was calculated as: the fresh weight of the aerial part of 12-month-old combination plants divided by the fresh weight of their roots. Biomass, expressed as g x $10^3$ $m^{-2}$, was calculated as: the sum of the fresh shoot- and root weight after uprooting, plus the total fresh weight of the harvested shoots of the 12-month-old combination plants.

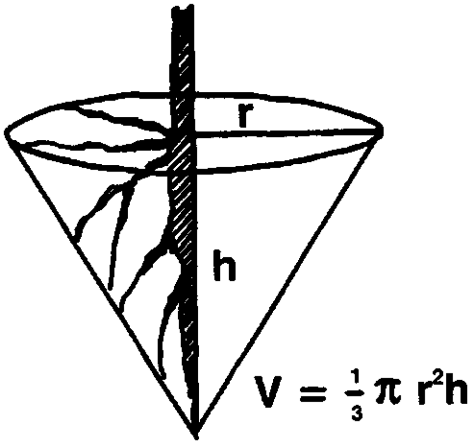

*Fig. 3.2. The volume of soil held by the root system of 12-month-old 'Sonia'-Edelcanina combination plants, expressed as an inversed cone.*

## 3.5. Results

### 3.5.1. *Experiment 1.* Variation within and between batches of *R.canina* 'Inermis'

The distribution of the ungraded 'Inermis' seedlings over the classes of root collar diameter (2<3, 3<4, ..., 10<11, 11<12 mm) is presented in Fig.3.3.. The mean diameter was 5.9 ± 1.83 mm. According to the generally applied grading standard (Section 3.2.3.), the population consisted of about 8% <4 mm, 39% 4<6 mm, 33% 6<8 mm, and 20% ≥8 mm.

Between several characters of the ungraded seedlings very significant correlations were computed. Fig.3.4. shows the number of shoots and of bottom-breaks to be negatively correlated, indicating that as seedlings had more shoots, the number of bottom-breaks became smaller. In each of the four root collar diameter classes, branching of the root system increased as the number of shoots increased (Fig.3.5.). An increase in root collar diameter was reflected in both increased branching of the roots (also clear from Fig.3.5.) and in an increase in the number of shoots (Fig.3.6.). Other correlations between plant characters were non-significant.

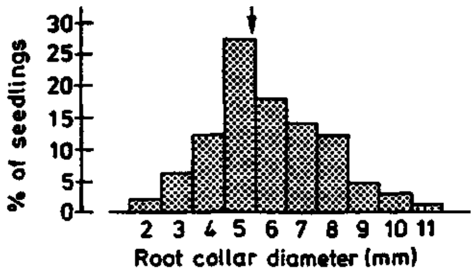

*Fig. 3.3. The distribution of one-season-old R.canina 'Inermis' seedlings over classes of root collar diameter (n = 177). Arrow indicates the mean diameter.*

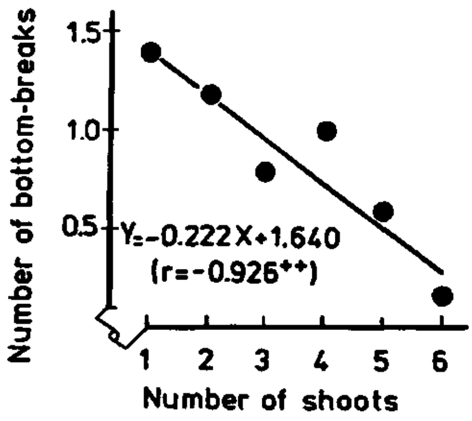

*Fig. 3.4. The relation between the number of shoots and the number of bottom-breaks of one-season-old ungraded R.canina 'Inermis' seedlings. Correlation significant at p = 0.01.*

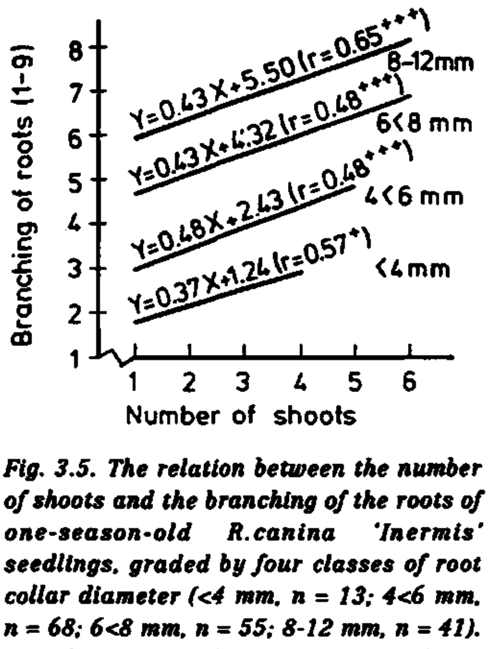

*Fig. 3.5. The relation between the number of shoots and the branching of the roots of one-season-old R.canina 'Inermis' seedlings, graded by four classes of root collar diameter (<4 mm, n = 13; 4<6 mm, n = 68; 6<8 mm, n = 55; 8-12 mm, n = 41). Correlations significant at p = 0.05 (+) or 0.001 (+++).*

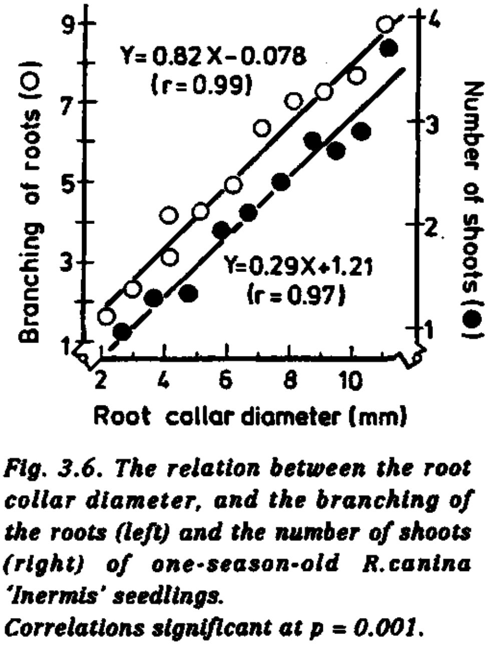

*Fig. 3.6. The relation between the root collar diameter, and the branching of the roots (left) and the number of shoots (right) of one-season-old R.canina 'Inermis' seedlings.*
*Correlations significant at p = 0.001.*

In spite of being graded by 8-12 mm, between the 28 batches 'Inermis' significant variation occurred for all characters assessed, including the root collar diameter (Table 3.2.). Per plant in a batch, the number of shoots varied from 3.1 to 6.8, the number of bottom-breaks from 0.3 to 2.0, the root collar diameter from 9.5 to 14.9 mm, and degree of branching of the root system from 3.8 to 8.8.

*Between* batches, significant correlations between characters occurred (Table 3.3.), indicating that as per batch the mean number of shoots per plant was larger, plants had fewer bottom-breaks and thicker root collars. Correlations *within* batches, viz. between individual plants, indicate that as the number of shoots increased, root collars were thicker and the root system branched better; when the root collar was thicker, the root system branched better. These correlations agree with those found in ungraded plants (Fig.3.6.), but coefficients were generally lower because variation between these previously graded plants was yet smaller.

*Table 3.2. F-values from analysis of variance (significant at p=0.01), minimum, maximum, means (s.dev.), and coefficients of variance (CV) for the number of shoots, number of bottom-breaks, root collar diameter, and branching of the root system of 28 batches of one-season-old R.canina 'Inermis' rootstock plants graded by 8-12 mm.*

| | Number of shoots | Number of bottom-breaks | Root collar diameter | Branching of the root system |
|---|---|---|---|---|
| *F-value* | *15.9* | *7.1* | *33.2* | *19.4* |
| *Minimum* | *3.1* | *0.3* | *9.5* | *3.8* |
| *Maximum* | *6.8* | *2.0* | *14.9* | *8.8* |
| *Mean (s.dev.)* | *4.7 ± 1.4* | *1.1 ± 1.0* | *11.8 ± 1.5* | *7.5 ± 1.8* |
| *CV (%)* | *29* | *94* | *12* | *24* |

*Table 3.3. Correlations between and within (in brackets) 28 batches of one-season-old R.canina 'Inermis' rootstock plants, for the number of shoots, the number of bottom-breaks, the root collar diameter, and the branching of the root system (correlations significant at p = 0.001).*

| | Number of shoots | Number of bottom-breaks | Root collar diameter |
|---|---|---|---|
| *Number of* | *- 0.60* | - - | - - |
| *bottom-breaks* | *(n.s.)* | - - | - - |
| *Root collar diameter* | *0.70* | *n.s.* | - - |
| | *(0.50)* | *(n.s.)* | - - |
| *Branching of root* | *n.s.* | *n.s.* | *n.s.* |
| *system* | *(0.29)* | *(n.s.)* | *(0.42)* |

### 3.5.2. *Experiment 2.* Effects of plant density in the field on *R.canina* 'Inermis'

Plant density exerted a pronounced effect on the distribution of seedlings over the nine classes of root collar diameter (Fig.3.7.). Hence, as the mean density increased from 30 to 190 plants per $m^2$, the mean root collar diameter decreased from 9.0 to 5.4 mm. The frequency distribution gradually shifted from positively skew (30 plants per $m^2$), via normal (90 plants per $m^2$), to negatively skew (150-190 plants per $m^2$). Except at 30 plants per $m^2$, where most plant fell into >10 mm class, the modal class was 6<8 mm, containing 36-48% of the plants of a density. Interplant variation for diameter, expressed by the coefficient of variance (CV), consistently increased with the plant density. The proportion of plants in the important diameter class ≥8 mm, which is used exclusively for bench grafting cut roses, decreased as the plant density increased, from about 65% at 30, to just over 5% at 190 plants per $m^2$, following an exponential curve (Fig.3.8.).

As the plant density increased from 30 to 190 plants per $m^2$, the mean height of plants in the 6<8 mm class increased from about 75 to 85 cm (Fig.3.9.). The mean number of shoots per plant, and the branching of the roots, decreased as plant density increased (Fig.3.10.). These effects were reflected in the mean shoot weight, which linearly decreased from 19 to 13 g, and in the mean root weight, which likewise decreased from 8.5 to 6.2 g (Fig.3.11.). Slopes indicate shoot weight to decrease more than root weight. In general, plant weight decreased as plant density increased.

The decreasing shoot/root (fresh) weight ratios (Table 3.4.) show plants to become 'rootier' as density increased. Except at 30 plants per $m^2$, where the highest number of bottom-breaks occurred, between 50 and 190 plants per $m^2$, the number of bottom-breaks increased from 0.80 to 0.98 per plant. Plant density had no consistent effect on the percentage of seedlings with a crooked root collar ('bents'). Plant density exerted a pronounced effect on the biomass of *R.canina* 'Inermis', which steadily increased until about 170 plants per $m^2$ (Fig.3.12.).

Other associations between plant characters which are not presented in Figures or Tables, are expressed as coefficients of correlation (d.f. = 95, $p = 0.001$, $r \geq 0.32$). They indicate (i) the plant height to decrease with increasing

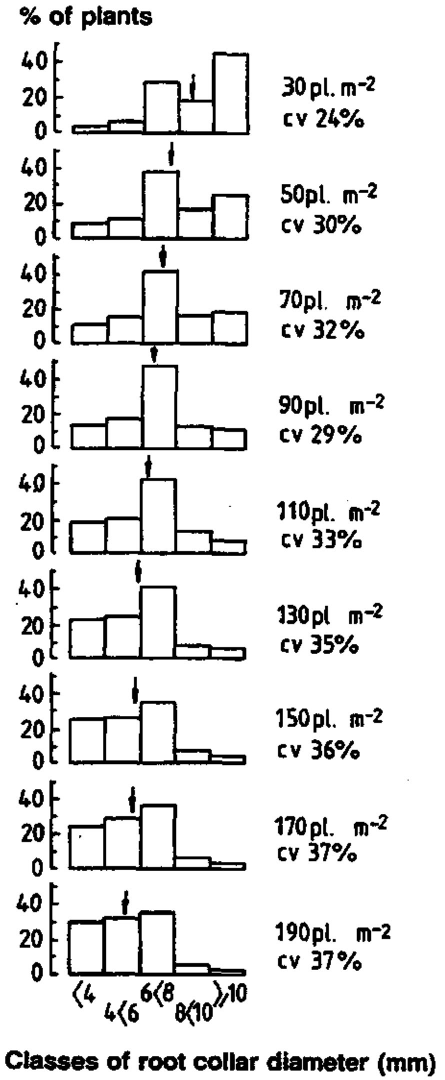

*Fig. 3.7. The distribution of one-season-old R. canina 'Inermis' seedlings, grown at nine plant densities, over five classes of root collar diameter. Arrows indicate means.*

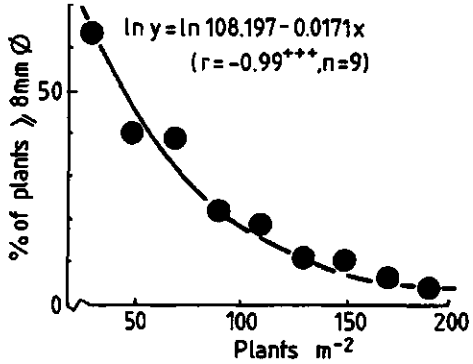

***Fig. 3.8. The relation between plant density and the percentage of one-season-old R.canina 'Inermis' seedlings in the diameter class ≥8 mm.***
***Correlation significant at p = 0.001.***

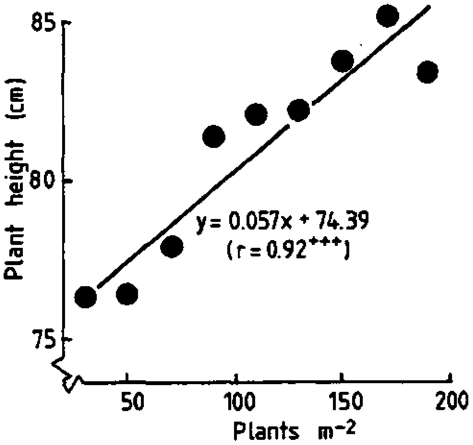

***Fig. 3.9. The relation between plant density and the mean height of one-season-old R.canina 'Inermis' seedlings graded by 6<8 mm.***
***Correlation significant at p = 0.001.***

**number of shoots per plant (r = - 0.41), (ii) the shoot weight per plant to increase with increasing number of shoots (r = 0.72), (iii) the number of shoots to increase with increasing root fresh weight (r = 0.49), and the shoot fresh weight to increase with (iv) increasing root fresh weight (r = 0.75) and (v) increasing branching of the root system (r = 0.58).**

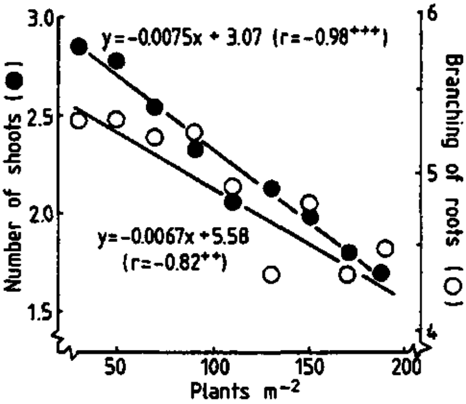

*Fig. 3.10. The relation between plant density and the number of shoots (left), or the branching of the roots (right), of one-season-old R.canina 'Inermis' seedlings graded by 6<8 mm. Correlations significant at p = 0.05 (+) or 0.01 (++).*

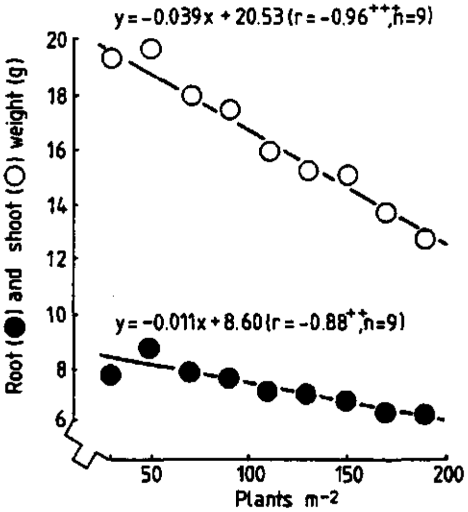

*Fig. 3.11. The relation between plant density and the mean root weight or the mean shoot weight of one-season-old R.canina 'Inermis' seedlings graded by 6<8 mm. Correlations significant at p = 0.01 (++) or 0.001 (+++).*

*Table 3.4. The shoot/root (S/R) fresh weight ratio, the number of bottom-breaks (Bb) per plant, and the percentage of 'bents', of one-season-old R.canina 'Inermis' rootstock plants, grown at nine plant densities.*

| Density (pl.m$^{-2}$) | 30 | 50 | 70 | 90 | 110 | 130 | 150 | 170 | 190 |
|---|---|---|---|---|---|---|---|---|---|
| *S/R ratio* | *2.4* | *2.3* | *2.3* | *2.3* | *2.2* | *2.2* | *2.1* | *2.0* | *2.0* |
| *Number of Bb's* | *1.0* | *0.80* | *0.81* | *0.84* | *0.82* | *0.85* | *0.89* | *0.92* | *0.98* |
| *Bents (%)* | *19* | *22* | *16* | *12* | *14* | *18* | *17* | *14* | *13* |

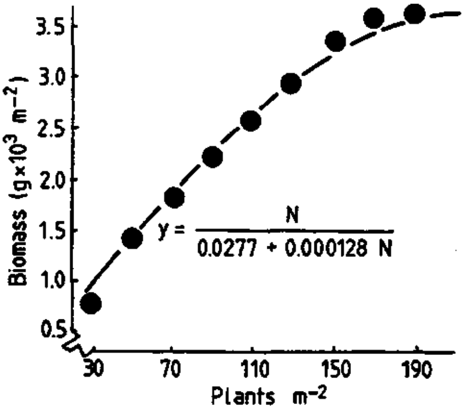

*Fig. 3.12. The relation between plant density and the biomass of one-season-old R.canina 'Inermis' seedlings graded by 6<8 mm.*

### 3.5.3. *Experiment 3.* The growth of 'Sonia' on Edelcanina of different root collar diameter

*Growth of the scion*

The first effects of rootstock diameter were observed in the length of the primary shoots of 'Sonia'. Measured 30 days after grafting, when in early plants anthesis was about to occur, shoots were longer as stocks had been thicker at grafting (Fig.3.13.). At the same initial stock diameter, primary shoots were generally longest on 'Inermis'. With respect to the time of emergence of bottom-breaks, the initial diameter of the root collar exerted marked effects as well. Trendlines (Fig.3.14.) indicate the first, second and third 'Sonia' bottom-breaks on the three rootstocks to emerge earlier as stocks had been thicker. In the same diameter class, the general sequence of bottom-break emergence was: 'Inermis', 'Brögs', 'Pollmers'. Difference in time of bottom-break emergence between stocks was small for the first bottom-breaks, but increased for the second and third ones.

Within each of the three Edelcaninas, the stock diameter at grafting induced significant variation in the number of harvested 'Sonia' shoots (Table 3.5.). Differences in yield between thinnest and thickest stocks were 28%, 32% and 48%, on 'Inermis', 'Brögs' and 'Pollmers', respectively. As illustrated by Fig.3.15., the number of harvested 'Sonia' shoots linearly increased with the diameter of the root collar at grafting. In the same diameter class, the general order of increasing yield was: 'Pollmers', 'Brögs' and 'Inermis'. On all stocks, both the shoot length (Fig.3.16.) and shoot weight (Fig.3.17.) of 'Sonia' linearly increased as root collars had been thicker at grafting. At the same diameter, shoots were markedly longer and heavier on 'Inermis' and 'Brögs', than on 'Pollmers'.

*Growth of the stock*

Assessed prior to grafting, in ungrafted rootstock plants of each of the three Edelcaninas, significant positive correlations occurred between the root collar diameter and the number of shoots or the fresh root weight, and between the fresh root weight and the number of shoots (Table 3.6.). This indicates that, just like found in Section 3.5.2., both the shoot number and the root weight of

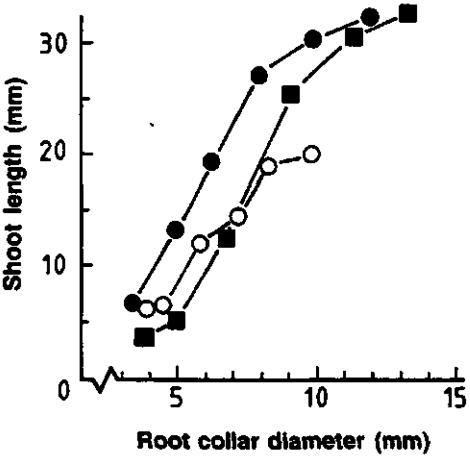

*Fig. 3.13. The relation between the initial root collar diameter of the Edelcanina rootstocks (● = 'Inermis', ○ = 'Brögs Stachellose', ■ = 'Pollmers'), and the length of the primary shoot of 'Sonia' 30 days after grafting on these stocks.*

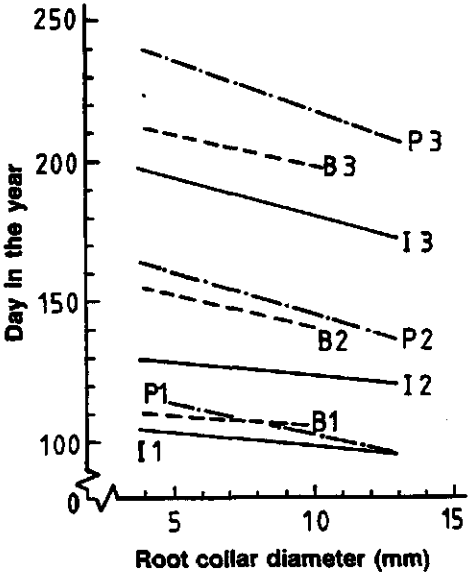

*Fig. 3.14. Trendlines for the date of emergence of the first (1), second (2) or third (3) bottom-break of 'Sonia', grafted on the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B) or 'Pollmers' (P), in relation to the initial root collar diameter of these stocks.*

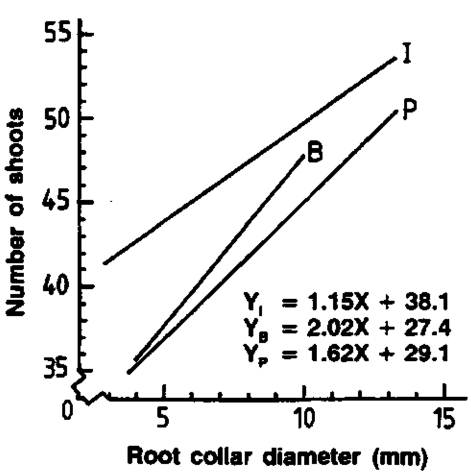

*Fig. 3.15. The relation between the initial root collar diameter of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B) or 'Pollmers' (P), and the number of shoots per plant harvested in 12 months from 'Sonia', grafted on these stocks. ($r_I = 0.95$, $r_B = 0.99$, $r_P = 0.97$, correlations significant at $p = 0.01$)*

*Table 3.5. The total number of shoots per plant harvested in 12 months of the glasshouse rose 'Sonia', bench grafted on R.canina 'Inermis', 'Brögs Stachellose' or 'Pollmers' rootstocks, each graded by root collar diameter in 6 classes, prior to grafting. Figures in one row followed by the same letter do not differ at p = 0.05.*

| | Diameter class | | | | | |
|---|---|---|---|---|---|---|
| **Rootstock** | **1** | **2** | **3** | **4** | **5** | **6** |
| *Inermis* | *41.5e* | *44.6cd* | *45.1cd* | *47.0bc* | *49.1b* | *53.1a* |
| *Brögs* | *35.4d* | *35.8d* | *39.1cd* | *40.9bc* | *44.3ab* | *46.8a* |
| *Pollmers* | *35.0c* | *37.3c* | *42.3bc* | *42.2bc* | *45.7b* | *51.8a* |

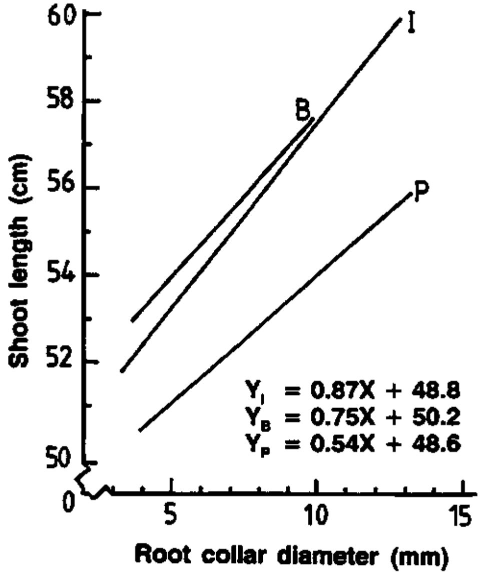

*Fig. 3.16. The relation between the initial root collar diameter of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B), 'Pollmers' (P), and the mean length of the flowering shoot of 'Sonia' grafted on these stocks, assessed between November and Februari. ($r_I = 0.96^{++}$, $r_B = 0.78^{+}$, $r_P = 0.79^{+}$, correlations significant at $p = 0.05$ (+) or 0.01 (++)).*

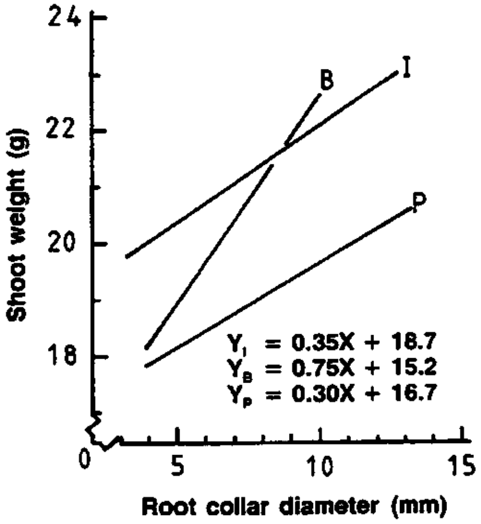

*Fig. 3.17. The relation between the initial root collar diameter of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B), 'Pollmers' (P), and the mean weight of the flowering shoot of 'Sonia' grafted on these stocks, assessed between November and Februari. ($r_I = 0.90$, $r_B = 0.89$, $r_P = 0.70$, correlations significant at $p = 0.1$ (P) or $p = 0.01$).*

seedlings increased with the root collar diameter, and the fresh weight with the number of shoots. Because of its probable significance for genotypic variation between the three stocks (see Section 3.6.4.), the relation between the root collar diameter and the number of shoots of seedlings prior to grafting is illustrated in Fig.3.18.. In spite of similarity of the relationship, at the same diameter 'Pollmers' plants had fewer shoots than those of 'Inermis', and 'Brögs'. In the short range of diameters available, plants of the latter stock had most shoots.

*Table 3.6. Correlations between the root collar diameter and: (i) the number of shoots per plant, (ii) the fresh root weight, and between (iii) the fresh root weight and the number of shoots, of ungrafted, one-season-old rootstock plants in batches of R.canina 'Inermis' (n=150), 'Brögs Stachellose' (n=175) or 'Pollmers' (n=185). (Correlations significant at p = 0.001).*

| | | Inermis | Brögs | Pollmers |
|---|---|---|---|---|
| *Diameter* | *- Shoot number* | *0.95* | *0.96* | *0.91* |
| *Diameter* | *- Root weight* | *0.97* | *0.99* | *0.99* |
| *Root weight* | *- Shoot number* | *0.97* | *0.95* | *0.97* |

Comparison of the initial and final root weights of the stocks of various diameters (Fig.3.19.), shows a linear relation between these parameters which, owing to the short range of available diameters, was not significant in 'Brögs'. Although weight increase followed similar course (tg φ about 0.5), at the same initial weight 'Inermis' root systems had gained markedly higher final weigths than 'Pollmers'. Fig.3.20. shows that the weight increase of the roots of the three Edelcaninas decreased in inverse proportion to the initial root weight. Over 12 months, the lightest root systems had increased about 20-fold, against the heaviest ones 2-5 fold only.

As the original root collar diameter increased from 3 to 13 mm, the volumeof soil held by the root system of all three Edelcaninas decreased from about 40 dm$^3$ to 10 dm$^3$ (Fig.3.21.), indicating that absolute root growth had been larger as stocks had been thinner at grafting.

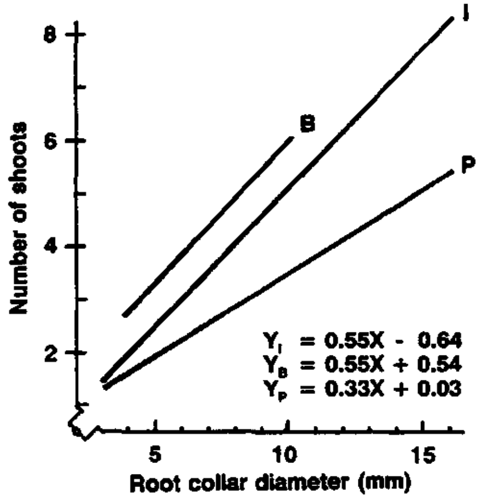

*Fig. 3.18. The relation between the root collar diameter and the number of shoots of one-season-old, ungrafted seedling plants of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B), 'Pollmers' (P). ($r_I = 0.95$, $r_B = 0.96$, $r_P = 0.91$, correlations significant at $p = 0.01$).*

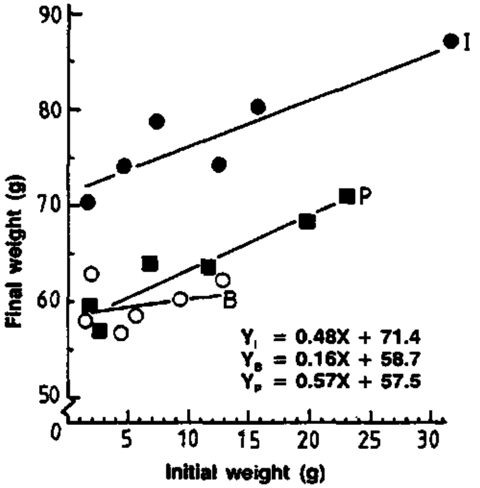

*Fig. 3.19. The relation between the initial and the final (fresh) root weight of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B) or 'Pollmers' (P), grafted with 'Sonia'. ($r_I = 0.87$, $r_B = 0.40^{ns}$, $r_P = 0.94$, correlations significant at $p = 0.01$).*

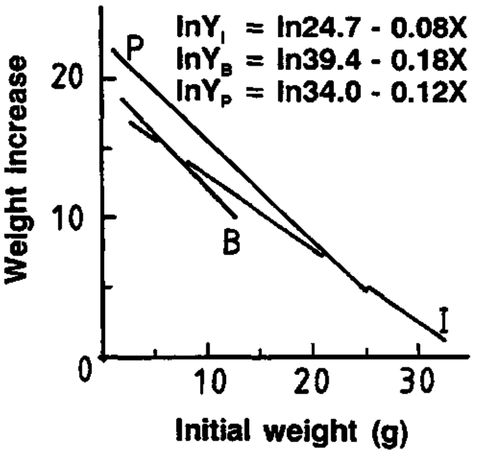

*Fig. 3.20. The increase in fresh weight in 12 months (final : initial weight) of the roots of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B) or 'Pollmers' (P), grafted with 'Sonia'. ($r_I = -0.95$, $r_B = -0.95$, $r_P = -0.91$, correlations significant at $p = 0.01$).*

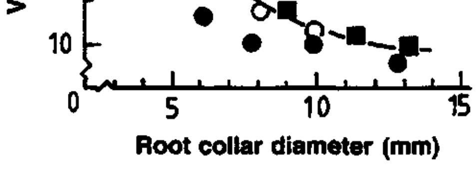

*Fig. 3.21. The volume of soil held by the 12-month-old root systems of the Edelcanina rootstocks (● = 'Inermis', ○ = 'Brögs Stachellose', ■ = 'Pollmers') grafted with 'Sonia', related to the initial root collar diameter of these stocks.*

### *Growth of combination plants*

In spite of the differences in root growth between thin and thick stocks, regression lines representing the relation between initial root collar diameter and S/R (weight) ratio of 12-month-old combination plants hardly diverged from the horizontal, indicating that in none of the three Edelcaninas the S/R ratio was affected by the original diameter (Fig.3.22.). However, whereas S/R ratio of 'Pollmers' differed only slightly from that of 'Inermis', the ratio for 'Brögs' was much higher.

Overall growth, expressed as total biomass produced in 12 months, was larger in all three stocks as their initial diameter had been larger. At all diameters, biomass was highest on 'Inermis' and lowest on 'Pollmers' rootstocks (Fig.3.23.).

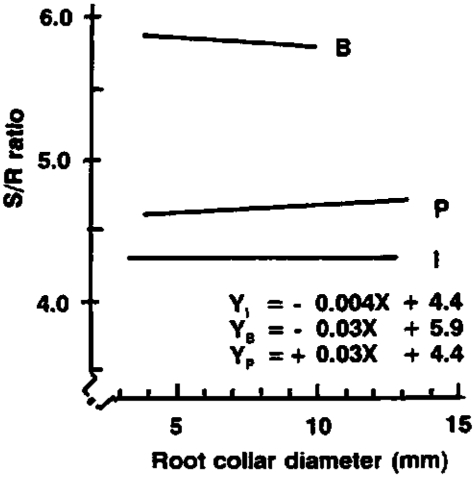

*Fig. 3.22. The relation between the initial root collar diameter of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B), or 'Pollmers' (P), and the shoot : root (S/R) fresh weight ratio of 12-month-old 'Sonia' combination plants.*

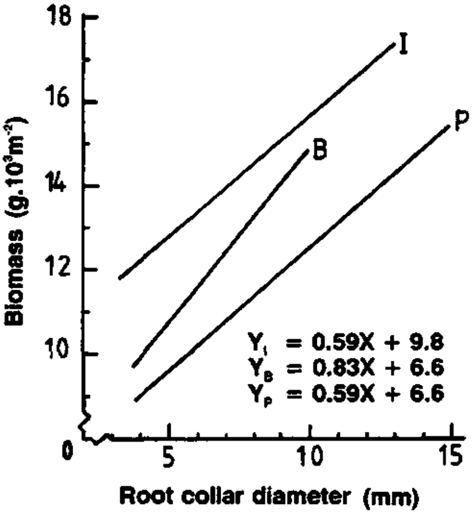

*Fig. 3.23. The relation between the initial root collar diameter of the Edelcanina rootstocks 'Inermis' (I), 'Brögs Stachellose' (B), or 'Pollmers' (P), and the fresh biomass of 'Sonia' combination plants produced in 12 months. ($r_I = 0.99$, $r_B = 0.95$, $r_P = 0.97$, correlations significant at $p = 0.01$).*

## 3.6. Discussion

### 3.6.1. Growth and development of seedling stocks

In the rose, in principle two categories of seedlings occur, viz. 'recurrent' flowering ones with a juvenile period between 20 and 40 days (DE VRIES, 1976a), and 'non-recurrent' flowering ones (DE VRIES & DUBOIS, 1978) with a juvenile period of 1 to 5 years. Once flowering has begun, recurrent genotypes continuously produce flowers (Section 2.3.), while non-recurrent do so in spring only. It is noteworthy, however, that in spite of differences in flowering habit, the morphology of recurrent and non-recurrent flowering seedlings is basically the same.

Since Edelcanina rootstocks belong to the non-recurrent flowering category (see also Section 6.2.3.), and have a juvenile period of 3-5 years, the seedlings presently studied were similar in that they were both non-recurrent and juvenile. In contrast to recurrent flowering plants, genotypic variation in plant development and selection based on this variation (DE VRIES, 1976a) has not been studied in non-recurrent plants.

Present results have demonstrated important and significant phenotypic variation of the root collar diameter, the number of shoots, the shoot length and the shoot weight, the number of bottom-breaks, the branching of the root system and the weight of the root system in ungraded, and even in graded batches of rootstocks (Tables 3.1., 3.2.). Notwithstanding large variation in the level of expression, correlations between these characters remained unbroken (Tables 3.3., 3.6.; Figs.3.5., 3.6.). Even at widely varying plant densities, the same correlations between characters occurred. Evidently, the above variation and relationships are characteristic of seedling (Edelcanina) stocks in general, rather than of the selections 'Inermis', 'Brögs' or 'Pollmers' in particular.

Bottom-breaks have significance in the ontogeny of (non-recurrent) flowering seedlings, which was described for *R.rubrifolia* Villars and *R.pendulina* L. by TROLL (1937). In the first month from seed germination, the main shoot of the seedling has grown to a length of 10-15 cm. Subsequently, the basal axillary buds of the main shoot sprout and form the lateral shoots observed in Experiments 1 and 2. In the field, most seedlings form bottom-breaks ('Erstarkungstrieben') when the canopy has closed. In course of the second or third year, when growth is not disturbed by uprooting, the first year's shoots gradually decline as the bottom-breaks grow out into 2-3 m long branches. These branches grow almost upright (orthotropic) for the first 1.5-2 m, and subsequently become spreading (anisotropic). This indicates juvenile, non-recurrent seedlings to show two main phases of development. In the first phase, which coincides with the first year, a number of relatively short laterals (70-80 cm) from the main shoot are formed. In the second phase, which was not included in our observations, bottom-breaks grow out towards their ultimate function, i.e. bearing the reproductive organs, in 2-5 years. Like in recurrent seedlings (see Section 4.5.1.), the time of occurrence (which was not recorded) and the number of bottom-breaks, might express individual 'earliness', and as such be based on genotypic rather than on phenotypic variation.

In the plant density experiment (Section 3.5.2), the number of bottom-breaks per plant slightly increased with the number of plants per m$^2$ (Table 3.4.). Simultaneously the number of shoots decreased from about 2.8 to 1.7 per plant (Fig.3.10.), so that the total number of shoots per plant (bottom-breaks plus shoots) still decreased as there were more plants per m$^2$. Also in an ungraded field crop there were more bottom-breaks as there were fewer shoots per plant (Fig.3.4.). Because the number of shoots also decreased as the root collar was thinner (Fig.3.6.), bottom-break number might be inversely related to the root collar diameter, which was not verified. Probable relations between number of bottom-breaks, number of shoots, supposed earliness and plant development in subsequent years, should be substantiated by further experiments.

In addition to large phenotypic variation within each rootstock selection, likely genotypic variation between 'Inermis', 'Brögs' and 'Pollmers' is indicated by a consequent difference in the number of shoots per rootstock plant of the same diameter (Fig.3.18.). Because the three types of stocks were grown at about the same number of plants per ha in the seedling field, the number of shoots per plant may result from genotypic differences, rather than from density effects (see Section 3.6.2.). This would mean that in general 'Pollmers' seedlings have fewest and 'Brögs' most shoots, which should be verified by studying a larger number of provenances.

### 3.6.2. Effects of plant density in the field

Our results show plant density to have a marked effect on the grading of *R.canina* 'Inermis' seedlings. As density increased from 30 to 190 plants per $m^2$, the root collar diameter decreased from 9.0 to 5.4 mm. This agrees with empirical knowledge (ASTREGO, 1955). Simultaneously the distribution over diameter classes shifted from mainly thick, to mainly thin stocks (Fig.3.7.). Except at 30 plants per $m^2$, where the >10 mm class dominated, seedlings in the 6<8 mm class were the most frequent at all densities. Interplant variation for diameter increased with increasing plant density, which agrees with assumptions of SPITTERS (1979). Because the shoot/root ratio of plants slightly decreased as plant density increased, competition between shoots (for light) appeared to be more serious than between roots (water, nutrition) (Table 3.4.). Although the situation in 'Inermis' was somewhat different, it should be noted that in wheat (NELSON, 1963) and as reported by BROUWER & KUIPER (1972) in pine seedlings, reduction of the light level caused an increasing S/R ratio.

As shown by the course of the hyperbola presenting the relation between plant density and biomass (Fig.3.12.), severe interplant competition occurred from about 170 plants per $m^2$ onwards when, in spite of increasing number of plants, biomass ceased to increase. For nurserymen, who generally require a majority of 6<8 mm stocks, this indicates that aiming at more than 170 x 6.666 = 1.133.220 plants per ha, is inadvisable. Without studying this matter further in depth, it should be noted that density effects in 'Inermis' agree with those observed in *Linum usitatissimum* (OBEID et al., 1967), *Zea mays* (DAYNARD & MULDOON, 1983), and forestry crops in general (CANNELL, 1983).

Contrary to specially designed density experiments, where plants are usually properly spaced at regular distance, in the present experiment plant-to-plant distance could vary considerably within a density class. Thus density has two aspects, (i) the mean number of plants per area, and (ii) distribution of the plants over this area. In addition to variation owing to density, there is variation in plant size owing to irregular time of germination. This indicates that when the canopy closes in August, and serious competition for light begins, the small plants and those at even distance in the row are at a disadvantage compared with large plants and with plants at the border of open spaces in the row or those in outer rows of a bed. Until the plants are uprooted in November, competition will increase, the more so when the root system becomes involved as well. Increasing interplant variation, occurring as plant density increases (Fig.3.7.), is likely to be explained from increasing differences between the well-developed plants at open spaces, and the properly spaced plants.

It is thus tentatively concluded that differences in plant size occurring in ungraded batches of Edelcanina, is caused in considerable degree by irregular distance in the row and by variation in plant age. In this reasoning the dominating role of environment in the expression of plant characters justifies the question whether Edelcanina selections behave as cultivars rather than as segregating populations. Possible genotypic variation as to plant size (vigour) may only be exposed when plants of the same age are planted properly spaced in homogeneous soil in the field. Only in such experiments the question may be answered whether and to what extent the diameter of the root collar of a certain provenance results from environment or from the genotype.

Our results indicate that according to standards in the trade, in which stocks with fibrous root systems are preferred to those with tap roots (Fig.3.1.), in the same diameter class seedlings from low plant density, that produce heavier and more fibrous roots (Figs.3.10., 3.11.) are more 'valuable' than those from high density. This conclusion does not necessarily mean financial returns from sparcely sown fields to be better than from densily sown ones. On the contrary, regardless of the branching of roots, the number of 6<8 mm stocks (modal class) generally determines the value of a hectare of stocks.

### 3.6.3. Improvement of external uniformity of Edelcanina

As expected, in ungraded batches of *R.canina* 'Inermis' rootstocks considerable variation of root and shoot characters occurred (Fig.3.5., Table 3.1.). Unexpectedly, however, also *within* and *between* different batches already graded by 8-12 mm root collar diameter, statistically significant variation for the number of shoots, number of bottom-breaks, and branching of the root system was present (Table 3.2.). Results of Experiment 3 show this situation to be similar in 'Brögs Stachellose' and 'Pollmers' stocks. There is no reason to assume that the situation in other Edelcaninas would be different. These results indicate grading by root collar diameter alone to be insufficient for the required external uniformity. They confirm the customers' complaints about lack of external uniformity of Edelcanina stocks to be fully justified.

In the present situation, in which dubious provenance of seeds often adds to low and erratic germination, the external uniformity of rootstocks may be improved in two ways, viz. in the field and/or after uprooting.

### *Measures in the field*

Owing to doubts about financial returns, measures to improve uniformity of plants in the field, like e.g. 'root pruning', are not generally applied in nurseries. However, the present results may offer new perspectives to increase uniformity. Because in commercial seedling fields sown at conventional density, the plant distance in the rows is smaller (3-4 cm) than between the rows (25 cm), the most severe competition effects expectedly occur in the rows. Uniformity of plant characters is expected to improve at equal plant distance in the row. Ideally, however, distance in the row is the same as between rows. With the preservation of the same number of plants per unit area, this may be achieved by both sowing more thinly in the row, and drawing the rows more closely together. It is realized that problems as to pest- and disease control may increase, although weed growth may be suppressed. A still more drastic measure may be the spaced *planting* of seedlings that have been germinated and pre-grown in the glasshouse.

The success of the above proposed measures and future advance, greatly depends on the improved control of the stratification and germination processes, and the effective separation of viable from non-viable seeds. Only when further research has succeeded in solving those problems, more advanced seed technology (HEYDECKER & COOLBEAR, 1977), such as pelleting or priming, may be applied to rose seeds.

### *Measures after uprooting*

Uniformity of root collar diameter being considered a character of rootstock quality (AKKERMAN, 1978a), the most important measure to improve external uniformity of Edelcanina has been the grading by root collar diameter. Although the significance of branching of the root system for the growth of combination plants has never been confirmed, in addition to uniform thickness, a well-branched (fibrous) root system is much appreciated.

Because the uniformity of root collar diameter and degree of branching of the roots are not necessarily connected (Fig.3.10.), the external quality of graded stocks may be considerably improved by additional grading by *branching of the roots*. Since 'branching of the roots' is correlated with 'number of shoots' (Fig.3.5.), actual grading for the latter trait, which is much more easily to assess, should be recommended. This combined grading for diameter and branching of the roots would be particularly beneficial to stocks in the 8-12 mm class which, being used for bench-grafting, are all handled individually by propagators.

### 3.6.4. Effects of the root collar diameter on the growth of 'Sonia' combination plants

It cannot be said, in generally accepted terms, that thin and thick stocks of the same selection differ in inherent vigour. However, the results of Experiment 3 show that from the start onwards, the original diameter of 'Inermis', 'Brögs' and 'Pollmers' stocks exerted pronounced effects on the growth of 'Sonia' combination plants. Apart from differences in level, these effects were the same for these three stocks. Hence, as the original stock diameter had been thicker, primary shoots were longer after 30 days (Fig.3.13.), the first, second and third bottom-breaks emerged earlier (Fig.3.14.), total shoot yield was higher (Fig.3.15.), whereas shoots were longer and heavier (Figs.3.16., 3.17.). Although in course of the second year, first year's differences between thin and thick stocks are expected to smooth out, empirical knowledge is that loss of shoot yield in the first year is not compensated in subsequent years. These results support the custom to use only thick stocks for grafting (usually 8-12 mm grading).

Comparing the three Edelcanina selections 'Inermis', 'Brögs' and 'Pollmers', the results indicate that at the same stock diameter, level of performance of 'Sonia' was highest on 'Inermis'. However, extrapolation of data for 'Brögs', which was only available up to 9.8 mm, suggest shoot yield on this stock to be at least equal to 'Inermis', shoot weight (quality) to be higher as diameter increased, and generally S/R ratio to be higher. Contrary to empirical knowledge, that there is little difference between the three stocks (compare Fig.4.4.), in present experiment 'Pollmers' performed least well. It might be concluded that to obtain superiorly performing clonal Edelcanina stocks (Section 6.1.3.), selection should be carried out in 'Inermis' and 'Brögs' seedling populations, rather than in those of 'Pollmers'. In spite of the consistent differences between the vigour of the three Edelcanina selections, the results demonstrate that these differences cannot be judged without considering the diameter of the stocks at grafting.

To a certain extent, our results confirm those with glasshouse-grown 'Sonia' on clonal 'Inermis', of which the yield tended to increase as stocks had been thicker at grafting (DE DOOD, 1989b). Also in a nursery experiment with *R.multiflora* and *R.canina* stocks budded with various outdoor cultivars, the plant height, the root collar diameter and the plant weight increased, as the original diameter increased from 3-5 mm through 8-12 mm (LUNDSTAD, 1973). Similar results had previously been obtained by KOSAKOF et al. (1970), but in addition, these authors reported a continuing lower flowering capacity on thin than on thick stocks in a period of three successive years.

The presently found effects of stock size on subsequent growth of rose scions, may have a more general significance. For example, when budded onto virus free M9, the apple cultivars 'Cox's O.P.' and 'Rode Boskoop' produced markedly more early laterals ('feathers') on thick (11 mm) than on thin (5 mm) stocks in the first year (VAN OOSTEN & DE GROENE, 1982), thus indicating a similar increase in vigour of the scion as rootstock diameter increased.

With regard to general understanding of present rootstock conduct, the performance of 'Sonia' at various stock diameter may be considered more detailed. In a growth analysis of 'Sonia', bench grafted onto uniform 'Inermis' 8-12 mm, DE VRIES & DUBOIS (1993a) demonstrated initial stock weight to decrease until about 50 days after grafting; not before about 40 days later (90 days after grafting) had the stock returned to its initial weight. This indicates that in the first weeks of growth, the scion's need for carbohydrates is mainly satisfied by reserves stored in the stock (VAN DE POL et al., 1988b). Obviously, imports from the stock and new production of carbohydrates by the leaves are not on an even base (PASIAN & LIETH, 1989) until the primary shoot is fully grown and bottom-breaks are about to emerge. In agreement with observations by LOESCHER et al. (1990) regarding the general role of roots of woody plants in the storage of carbohydrates, the present performance of 'Sonia', may be explained from initially different reserves in the stock. In addition, the root surface area which is of importance for uptake of water and nutrients (DE WILLIGEN & VAN NOORDWIJK, 1987) is supposed to be larger in heavy (thick) than in light (thin) stocks. It should be noted that initially smaller carbohydrate reserves in light than in heavy stocks, may disagree with subsequent better root growth of light stocks, that was reflected in higher weight increase (Fig.3.20.) and larger volume of soil held by the roots (Fig.3.21.). To answer the question what causes the root growth of combination plants to be more vigorous (in a relative sense) on light than on heavy stocks (Fig.3.20.), it should be remembered that initial variation in rootstock size is due to variation in plant age, environmental conditions in the seedling field and, probably, genotypic variation in vigour. In this reasoning, light stocks likely were retarded in their development. Presuming the root growth of heavy stocks in the field to have been optimal for development in the first growing season, light stocks might make up for arrears in development in the glasshouse.

In view of the foregoing, it is of interest to consider root growth in the light of a common striving of (combination) plants towards a functional equilibrium between shoot and root growth in a certain environment (BROUWER, 1983; KLEPPER, 1991). In grafting 'Sonia' scions of about the same weight onto stocks of increasing weight (Table 3.1.), a series of young combination plants was created with imposed decreasing S/R ratio. Hence, in the thinnest rootstocks, shoots and roots supposedly had about the same weight at grafting (S/R ratio about one), whereas stocks were heavier, the ratio decreased. After twelve months in the glasshouse, however, initial differences had levelled out, so that the combination plants of one Edelcanina had the same S/R ratio (Fig.3.22.). Considering better root growth of thin than of thick stocks, which might suggest a lower S/R ratio in the former category, this situation is somewhat unexpected. On the other hand, a common striving towards an equilibrium between aerial and subsoil parts in plants composed of the same scion and rootstock genotypes, which expectedly has established after 12 months of cultivation, agrees with the actual situation. The S/R ratio of harvested roses will be further considered in Chapter 5.

Differences in subsequent performance between one-season-old stocks of different diameter cannot be explained without further experiments, in which preferably the growth and development of both (ungrafted) seedling and clonal stocks of different diameter should be followed over a prolonged period.

# Chapter 4

# Scion-rootstock relationships as to vigour

*'.... We have never asked: who is the controller ? The controller is put together in the past, the past which is knowledge, which is thought. Thought has separated itself as the controller and the controlled. Concentration is the operation of that. Understanding that, we are asking a much more fundamental question, which is: can one live in this world, with a family and responsibilities, without a shadow of control ? '*

*J.Krishnamurti, 1982. The network of thought. London, p.79.*

# Chapter 4. Scion-rootstock relationships as to vigour

## 4.1. Summary

In three different experiments in the glasshouse, each running 12 months, replicated in two or three years, aspects of scion-rootstock relationships in the rose were studied. Plant material consisted of different batches of cut rose genotypes, grown on their own (seedling) roots in the first year, and as clones on the rootstock *R.canina* 'Inermis' in the second year.

The numbers of bottom-breaks and of harvested shoots in seedlings and clones were not affected by scion-rootstock interactions. Allowing for differences in level, seedlings and clones performed similarly as to vigour.

When genotypes were more vigorous, the axillary bud of scions sprouted sooner after grafting on the rootstock 'Inermis' and more bottom-breaks emerged earlier; after 12 months, shoot yield was higher, and root weight of the stock increased. In general, a certain equilibrium between aerial and subsoil parts of harvested cut rose plants occurred.

The value set in practice on a high number of bottom-breaks as a basis for high flower production was confirmed. In selecting high yielding cultivars, breeders are recommended to pre-select for number of bottom-breaks and shoot yield in the seedling stage.

In clones of weak Hybrid Tea seedlings, the rootstock 'Inermis' promoted the vigour of combination plants, but as the original seedlings had been more vigorous, the vigour of combination plants increased less. In combination plants on one type of stock the vigour is determined by the scion variety rather than by the stock. The high cultural value attached to 'Inermis' as a rootstock, does not seem justified.

The branching capacity of scion varieties is a major factor of vigour. Since branching capacity of scion varieties depends on degree of correlative inhibition, variation in the ratio of IAA (synthesized in the shoot) and cytokinins (produced in the root), is supposed to be the controlling mechanism of bud-break. The lead in growth of vigorous over weak scion genotypes is owing to a better branching capacity, contributing to a larger leaf area per plant.

## 4.2. Introduction

### 4.2.1. Scion-rootstock relationships. *Terminology*

In grafting a scion variety onto a rootstock, a 'compound', 'composite' or 'combination' plant is created. A combination plant generally consists of two different genotypes, each striving for expression of its own combination of genes, and in that process interacting with its counterpart (ROBERTS, 1949; FRIEDRICH et al., 1986).

In most crops, other than those easily raised on their own roots, *first* interest in rootstocks has lain in the rapid yet economic multiplication of desirable scion varieties, rather than in controlling scion growth, ultimate plant size, precocity of flowering, fruitfulness, fruit quality or disease resistance (TUBBS, 1973a; 1973b). But, ever since seedlings began to give way to clonal stocks, consistent influence of the clonal stock on performance of the scion variety has been noted by horticulturists. In top fruit, properties of clonal stocks to dwarf the tree or to overcome some of the hazards encountered by the tree in the orchard, were exploited as early as the mid-nineteenth century (CUMMINS & ALDWINCLE, 1983; ROM & CARLSON, 1987). In non-woody crops, like tomato or cucumber, rootstocks have been used to circumvent soil-borne diseases (KRUG, 1986).

Since scion-rootstock relationships have primarily been studied in fruit trees, the terminology as to the plant parts used, the expression of vigour of combination plants and methods of research, have served as models for other crops. In course of time the term 'scion-rootstock relationship' has been used for various phenomena, viz.:

- (in)compatibility between scion and rootstock (SIMONS, 1987)
- manner or degree in which the stock affects the scion variety (BEAKBANE & ROGERS, 1956)
- manner or degree in which the scion variety affects the stock (LINCOLN, 1941)
- manner or degree in which scion and stock contribute to the growth of the combination plant (VYVYAN, 1955; TUBBS, 1967).

In the present Chapter, 'scion-rootstock relationship' concerns the variation in the vigour of rose combination plants, resulting from variation in the individual vigour of scion varieties and rootstocks. According to our agreements in Section 2.4., vigour of combination plants will be commonly expressed as 'shoot yield in a certain period of time'.

Graft (in)compatibility of scion and rootstock, which evidently raises little problems in the rose (DUBOIS et al., 1990a), is not considered in this study.

### 4.2.2 Contribution of scion and stock to the vigour of combination plants. *General*

Once clonal stocks were in vogue, it has been asked to what extent their effects on the growth of combination plants would be predictable. This question, which applies to all grafted crops, was first encountered by fruit growers.

Around 1915 (HATTON, 1917), East Malling Research Station released a series of clonal apple stocks ranging from 'weak' to 'vigorous' which reliably control the vigour, i.e. the vegetative growth of combination trees (FERREE & CARLSON, 1987; Section 6.1.2.). Besides vigour, however, apple stocks affected precocity of flowering and onset of fruiting of the cultivar in a way that was not correlated with their growth on stoolbeds. Numerous and exhaustive experiments, both in the nursery and in the orchard, have been carried out to understand the relation between rootstock vigour and precocity of flowering, and to unravel the relative contribution of scion and rootstock to performance of the combination tree (BLAIR, 1938; VYVYAN, 1955; BEAKBANE & ROGERS, 1956; MARTIN, 1980; see also Section 6.1.2.).

In course of time, early controversies as to the relative importance of the scion or the stock to the performance of combination fruit trees in the nursery or the orchard, have gradually been replaced by a "far more constructive understanding of the need to evaluate and codify the effects of the mutual interactions of specified stocks and scion cultivars" (TUBBS, 1974). Graft incompatibility not taken into account, it is now generally understood in both woody (VYVYAN, 1955; BRYNDUM, 1965; TUBBS, 1967; TROWELL, 1972) and non-woody species (DEN NIJS, 1985; ZIJLSTRA & GROOT, 1988), that in spite of disturbing factors like soil conditions, pruning, onset of flowering, fruiting or alternating bearing, the contributions made by scion and rootstock as to various aspects of the growth (vigour) of combination plants, are *largely additive* (TUBBS, 1976; 1977; 1980; MARTIN, 1980).

The above conclusion excludes general occurrence of so-called 'scion-rootstock interaction' as to vigour. This concept needs closer consideration. Scion-rootstock interaction refers to (i) the inconsistency in the sequence of the individual vigour of scion varieties on diverse rootstocks or, (ii) the inconsistency in which the vigour of individual rootstocks recurs in combination with various scion varieties. This means that when scion-rootstock interaction as to vigour is absent (i) the sequence in vigour of a range of scion varieties is not affected by any rootstock or, (ii) the sequence in vigour of range of rootstocks is the same for any scion variety.

The presence of interactions is generally uncovered in an analysis of variance (FREEMAN, 1973), but a judgement of interaction may also be obtained by graphical presentation, a procedure that has been pursued in this study. As to vigour, which may be expressed by different parameters, such graphs are obtained by plotting the individual vigour of scion varieties on each rootstock (ordinate) against the means for vigour of scion varieties on a certain rootstock (indicated by arrows on the abscissa) (YATES & COCHRAN, 1938; EBERHART & RUSSELL, 1966). When the rootstocks are arranged for vigour, the vigour of a scion variety commonly follows an ascending line; when interaction is absent, ideally, ascending lines for various scion varieties would run parallel. In presence of interaction, lines for one or more scion varieties would significantly deviate from parallelism or show an erratic pattern.

Scion-rootstock interaction as to vigour has been studied in a number of crops, including apple (VYVYAN, 1955; MARTIN, 1980), *Abiës* (BRYNDUM, 1965) and cucumber (ZIJLSTRA & GROOT, 1988). Additive vigour of scion and rootstock (absence of scion-rootstock interaction as to vigour) in combination plants of these crops is illustrated in Figs.4.1., 4.2. and 4.3., which were recalculated from originally tabulated values; vigour is expressed as 'dry weight', 'plant height' or 'length increase per day', respectively.

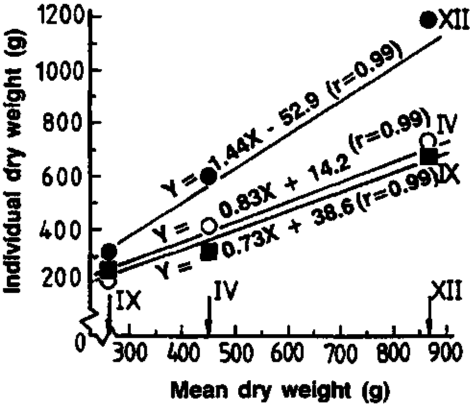

*Fig. 4.1. The relationship between the overall mean dry weight of 3-year-old apple trees grafted on the rootstocks MIX, MIV and MXII (indicated by arrows), and the individual dry weight of trees of MIX, MIV and MXII grafted as a scion variety on these stocks. Correlations significant at p = 0.01. (Figure plotted after data by VYVYAN, 1955).*

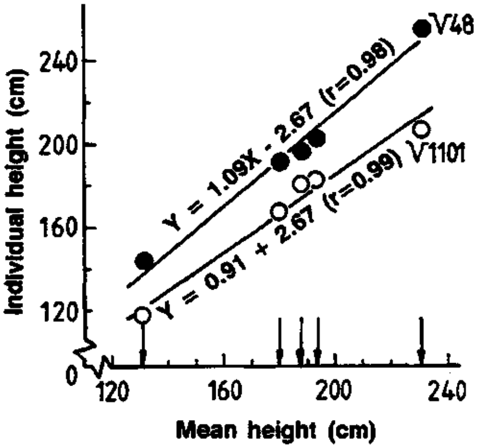

*Fig. 4.2. The relationship between the overall mean height of 11-year-old Picea trees on five different Picea rootstocks (indicated by arrows), and the individual height of the P.abies varieties V48 (vigorous) and V1101 (weak) on these stocks. Correlations significant at p = 0.001. (Figure plotted after data by BRYNDUM, 1965).*

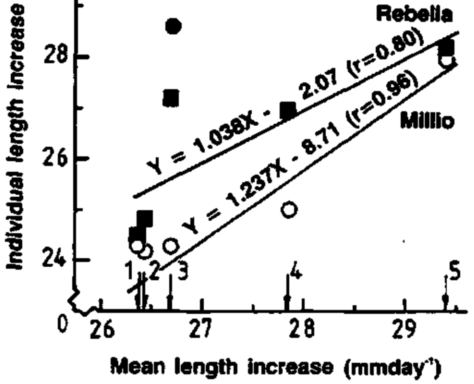

*Fig. 4.3. The relationship between the overall mean daily length increase of cucumber plants grafted on five different rootstocks (indicated by arrows), and the individual daily length increase of 'IVT-line 1', 'Rebella' or 'Millio' grafted on these stocks. Correlations significant at p = 0.05. (Figure plotted after unpublished data by S.Zijlstra and S.Groot, CPRO-DLO, Wageningen).*

### 4.2.3. Scion-rootstock relationships in the rose

Surprisingly, first application of rootstocks in the rose was as a useful agent in producing more self-rooted plants of valuable cultivars (BUCK, 1951; EDWARDS, 1955). In that propagation process, temporary combination plants were stooled. After self-rooting, the scion variety was removed from the stock. Only when roses became popular as garden plants and demand for large numbers of a cultivar increased, stocks were used for permanent cultivation of combination plants.

In the development of rose stocks and in their use, both similarities and differences with fruit stocks occur. A gradual change from the use of seedling to that of clonal rootstocks, which has happened in e.g. the apple, is not described for the rose. On the contrary, ever since stocks are mentioned in the literature, seedlings and clones have gone side by side, the use of either type being determined geographically. Distinction between seedling and clonal rose stocks is only partly explained by the fact that most *seedling* stocks are recalcitrant in vegetative propagation (FERGUSON, 1933; DUBOIS & DE VRIES, 1992), and that most *clones* used are not winter hardy.

Unlike various fruit crops, where clonal stocks of different vigour may control the growth of the combination tree according to the grower's desires or soil conditions (ROM & CARLSON, 1987), such a range is not available in the rose. This is partly connected with the fact that the seedling stocks currently used for cut roses differ little in vigour, partly with the fact that cut rose growers are interested in vigorous rather than in weak stocks.

In contrast to forest or fruit trees, the vigour of rose combination plants is not known to be affected by the onset of flowering of the scion variety. Recurrent flowering cut rose genotypes are genetically programmed, in that each shoot segregates a more or less fixed number of leaves before the apical flower bud is initiated. Another difference is that fruit trees are usually pruned when dormant, whereas roses are continuously pruned (harvested) while actively growing. Anticipating our discussion in Section 4.6.5., it is expected that continuous harvesting of rose plants exerts effects on the growth of both the scion variety and the stock.

Research into scion-rootstock relationships in the rose, as it was carried out at horticultural institutions in the past 70 years, has been dedicated exclusively to the variation in shoot yield of a relatively small number of cultivars, as induced by a large number of diverse kind of stocks. Analysis of more than 40 rootstock experiments with cut roses under glass, showed most of the trials to be highly repetitive and serving mainly local interest (DUBOIS et al., 1990a). In addition, the majority of results lacked any statistical basis, were often confusing, and sometimes contradicted previous results. Even recent experiments with clonal stocks (KROMWIJK & VAN MAURIK, 1991) hardly diverged from that traditional pattern.

In spite of rather one-sided approach of scion-rootstock relationships in the above experiments, DUBOIS et al. (1990a) drew a number of important conclusions. Hence, (i) stocks significantly affect the shoot yield of combination plants, (ii) shoot yield of combination plants is a useful parameter of rootstock vigour, (iii) the yield of self-rooted cultivars is inferior or at best equal to that of the same cultivars grown on a rootstock, (iv) when seedling and clonal stocks are used for the same cultivars, clones (*R.indica* 'Major', 'Manettii' and *R.multiflora*) always yielded higher than seedlings (Fig.4.4.). It is remarkable, therefore, that vigorous clonal stocks have remained so unpopular in The Netherlands.

An important effect of rootstock experiments has been the gradual discarding of weak stocks from collections. However conducive this selection may be to the general level of shoot yield, lack of weak stocks creates a difficult situation when genotypic rootstock variation for vigour is to be studied.

Presence of scion-rootstock interaction as to vigour was not reported in the literature of the rose. On the contrary, in an experiment with eight garden roses grafted on eight different stocks, ROWLEY (1961) reported absence of scion/stock interactions. Also in the review by DUBOIS et al. (1990a), no evidence of that phenomenon was found. This indicates, as has been found for a number of species, that the vigour of rose combination plants largely consists of the additive vigour of the scion variety and the rootstock (Section 4.2.2.). Hence, when two or more cultivars are grafted onto a series of stocks that are arranged for vigour, it is commonly seen that (i) cultivars differ in level of yield, (ii) the sequence of rootstock-induced vigour (yield) is the same for each cultivar, (iii) the vigour of the combination plant is determined by the

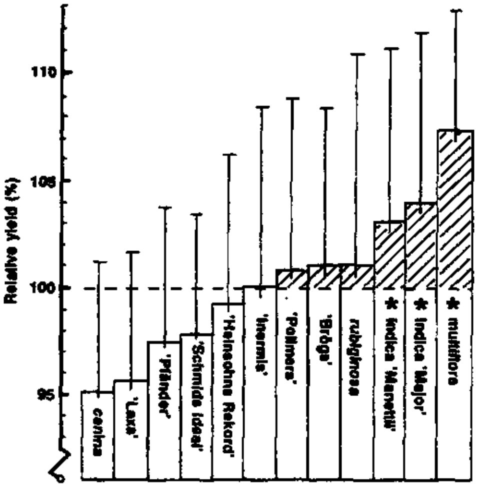

*Fig. 4.4. The mean flower yield of various cut rose cultivars induced by 12 different rootstocks used in 23 experiments, expressed as the overall mean percentage.*
*Bars indicate standard deviation; ★ indicate clonal stocks. (Figure after DUBOIS et al., 1990a).*

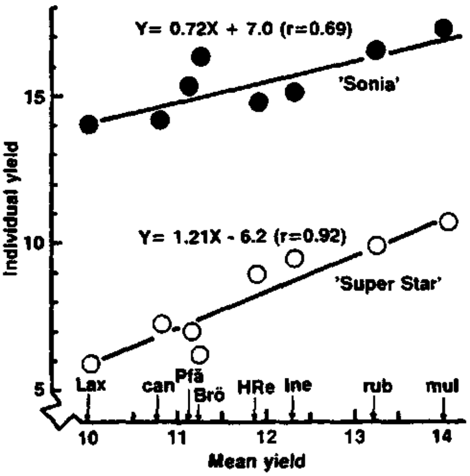

*Fig. 4.5. The relationship between the overall mean flower yield in the second year of rose cultivars grafted on eight different rootstocks (indicated by arrows), and the individual yield of 'Sonia' and 'Super Star' grafted on these stocks. Correlations significant at p = 0.05(+) or 0.01(++). (Figure after DUBOIS et al., 1990a).*

individual vigour of scion and stock. This is illustrated for (i) and (ii) by the scion varieties 'Sonia' and 'Super Star' (Fig.4.5.), where the individual shoot yield of these cultivars grown on eight stocks (ordinate), is plotted against the overall mean yield of each stock (abscissa) (Section 4.2.2.). General absence of scion-rootstock interaction as to vigour in the rose indicates, that the preference of growers and propagators for specific cultivar-rootstock combinations, must be based on shoot quality or the availability of certain stocks, rather than on yield capacity. As in apple (HATTON, 1917), absence of scion-rootstock interaction for yield also indicates the use of one scion variety to test the vigour of rootstocks, to be justified in the rose.

A particular relation between scion and rootstock, which has not yet been investigated, occurs in the breeding of new cut rose cultivars. In that procedure, promising (own-rooted) seedlings are selected from segregating populations at anthesis in the first year (DE VRIES, 1976a; 1976b). Selection is commonly based on *direct* characters, viz. those that are not or hardly modified after grafting on a rootstock, like flower colour, petal number or thorniness.

In spite of good possibilities of *indirect* selection (GALLAIS, 1983) for yield, based on a correlation with the juvenile period of seedlings (DE VRIES, 1976a; 1976b), this method is not applied by breeders because it would be 'too laborious'. This means that the shoot yield of otherwise promising genotypes is not assessed before cultivation on a rootstock in the next year (DE VRIES & DUBOIS, 1977). As the above selection procedure has been followed ever since breeding was aimed at cultivars for the glasshouse, it is evident that (i) breeders pay insufficient attention to selection for vigour, and (ii) this situation is undesirable, because far too many genotypes are unnecessarily propagated. Because the breeder's choice of desirable seedlings determines future performance of cultivars, it has yet to be investigated whether seedling behaviour as to vigour is indicative of that of their clones on a rootstock.

Another aspect of scion-rootstock relationship which has been neglected in the rose, is a comparative study of the growth and development of scion varieties of different vigour, either on their own roots or in combination with a rootstock. Hence, the early stages of plant growth in the nursery, the subsequent development of combination plants in the glasshouse, the function of bottom-breaks, and the consequences of variation in correlative inhibition (Section 2.6.) in relation to expression of vigour, are unclear.

## 4.3. Aims of present chapter

In rose rootstock experiments, predominantly the vigour (yield) of scion varieties grafted on various stocks has been investigated. Relations between own-rooted seedlings and their clones on a stock, have not been studied as a basis for efficient breeding. Based on the parameter 'shoot yield', the vigour of scion varieties may be assessed after one or more years of cultivation. However, basic differences between the growth and development of weak and vigorous scion genotypes are yet unclear. In addition, effects of scion vigour on the growth of the root system of combination plants have not been studied in the rose.

The *first* aim of this chapter is to study relationships as to the vigour of cut rose genotypes grown as *own-rooted* seedlings and as their *clones* grafted on the rootstock *R.canina* 'Inermis'. Special attention is paid to the time of emergence and number of bottom-breaks in relation to the vigour of genotypes.

The *second* aim is to study the growth and development of cut rose genotypes of different vigour, starting at the time of grafting on the rootstock 'Inermis' in the nursery, until 12 months of cultivation in the glasshouse.

Our *third* aim is to investigate the influence of cut rose genotypes of different vigour on the growth of 'Inermis' root systems.

## 4.4. Material and methods

### 4.4.1. *Experiment 1*. Vigour of own-rooted Hybrid Tea seedlings and their clones on *R.canina* 'Inermis' stocks

The vigour of different own-rooted Hybrid Tea rose seedlings in the first year, was compared with that of their clones on *R.canina* 'Inermis' in the following year. The experiment was replicated in three different years, each replication involving batches of different genotypes.

#### *Plant material*

In the spring of 1978, 1979 and 1980, plants were the seedlings of various populations that arose from crossing different Hybrid Tea progenitors in each previous year. After 3-4 months stratification and subsequent germination of the seeds, young seedlings in the cotelydon stage were transplanted in 7x7 cm flower pots in March. At first flowering in May, individual Hybrid Tea seedlings were selected in a *direct* way for cut rose properties, viz. upright habit, long shoots with few thorns, and well-shaped flowers composed of 20-35 petals of attractive colour. Care was taken, to select as much as possible, for uniform shoot length. In that procedure, which is a custom in rose breeding (DUBOIS & DE VRIES, 1987), about 2% of the seedlings of a population were retained each year. The selected seedlings were randomly planted in the glasshouse in soil, in two-row beds. Glasshouse conditions were:

16°C during the night and 19°C during day-time, with automatic ventilation starting at 22°C. Contrary to practice, these own-rooted seedling plants were treated as cut rose combination plants (ANON., 1987; Section 2.4.), viz. the bottom-breaks were soft-pinched and shoots were uniformly harvested by cutting just above the third five-leaf from below, when the colour of the petals became visible between the sepals.

In December of the years 1978, 1979 and 1980, when the shoot yield of the seedling plants had been recorded over a period of about six months, batches of respectively 38, 51, and 30 plants were chosen for clonal propagation. These genotypes, that were satisfactory for cut rose properties, but greatly varied in yield, were visually selected for uniformity of shoot length, number of leaves per shoot and leaf size. In January of each next year (1979, 1980 and 1981), the genotypes were bench grafted onto 8-12 mm *R.canina* 'Inermis' (seedling) stocks (Section 2.2.), provenance Verschuren, Oeffelt. Per genotype, 25-30 scions were grafted. When the axillary sprout of a scion was about 10 cm long, combination plants were planted in the glasshouse, in two-row beds in February; a clone consisted of 15 uniform combination plants. As the Hybrid Tea seedlings were necessarily grown as single plants, their clones were neither replicated and planted in random order.

Glasshouse conditions and treatment of the combination plants were similar to those described for the seedlings. The first basal bottom-breaks were soft pinched to about 40 cm height (Section 2.4.); subsequent basal and axillary bottom-breaks were pinched depending on the level of shoot harvest at that time. Shoots were harvested twice weekly. Combination plants were grown for about 12 months.

### *Observations*

Of each seedling and clonal plant the date of pinching of bottom-breaks and the number of harvested shoots were recorded. ***Time of bottom-break emergence*** is defined as the number of days from bench grafting until the pinching of a bottom-break. Actual emergence of a bottom-break, which is a delicate observation, occurred several weeks previously.

### 4.4.2. *Experiment 2.* Growth and development of Hybrid Tea clones on *R.canina* 'Inermis' stocks

The growth and development of cut rose genotypes of different vigour was studied from the time of sprouting of the scion after grafting in the nursery, until about 12 months of cultivation in the glasshouse. The experiment was replicated in three different years, each replication involving batches of different genotypes.

#### *Plant material*

In 1978, 1979 and 1980, plants were Hybrid Tea rose seedlings similar to those involved in Experiment 1, but of different descent. Selection for desirable traits, as well as nursery and glasshouse conditions for seedlings and their clones, were the same as described in Section 4.4.1.. At the end of December of each of the years 1978, 1979, 1980, batches of respectively 60, 53 and 40 (about 6-month-old) seedlings were labelled for clonal propagation. Early in January of each following year (1979, 1980 and 1981), these seedling plants were bench grafted on 'Inermis'.

Because uniform sprouting *within* clones, and detection of differences in time of sprouting *between* clones, were the aims in this experiment, scions were only cut from the four central internodes of seedling shoots of which anthesis was about to occur. Per clone, 25-35 scions were grafted onto 8-12 mm *R.canina* 'Inermis' (seedling) stocks, provenance Verschuren, Oeffelt. These stocks had been carefully selected for uniform branching of the root system. When the sprouts of scions were about 10 cm long, 15 uniform combination plants of each clone were planted in a three-row bed in a glasshouse. Plant treatment was similar to that described in Section 4.4.1.. Shoots were harvested twice weekly. The experiment ran about 12 months.

#### *Observations*

In the nursery glasshouse, the dates of grafting and sprouting of each scion were recorded in 1980 and 1981. In the glasshouse, the dates of pinching the bottom-breaks of each plant, and the number of harvested shoots per clone were recorded in 1979, 1980 and 1981. *Time of sprouting of the scion* is defined as the number of days from grafting until the individual sprout of a plant was 1 cm long (VAN DEN BERG, 1987). *Time of bottom-break emergence* is defined as the number of days from sprouting of the scion in the nursery until the first bottom-break of each individual plant was pinched; actual emergence of a bottom-break occurred several weeks earlier.

### 4.4.3. *Experiment* 3. Root weight, root collar diameter, bottom-breaks and shoot yield of Hybrid Tea clones on *R.canina* 'Inermis' stocks

The relations between the root (fresh) weight, the root collar diameter, the number of bottom-breaks and number of harvested shoots of various cut rose genotypes were studied. The experiment was replicated in two different years, each replication involving batches of different Hybrid Tea rose genotypes.

#### *Plant material*

Plants were the clones of 71 and 52 different own-rooted cut rose genotypes of various origin, selected in 1978 and 1979 on a similar basis as in Experiment 1. These genotypes were cloned by bench grafting onto 8-12 mm *R.canina* 'Inermis' (seedling) rootstocks, provenance Verschuren, Oeffelt, in January of respectively 1979 and 1980, under conditions similar to those described in Section 4.4.1.. Of each genotype 10 combination plants were planted in the glasshouse about three weeks after grafting. Glasshouse conditions, cultural measures and harvesting disciplines were likewise similar to those described in Section 4.4.1.. Plants of 12 months old were uprooted; then shoots and roots were separated at the graft union.

#### *Observations*

Prior to grafting, the individual root fresh weight of 100 uniform stocks to be used for grafting was assessed. In the glasshouse, the numbers of bottom-breaks and of harvested shoots were recorded. The transverse diameter of the root collar (graft union), and the fresh weight of the root part free of adherent soil, were recorded after uprooting.

## 4.5. Results

### 4.5.1. *Experiment 1.* Vigour of own-rooted Hybrid Tea seedlings and their clones on *R.canina* 'Inermis' stocks

In each of the three years, the mean number of bottom-breaks per plant tended to be larger in own-rooted Hybrid Tea seedling plants than in their clones on 'Inermis' in the following year (Table 4.1.). Probably because the cultivation period was about 4 months longer in clones (12 months) than in seedlings (7 months), the mean shoot yield per plant was higher in clones than in the original seedlings. Significant positive correlations between the number of bottom-breaks and the number of harvested shoots in both own-rooted seedlings (Fig.4.6., left) and their clones on 'Inermis' (Fig.4.6., right), occurred in each of the three years. This indicates, both in own-rooted seedlings and in their clones, the shoot yield to be highly dependent on the number of bottom-breaks. Remarkable agreement between the regressions and levels for clones may be due to selection of uniform 'Inermis' stocks prior to grafting, the same growing period, and/or selection for the same plant habit in genotypes from a similar gene pool in the three years.

In each of the three batches of Hybrid Tea plants, the number of bottom-breaks of seedlings in the first year, and that of their clones in the following year, were significantly correlated. The relation was linear and approximately the same for each batch (tg $\varphi = 0.2$) but years differed in level (Fig.4.7., left). Regression formulae show plants with few bottom-breaks in the seedling stage to have a somewhat higher number in the clonal stage. However, as the number of bottom-breaks of seedlings increased, the number of bottom-breaks in their

*Table 4.1. The number of bottom-breaks and of harvested shoots per plant of batches of own-rooted Hybrid Tea rose seedlings in the first year, and those of their clones on R.canina 'Inermis' stocks in the second year, in three different years.*

| | 1978 | 1979 | 1980 | 1981 |
|---|---|---|---|---|
| *Bottom-breaks seedlings* | *2.9 ± 2.6* | *2.8 ± 2.7* | *2.1 ± 2.2* | - - |
| *Bottom-breaks clones* | - - | *2.2 ± 2.5* | *1.7 ± 2.0* | *1.7 ± 2.1* |
| *Shoot yield seedlings* | *11.7 ± 9.1* | *5.2 ± 4.8* | *6.4 ± 5.9* | - - |
| *Shoot yield clones* | - - | *13.2 ± 5.1* | *11.6 ± 4.7* | *8.8 ± 3.6* |

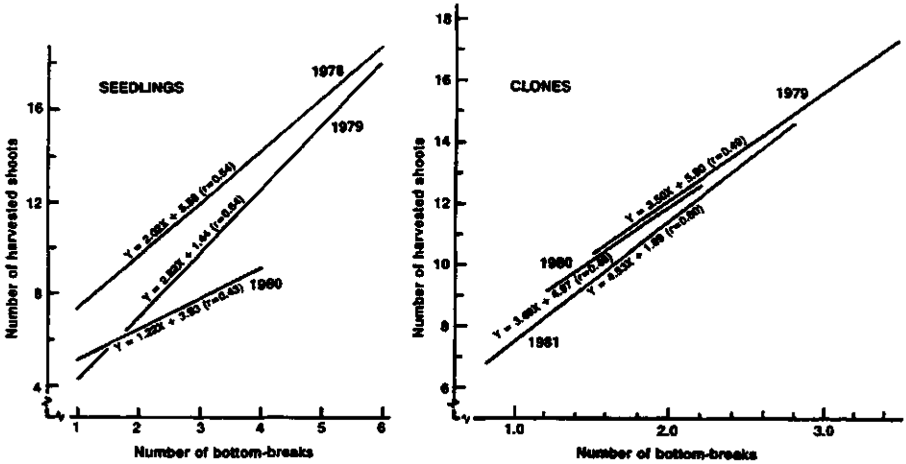

*Fig. 4.6. The relation between the number of bottom-breaks and harvested shoots, in 3 batches of own-rooted seedlings (left) and in their clones on R.canina 'Inermis' (right), in 3 years. Correlations significant at p = 0.01.*

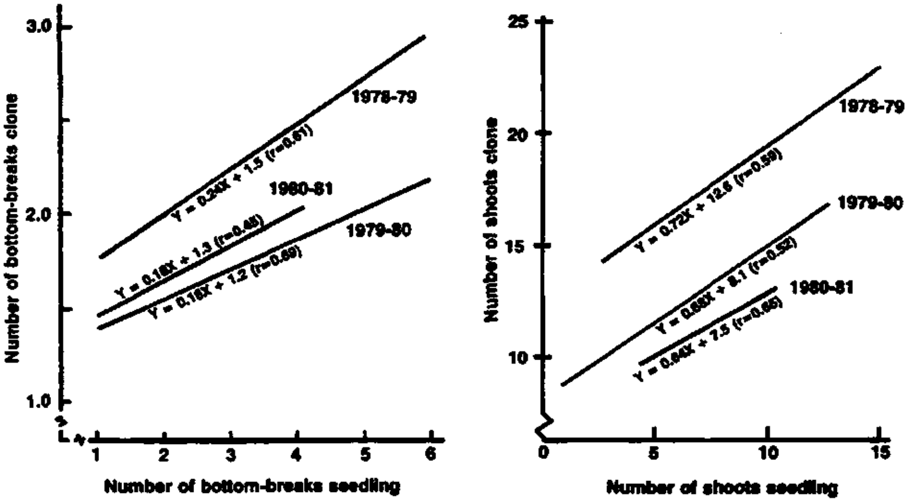

*Fig. 4.7. The relation between the numbers of bottom-breaks (left) or of harvested shoots (right), in 9-month-old own-rooted seedlings in the first year, and in their 11-month-old clones on R.canina 'Inermis' in the following year. Correlations significant at p = 0.01.*

clones did not increase correspondingly. Also the number of harvested shoots of seedlings in the first year and that of their clones in the following year, were significantly correlated (Fig.4.7., right). In genotypes with low shoot yield in the seedling stage, yield was augmented by the rootstock but, like the bottom-breaks, this situation was reversed in high yielding genotypes. As a consequence of these effects of 'Inermis', both the numbers of bottom-breaks and of harvested shoots of potentially high yielding genotypes, were markedly reduced.

### 4.5.2. *Experiment 2.* Growth and development of Hybrid Tea clones on *R.canina* 'Inermis' stocks

Between the years 1980 and 1981, the number of days from grafting various Hybrid Tea genotypes on 'Inermis' to sprouting of their scion in the nursery, did not differ significantly (Table 4.2.). Also the time of bottom-break emergence of the clones was about the same in the three years. The number of bottom-breaks tended to decrease from 1979 to 1981, as was also reflected in a decreasing number of shoots harvested per plant. However, differences between years were not significant.

In 1980 and 1981, within each group of clones, the time of sprouting of the scion was correlated with (i) the time of bottom-break emergence (positively) and (ii) the number of bottom-breaks (negatively) (Table 4.3.). This indicates that as the scion of genotypes sprouted earlier in the nursery, the bottom-breaks of such clones emerged both earlier and in larger numbers. Correlations between time of sprouting and number of harvested shoots, however, were not significant. *Time* of bottom-break emergence was negatively correlated with both the *numbers* of bottom-breaks and of harvested shoots. Finally, the number of bottom-breaks of clones was positively correlated with the number of harvested shoots. This indicates that as clones produced more bottom-breaks in an earlier stage, the yield of such clones was correspondingly higher.

The course of bottom-break emergence, progressing similarly for all clones in each year, is illustrated for the year 1979 (Fig.4.8.). Earliest bottom-breaks emerged at the end of April, about 14 weeks after the scion had sprouted;

*Table 4.2. Times of sprouting of the scion and of bottom-break (Bb) emergence (day in the year), mean number of Bb's per plant, and mean number of shoots harvested per plant of three different batches of clones of cut rose grown on R.canina 'Inermis' stocks in the glasshouse in 3 different years.*

| | 1979<br>(n = 60) | 1980<br>(n = 53) | 1981<br>(n = 40) |
|---|---|---|---|
| *Time of sprouting (d)* | - - | *16.0 ± 2.3* | *13.5 ± 2.6* |
| *Time of Bb emergence* | *101.0 ± 7.9* | *111.1 ± 10.7* | *111.4 ± 10.9* |
| *Number of Bb's* | *2.3 ± 0.5* | *1.8 ± 0.3* | *1.6 ± 0.4* |
| *Number of shoots* | *13.2 ± 3.9* | *11.6 ± 4.4* | *8.8 ± 2.8* |

*Table 4.3. Interclonal correlations between the time of sprouting of the scion in the nursery, the time of bottom-break (Bb) emergence, the number of bottom-breaks and the number of harvested shoots, in three different batches of clones of cut rose grown on R.canina 'Inermis' stocks in the glasshouse in 3 different years (correlations significant at p = 0.01).*

| | | 1979 (n = 60) | 1980 (n = 53) | 1981 (n = 40) |
|---|---|---|---|---|
| *Time of sprouting* | *-Time of Bb emergence* | - - | *+0.45* | *+0.48* |
| | *-Number of Bb's* | - - | *-0.47* | *-0.46* |
| | *-Number of shoots* | - - | *n.s* | *n.s* |
| *Time of Bb emergence* | *-Number of Bb's* | *-0.49* | *-0.45* | *-0.42* |
| | *-Number of shoots* | *-0.54* | *-0.48* | *-0.55* |
| *Number of Bb's* | *-Number of shoots* | *+0.49* | *+0.48* | *+0.60* |

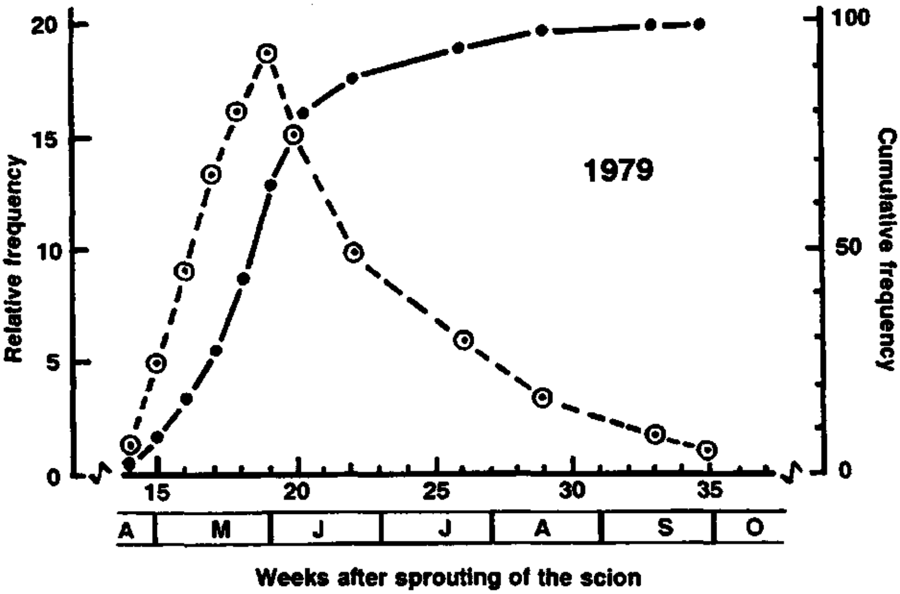

*Fig. 4.8. The relative (⊙) and cumulative (●) frequencies of bottom-break emergence in 60 cut rose clones on R.canina 'Inermis' stocks in the glasshouse in 1979 (100% = 2.32 Bb's per plant).*

highest emergence frequency occurred about five weeks later, when approximately 65% of the total number was present. From that time, frequency gradually declined to the 36th week after sprouting (late September), when the process of emergence had finished.

### 4.5.3. *Experiment 3.* Root weight, root collar diameter, bottom-breaks and shoot yield of Hybrid Tea clones on *R.canina* 'Inermis' stocks

Root collar diameter (graft union), root weight, number of bottom-breaks and number of harvested shoots per Hybrid Tea clone, differed insignificantly between the two years (Table 4.4.). Compared with the initial root weight (13.0 ± 3.6 g), stocks had increased approximately 2.5 times in weight in about 12 months. Table 4.5. shows significant *interclonal* correlations between the root collar diameter (graft union) and root weight, and between the diameter and number of bottom-breaks, indicating that as the diameter of the root collar (graft union) of clones increased, root weight and number of bottom-breaks were correspondingly larger. For each year, these relationships are illustrated in Fig.4.9., which shows that the regressions were about the same in the two years. Significant correlations (Table 4.5.) occurred between (i) root weight and number of bottom-breaks, and (ii) between number of bottom-breaks and number of shoots (see also Section 4.5.1.), indicating that (i) the number of bottom-breaks per clone was larger as root weight was higher, and (ii) as clones had formed more bottom-breaks, shoot yield was correspondingly higher. Correlations between (i) the root collar diameter (graft union) and number of shoots and (ii) root weight and number of shoots were not significant.

Like *between* clones, *within* each clone correlations (significant at $p = 0.05$, when $r \geq 0.63$) occurred between root collar diameter (graft union) and root weight ($0.54 \leq r \leq 0.92$, n= 10), between root collar diameter (graft union) and the number of bottom-breaks ($0.42 \leq r \leq 0.92$, n= 10), and between root weight and number of bottom-breaks ($0.25 \leq r \leq 0.83$, n= 10). Like between clones, the latter association was rather weak and significant for a few clones only.

*Table 4.4. Means of the root collar diameter (graft union), the root weight, the number of bottom-breaks and the number of shoots harvested in two batches of 12-month-old clones of cut rose grown on R.canina 'Inermis' stocks, in 1979 and 1980.*

| | 1979 (n = 71) | 1980 (n = 52) |
|---|---|---|
| *Diameter (mm)* | *21.2 ± 2.2* | *20.8 ± 1.8* |
| *Root weight (g)* | *32.1 ± 6.3* | *30.0 ± 5.3* |
| *Number of bottom-breaks* | *2.3 ± 0.5* | *1.8 ± 0.3* |
| *Number of shoots* | *13.2 ± 3.9* | *11.6 ± 4.4* |

*Table 4.5. Interclonal correlations between the root collar diameter (graft union), the root weight, the number of bottom-breaks (Bb) and the number of harvested shoots in two batches of 12-month-old clones of cut rose grown on R.canina 'Inermis' stocks, in 1979 and 1980 (correlations significant at p = 0.01).*

| | | 1979 (n = 71) | 1980 (n = 52) |
|---|---|---|---|
| *Diameter* | *-Root weight* | *0.70* | *0.76* |
| | *-Number of bottom-breaks* | *0.57* | *0.62* |
| | *-Number of shoots* | *n.s* | *n.s* |
| *Root weight* | *-Number of bottom-breaks* | *0.35* | *0.39* |
| | *-Number of shoots* | *n.s* | *n.s* |
| *Number of Bb* | *-Number of shoots* | *0.49* | *0.50* |

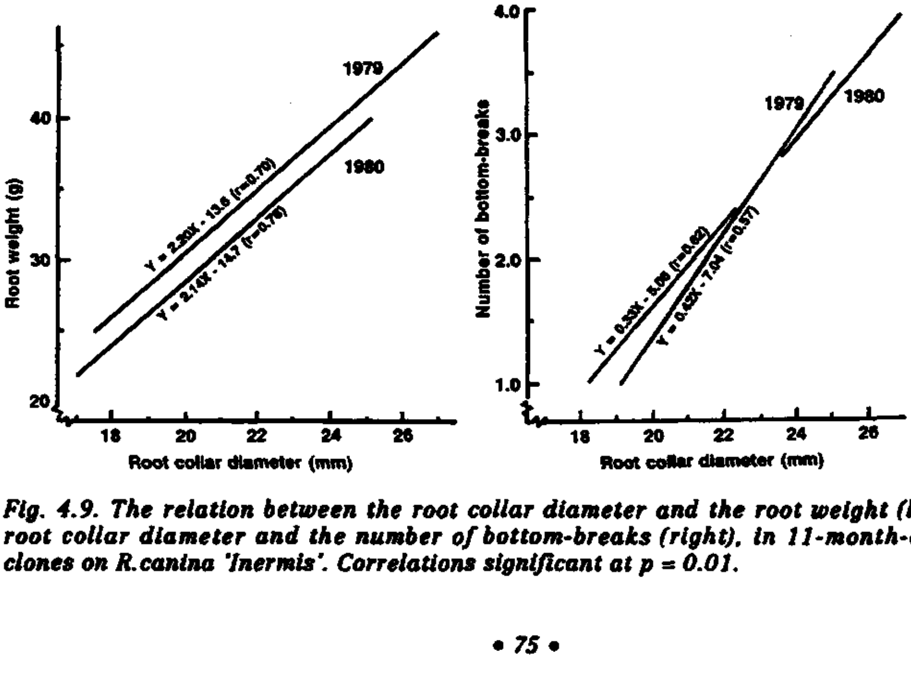

*Fig. 4.9. The relation between the root collar diameter and the root weight (left) and the root collar diameter and the number of bottom-breaks (right), in 11-month-old cut rose clones on R.canina 'Inermis'. Correlations significant at p = 0.01.*

## 4.6. Discussion

### 4.6.1. Scion-rootstock relationships as to scion vigour; seedlings-clones

Our results demonstrate consequent genotypic expression of scion varieties as to vigour. Hence, significant positive correlations between the numbers of bottom-breaks and of harvested shoots of own-rooted Hybrid Tea rose seedlings and their clones on 'Inermis' indicate that, when arranged for increasing vigour, viz. for number of bottom-breaks and/or of shoot yield (Fig.4.7.), the order of own-rooted seedlings and their clones was basically the same. These results agree with a general absence of scion-rootstock interaction as to vigour in the rose, as reported for numerous rose cultivars on various stock (ROWLEY, 1961; DUBOIS et al., 1990a).

The fact that the growth and development of Hybrid Tea genotypes, either as a seedling or as a clone on 'Inermis' were fundamentally the same, indicates that the ontogeny of the original seedling is repeated in the clonal stage. In that reasoning the primary shoot of the combination plant is comparable to that of the shoot of the seedling, while bottom-breaks and their laterals do not differ in either plant type.

It may be realized that in terms of 'scion-rootstock relationships', assessing the vigour of own-rooted seedlings may be considered an experiment without replications, in which many unknown scion varieties are grown on as many unknown rootstocks. In contrast to usual rootstock experiments, however, the scion and the stock are of the same genotype. Leaving aside differences in the level of vigour, it was shown that despite the use of different 'rootstocks', the order in vigour of the 'scion varieties' was the same on 'Inermis' roots. This might indicate that, broadly speaking, the vigour of a combination plant is determined by the scion variety, rather than by the stock.

Consistent order of the vigour of scion varieties has also important consequences for the selection for vigour (yield) in cut rose seedlings. As expounded in Section 4.2.3., breeders commonly follow a time and area consuming procedure, in which the seedlings that are selected at first flowering on the basis of direct characters in April-May, are virtually neglected until December-January. Only from that time, in addition to other characters, the yield of 5-10 clonal plants on a suitable rootstock is assessed in the glasshouse for about 12 months. Subsequently, the best genotypes from this first clonal cycle are propagated once more, usually in quantities of 25-50 plants per clone (DUBOIS & DE VRIES, 1987). Only after two or more clonal cycles, promising genotypes are distributed over different nurseries.

On account of the correlations between the vigour of seedlings and their clonal plants (Fig.4.7), efficiency of the procedure of selecting cut rose cultivars from groups of seedlings may be improved. Cultivation of own-rooted seedlings and treating them like cut rose plants from selection at first flowering until December, may largely contribute to that aim. During this about 6-month period, the choice made at anthesis may be verified. Most important, however, is that the vigour of genotypes can be assessed (DE VRIES & DUBOIS, 1977). As a consequence of disappointing flower quality and/or plant habit, vase life, but particularly of insufficient vigour, very many fewer genotypes need to be retained for the first clonal selection (DE VRIES, 1976b). It is our experience that, depending on the parentage, only 5-10% of the seedlings selected at first flowering are retained for the first clonal cycle. Taking into account that at first flowering about 2% of the population was retained, this means that 1/50 x 1/20 (1/10) = 0.1-0.2% of the plants of a population attains the first clonal selection.

Summarizing the foregoing, it is seen that by exploiting the 6-month period that is otherwise wasted, the information about genotypes is closely similar to that traditionally obtained after 18 (6 + 12) months. The advantages are: a shorter selection cycle and a reduction of financial expenses by economizing on glasshouse area and labour.

It is noteworthy that *indirect* selection in populations for shoot yield on the basis of 'earliness' of genotypes, which is correlated with shoot yield (DE VRIES, 1976b; Section 4.2.3.), would even more augment selection for vigour, as well as reduce the number of seedlings to be selected in.

### 4.6.2. Genotypic variation as to scion vigour

The results demonstrate marked variation in the capacity to produce shoots among numerous genotypes (Fig.4.6.) of which the seedling habit differed only little when selected at first flowering (Section 4.4.1.). The tremendous importance of bottom-breaks for the shoot yield of cultivars, was demonstrated by significant correlations between the numbers of bottom-breaks and of harvested shoots (Fig.4.6.; Table 4.3.). These results warrant efforts to enhance the number of bottom-breaks in cultivars that are naturally reluctant producers of such shoots (ASEN & HAMNER, 1953; CARPENTER & RODRIGUEZ, 1971; ZIESLIN et al., 1976b; Section 2.5.), and should be a stimulation for further research.

Variation in the vigour of genotypes is revealed as variation in the development of the grafted scion and, twelve months later, in that of shoot yield. Our results have shown that the first genotypic differences are discernable from about 10 days after grafting, as variation in the time of sprouting of the axillary bud of the scion (Table 4.2.), which announces the growth of the primary shoot. Subsequent differences occur in the number of bottom-breaks (Fig.4.6.) and probably in the time of their emergence; the most important differences occur between the number of shoots harvested per plant per annum (Fig.4.6.). When a set of clones of cut rose genotypes are arranged for increasing vigour, the growth and development of vigorous clones, relative to weak ones, may be described as follows. Owing to a lower degree of inhibition, the quiescent buds of scions break sooner after grafting, resulting in primary shoots that flower sooner; also the distal axillary buds of these primary shoots break sooner, which results in longer laterals of that shoot. As a consequence of this earlier development, bottom-breaks emerge sooner and, again owing to less inhibition, more of the lower buds of the original scion will break, which promotes the number of bottom-breaks; both earlier and more bottom-breaks ultimately result in higher shoot yield. As will be elaborated in Section 5.6.2., also at harvesting level there are more axillary buds that break sooner after each harvest, which in turn contribute to higher shoot yield.

It is thus concluded that the lead in growth of vigorous over weak genotypes is mainly due to the earlier breaking of more quiescent buds after grafting and cut-back or, otherwise stated, a larger 'branching capacity'.

As demonstrated by DE VRIES (1976b) and DE VRIES & DUBOIS (1977), the shoot yield (vigour) of rose seedlings assessed over a 6-month period is significantly correlated with the 'juvenile period' or 'earliness'. Hence, as the juvenile period of genotypes (defined as: number of days from seed germination to first flowering) was shorter, the vigour of these genotypes, both own-rooted and on a rootstock, was higher. Since the present results have shown the vigour of genotypes to be closely related to degree of bud inhibition, a general understanding of juvenility might be advanced by studying the relation between earliness and degree of bud inhibition.

The time of sprouting of rose scions grafted on 'Inermis', is an early parameter of bottom-break formation which, in turn, is correlated with yield (Table 4.3.). Because of this relation it would be of interest to rootstock breeding to investigate if, and to what extent, the time of sprouting of the scion is affected by the stock. In this reasoning, axillary buds of scions of the same genotype are expected to sprout earlier on vigorous than on weak stocks, which should be investigated.

### 4.6.3. Correlative inhibition and scion vigour

As was elucidated in Section 4.6.2., a major part of variation in vigour of cut rose genotypes is due to variation in the release from inhibition of axillary buds in various stages of plant development, resulting in different branching capacity. As bud inhibition in the rose is the result of apical dominance, variation in the vigour of scion varieties is tentatively considered against the background of probable endogenous hormone action (Section 2.6.).

With *Pisum* and *Vicia* as model plants, WICKSON & THIMANN (1958), SACHS & THIMANN (1967) and RUSSELL & THIMANN (1988) were the first who explained release from inhibition of axillary buds from an antagonism between auxins formed in the shoot and cytokinins formed in the root. In a review on apical dominance, CLINE (1991) noted that this original concept has not been contradicted but that, like auxin (Section 2.6.), views about the mode of action of cytokinins have changed in course of time. The advantage of this concept is that other endogenous hormones which might play a role in bud inhibition, are not considered. There is, however, the danger of oversimplification. Moreover, many conclusions about antagonism are based on *in vitro* experiments with synthetic hormones. On the other hand, variation in branching capacity in *in vivo* roses has been attributed to variation in the ratio of auxins : cytokinins, synthesized in the shoot and the root respectively, by PARUPS (1971) and MOR & ZIESLIN (1987). This antagonism, therefore, is used to explain the variation in branching capacity of scion varieties as observed in our experiments.

Hence, in the rose, own-rooted genotypes (seedlings) have fewer bottom-breaks and fewer shoots as the ratio of auxins : cytokinins shifts in favour of auxins, or more bottom-breaks and shoots as the ratio is in favour of cytokinins. In the clonal plants of these genotypes the original ratio is disturbed by grafting on 'Inermis'. Assuming 'Inermis' on average to produce about the same (relatively low) amount of cytokinins in combination with each genotype, in combination plants the ratio auxins : cytokinins is mainly controlled by the scion variety (F.W.A.Verstappen, CABO-DLO, Wageningen, Personal Communication). From this concept, the levelling-down effect on bottom-break number and shoot yield by the 'Inermis' stocks (Fig.4.7.; Section 4.5.1.) may be explained as follows. In plants with a low number of bottom-breaks in the seedling stage, 'Inermis' produces more cytokinins than did the original roots, thus inducing more bottom-breaks and shoots. However, in plants with a high number of bottom-breaks and shoots in the seedling stage, 'Inermis' produces less cytokinins than did the original root, and consequently induces fewer bottom-breaks and shoots. Our concept offers an explanation on a hormonal basis for the mediocre performance of 'Inermis' and probably of any currently available Edelcanina as a rootstock for cut rose cultivars (Fig.4.4.).

It is concluded, that selection and/or breeding of rootstocks that more efficiently control scion vigour should be encouraged. It should be repeated (Section 4.2.3.) that, contrary to fruit growing in which 'control' usually means a combination of reduced vigour, precocity and productivity, in roses 'control' should mean: high vigour, the ability to stand continuous harvesting (pruning) of the scion and to maintain these properties under different environmental conditions.

In current clonal rootstocks, Hybrid Tea genes have rarely been incorporated. With regard to the superior performance of some vigorous own-rooted Hybrid Tea seedlings, the use of their root system as a stock might be considered.

### 4.6.4. Consequences of variation in branching capacity

In the foregoing Sections it was made clear that the term 'bud-break' comprises two phenomena, viz. the *time of breaking* of quiescent buds after grafting or harvest, and the *number of buds* that break on those occasions. Our results indicate that in young plants the time of bud-break and the number of buds that break are linked, viz. early bud-break is usually correlated with numerous broken buds and vice versa (Table 4.3.). Bud-break after harvest, as influenced by temperature (and light) has been studied in detail by VAN DEN BERG (1987). In the cultivar 'Sonia' the time of bud-break varied from 10 days after harvest at 15°C to about 5 days at 20°C. Depending somewhat on the time of year (natural irradiation), the number of days to bud-break took about 15% of the total time between two harvests in that cultivar. The rate of bud-break (percentage of broken buds) observed 21 days after harvest in seven cultivars grown at 15°C, varied from about 10% for 'Ilona' to about 95% for 'Ilseta', thus indicating genotypic variation for bud-break. It may be emphasized that the time of bud-break has a repeated impact on the duration of each harvest cycle, whereas the number of broken buds is directly related to the number of shoots of each subsequent harvest.

Variation in correlative inhibition clearly is the basis of branching, but ultimate variation in number of shoots measurable as yield (vigour), is not explained by variation in branching alone. The variation in number of shoots is inevitably associated with the leaf area and consequently with photosynthesis. In established combination plants of *the same age*, but with differing correlative inhibition, it is seen that genotypes with strong inhibition have fewer shoots than those with weak inhibition. Because the plants involved in present experiments had been selected for uniformity of habit (stem length, number of leaves per shoot, leaf size [Section 4.4.1.]), it should be assumed that at the same age, the total leaf area of plants with weak inhibition is (much) larger than in those with strong inhibition. As a consequence of difference in leaf area, genotypes with weak inhibition have a more vigorous growth than those with a strong inhibition.

Effects of different leaf area per plant on growth are enlarged by the harvesting regime. In the present genotypes shoots usually bore 10-15 leaves, which agrees with those of the well-known cultivars 'Sonia' and 'Ilona' (VAN

DEN BERG, 1987). Taking into account that a length of shoot bearing 3-4 leaves is left on the plant (Section 2.4.), 70-80% percent of the leaf area of a shoot is removed at each harvest. Because a cut rose bush bears shoots of different age, harvesting of shoots in the marketable stage is a process that continuously interferes with the photosynthetically active area. Loss of carbohydrates is compensated by the shoots that are not yet marketable, by the remaining parts of harvested shoots, and probably by the roots. But as capacity of compensation is smaller in plants with few than with many shoots, impact of harvest is more serious on genotypes with strong than with weak correlative inhibition.

With regard to photosynthetically active area, our results are supported by those of an experiment by DE VRIES & DUBOIS (1993b), in which the 'natural' vigour of 'Sonia' and 'Baccara' cut rose plants was enhanced by grafting *two* scions of the same cultivar (instead of *one*) on one 'Inermis' stock. Compared with one scion per stock, plants raised from two scions had a consistently larger leaf area and more bottom-breaks, effecting an about 20 % higher shoot yield (vigour) in both cultivars in a 12-month period. It is thus concluded that variation in the vigour of scion genotypes is largely determined by variation in correlative inhibition, effecting variation in number of buds broken, which is associated with variation in photosynthetically active area.

However, our conclusions inevitably contain some assumptions. The first one, which will be confirmed in Chapter 5 as to rootstock action, is that genotypic variation in branching capacity is present both in the lower plant parts and at harvesting level. The second assumption is that genotypic variation for shoot length, number of leaves per shoot and leaf area per shoot *of the genotypes involved* (resulting from selection for uniformity) was relatively small (Section 4.4.1.). Our third assumption is that, as was reported for several cultivars (AIKIN & HANAN, 1975; PLAUT et al., 1975; JIAO et al., 1988; PASIAN & LIETH, 1989; ZIESLIN & MOR, 1990), the net photosynthesis per unit leaf area is of about the same order among various genotypes grown in the same environment. It should be remarked, finally, that in addition to the major effects of correlative inhibition and leaf area on the vigour of cut roses, possible variation in daily increments in length of shoots, of internode length and diameter, as well as of rootstock effects should be taken into account.

### 4.6.5. Scion vigour and stock growth

Our results demonstrate close, but mainly indirect relations between the growth of aerial and sub-soil parts of combination plants with 'Inermis' as a stock (Table 4.5.; Fig.4.9.). It is noteworthy that the significance of correlations between the characters was higher as the plant parts involved were physically closer. In agreement with these correlations, a general relationship between aerial and subsoil parts may be described as follows. As the vigour of scion varieties increases, combination plants (on the rootstock 'Inermis') have more bottom-breaks which result in higher shoot yield; as the bottom-break number increases, the root weight increases correspondingly. As bottom-break number and root weight increase, the root collar diameter (graft union) of plants increases as well. These relations, which hold both between and within clones, show great similarity to those in deciduous fruit crops. For instance, *between* Sweet Cherry cultivars on F12/1 rootstock, crown volume, trunk girth and diameter of the root system were very closely correlated (MAURER, 1971). Also *within* apple clones the weights of the root system, stock, trunk, branch and of accumulated prunings as induced by the stock, were very significantly correlated (MOORE, 1978).

In general, in plants that are regularly pruned, either as a cultural measure or for experimental purposes, a kind of equilibrium between the weight of aerial and subsoil parts, characteristic for the conditions prevailing seems to be reached after some time (BROUWER, 1983; VISSER, 1969; WAREING, 1970; LAMBERS, 1983; KLEPPER, 1991). Although the shoot/root weight ratio was not determined in Experiment 3, our results suggested a certain equilibrium between the growth of the aerial and subsoil parts of harvested cut rose clones of different vigour on the rootstock 'Inermis'. Since vigorous clones are harvested much more frequently than weak ones, an equilibrium would indicate total regrowth after harvest to be much better in vigorous than in weak genotypes. This agrees with our considerations in Section 4.6.4., where the advantage of a larger leaf area per plant of vigorous genotypes was expounded.

Occurrence of an equilibrium, functional for harvested cut rose plants was also shown by DE VRIES & DUBOIS (1993a). Comparison of harvested and non-harvested 'Sonia' on 'Inermis', showed an approximately constant S/R ratio in harvested plants (about 4 on fresh weight basis) to establish about five months from grafting. In non-harvested plants, however, the ratio continued to increase (>10) until the plants were uprooted after 12 months. In Section 3.5.3., about similar S/R (fresh) weight ratios of harvested 'Sonia' combination plants on 'Inermis' (Fig.3.22.) were encountered. In various, assumedly unpruned woody plants, S/R ratios between 4.0 and 9.1 are reported (KLEPPER, 1991).

Since the sequence in vigour of cut rose genotypes is not affected after grafting on a rootstock ('Inermis'), an equilibrium between shoot and root growth of approximately four, may indicate that the overall growth of a rose combination plant is determined by the scion rather than by the stock (Section 4.6.1.). However, between stocks different ratios occurred (Section 3.5.3.). This equilibrium, of which the relation with the total vigour of combination plants has not been investigated, is indicated as rather sensitive to environment (HUNT, 1982), including the pruning (harvesting) regime applied. With regard to the foregoing, it seems worthwhile to investigate the role of equilibrium between shoot and root weights in relation to additive vigour of the scion variety and the stock (Section 4.2.2.).

# Chapter 5

# Genotypic variation in rootstocks

> *" Hij die zichzelf vrij weet is inderdaad vrij, en hij die zichzelf gebonden acht is inderdaad gebonden. - Zoals de gedachte is, zo is het bereikte - is een algemeen gezegde in deze wereld, en het is waar."*
>
> *Ashtavakra Gita, Ch.1, Sl.11.*

# Chapter 5. Genotypic variation in rootstocks

## 5.1. Summary

Genotypic variation of *R.canina* 'Inermis' was studied as to plant characters and adventitious root formation of softwood cuttings. Variation in the growth and development of 'Sonia' combination plants was studied relative to clonal 'Inermis', 'Brögs' and Hybrid Tea stocks of different vigour.

After 6 months in the glasshouse, originally uniform 'Inermis' seedling stocks appeared to differ in internode length, number of leaflets per leaf and the leaf area. They also differed in the time of axillary bud-break, axillary sprout length and weight of adventitious roots of their 23-day-old softwood cuttings. Clonal root weight of cuttings was correlated with: number of leaflets per leaf, leaf area, and days to axillary bud-break.

'Sonia', grafted on different 'Inermis' and 'Brögs' rootstock clones, varied for the dates of emergence of the first and second bottom-break (Bb), the number of Bb's, and the number of harvested shoots in 12 months. Correlations between the root weight and the diameter of the graft union were significant for both 'Inermis' and 'Brögs'; at the same root weight, graft unions of 'Brögs' were always thickest. Genotypic variation of Edelcanina is attributed to hybridization.

In a Hybrid Tea (HT) rose seedling population, shoot yield of own-rooted seedlings in 8 months was negatively correlated with the time from seed germination to first flowering. The shoot yield of 'Sonia', grafted on rootstock clones of low or high yielding HT-seedlings, was positively correlated with the yield of the own-rooted HT-seedlings. The root weight of the clonal HT-stocks was positively correlated with the yield of 'Sonia'.

In all experiments it was demonstrated that as rootstock clones induced a first Bb earlier, the second one emerged earlier as well; clones with early Bb's induced more Bb's per plant and more shoots than clones with late Bb's. The number of Bb's per plant per rootstock significantly determined the shoot yield of 'Sonia'. The Bb diameter at emergence and the number of harvested shoots of a clone were not significantly correlated.

The vigour of rose genotypes is an inherent character, that is expressed in both the aerial and subsoil parts. In 'combination-plants' the vigour of the

rootstock genotype is transmitted to the scion variety. A major effect of vigorous rootstocks is increased branching capacity of the scion variety, which is visible as earlier and more profuse axillary bud-break in all stages of plant development. Owing to a larger branching capacity, scion varieties on vigorous stocks have a larger photosynthetically active area already in an early stage of plant development than scions on weak stocks. This results in a lead in growth. Important differences in the vigour of rootstocks are attributed to endogenous hormone action, a concept in which rootstocks supposedly differ for cytokinin synthesis. A model of endogenous hormone action and its effects on the axillary bud-break and subsequent growth of combination plants is tentatively proposed.

## 5.2. Introduction

### 5.2.1. The breeding system of *R.canina* L.

Because (Edel)caninas may produce rather uniform offspring but do not conspicuously hybridize, initially they were supposed to propagate apomictically. That concept was strengthened by the occurrence of numerous, clearly separated microspecies (KROON & ZEILINGA, 1974). Several authors, however, have doubted the occurrence of apomixis in the rose (HURST, 1931; FAGERLIND, 1940; BLACKHURST, 1948).

An alternative explanation of uniformity of offspring is the phenomenon termed *heterogamy*, occurring exclusively in roses of the *Caninae*-section (TäCKHOLM, 1920; 1923; BLACKBURN & HARRISON, 1921). In that system, the pentaploid ($2n=5x=35$) Edelcaninas form only 7 bivalents in meiosis, so that 21 univalents remain unpaired. During *microspore* formation the univalents are eliminated, resulting in haploid pollen, containing 7 chromosomes. During the formation of *macrospores*, univalents are not lost, so that egg-cells contain 28 chromosomes (tetraploid). After fertilization, plants containing 35 chromosomes are obtained. Because three sets of chromosomes are transmitted without any genetic recombination by the female gamete, the breeding system of Edelcaninas has been termed 'sub-sexual' or 'semi-apomictic' by WYLIE (1976). Because in some Edelcaninas seeds have been obtained in low frequency without previous pollination, indications are that apomixis may yet sometimes occur (ZEILINGA, 1969; KROON & ZEILINGA, 1974).

The foregoing indicates that Edelcaninas 'breed true' not because they are homozygous lines, but because of strong maternal influence. The same effects of heterogamy that are favourable to keep Edelcanina selections more or less-true-to type, may considered a serious drawback in creating new Edelcaninas by cross-breeding (Chapter 6).

### 5.2.2. Origin of genotypic variation in Edelcanina

Owing to the typical breeding system of *R.canina* L., the mother plants of each Edelcanina selection might produce a relatively homogeneous offspring. However, complaints about heterogeneity of Edelcaninas have increased since they were used on a large scale (FLOOR, 1955; KROON, 1975). Part of the external heterogeneity is the result of environmental effects (Chapter 3), but variation in thorniness, number of leaflets per leaf and flower colour are likely to be genetic. A large part of variation remains concealed, because the majority of stocks is handled in bench grafting when plants are quiescent and practically without shoots. External heterogeneity, therefore, is mainly visible in the nursery field where stocks do produce shoots with leaves prior to budding. In addition to discontent with the external homogeneity of plants within Edelcanina selections, complaints about the performance of stocks in combination with a scion variety have been voiced by both plant-producing nurserymen and cut rose growers. These usually concern variation in the growth of combination plants in the nursery in general, and plant-to-plant variation in the vigour (shoot yield) of one scion-rootstock combination in the glasshouse in particular.

In pollination experiments KROON & ZEILINGA (1974) demonstrated that, contrary to general opinion, Edelcanina selections may hybridize among themselves and with other species. As hybridization progresses slowly, its visual effects may be delayed for several generations. This means, that if seed gardens contained clonal Edelcanina mother plants, were mono-clonal or were maintained over a long range of years, hybridization might be kept relatively constant or on a low level. However, in current seed gardens various Edelcaninas and other species used as stocks are planted together and flower about simultaneously. In this situation which is ideal for cross-pollination, undesired hybridization may be common rather than exceptional. Moreover, seed gardens are regularly uprooted and replaced with 'true to type-looking' seedlings obtained from seedling mother plants. It is presumed that owing to that policy, effects of hybridization that initially were suppressed, have gradually appeared.

Although the judgement of homogeneity may have changed in course of time, it must be assumed that Edelcanina selections like 'Inermis' or 'Brögs Stachellose' were more uniform in the first decades after their introduction than today.

In spite of the importance to rose growing, so far the effects of hybridization in Edelcanina have neither been studied as to variation in the morphology of rootstock plants, nor in relation to the performance of cut rose combination plants.

## 5.3. Aims of present chapter

Environmental effects on the variation of Edelcanina stock with respect to the vigour of 'Sonia' combination plants were studied in Chapter 3. Genotypic variation in the vigour of *scion varieties* in combination plants with 'Inermis' as a stock, was investigated in Chapter 4. In the present Chapter aspects of genotypic variation of *rootstocks*, individually or in combination with 'Sonia' as a scion are examined. As a start, variation of (i) plant characters, (ii) rooting capacity of cuttings and (iii) vigour were studied in Edelcanina stocks. Because Edelcanina plants in commercial batches give no indication as to their inherent vigour, experiments were continued with Hybrid Tea seedlings that after selection for shoot yield (vigour), were used as a stock for 'Sonia'.

The *first* aim of this Chapter is to reveal effects of hybridization in Edelcanina, on the variation in plant characters, on the formation of adventitious roots in softwood cuttings, and on the variation in induced vigour when used as a stock for a scion variety.

The *second* aim is to study variation in the growth and development of 'Sonia' combination plants, as induced by rootstock clones of Edelcanina and Hybrid Tea seedlings of different vigour.

The *third* aim concerns the mode of action of rootstocks of different vigour.

## 5.4. Material and methods

### 5.4.1. *Experiment 1.* Variation of plant characters and of the performance of softwood cuttings of uniform 'Inermis'

Externally uniform 8-12 mm 'Inermis' seedlings were planted in the glasshouse. Individual plant characters were assessed; adventitious root formation and sprouting of the axillary buds of single-node softwood cuttings were studied.

*Plant material*

Plant material, consisting of a random batch of one-season-old commercial *R.canina* 'Inermis' rootstock seedlings in the grade 8-12 mm, that would otherwise have been used for grafting with cut rose cultivars, was obtained from Messrs Olij, cut rose propagators, De Kwakel, The Netherlands. Thirty seedlings, to be used as source plants, were selected for uniformity of the root system. They were planted in a heated glasshouse in January, about 40 cm apart in a row, and arbitrarily numbered from 1 to 30. The plants were deeply cut back in April. The profusely occurring new shoots of each source plant bore no flowers and were presumably juvenile. In June they were used for softwood cuttings. To that end, from each 'Inermis' source plant, 15 single-node softwood cuttings were taken from the part of a shoot that was neither too herbaceous nor too lignified. A cutting consisted of the full length of an internode with an attached leaf and one quiescent axillary bud on the distal end (DUBOIS & DE VRIES, 1991). Within a clone (viz. the cuttings of one individual source plant), cuttings were selected for external uniformity. To promote adventitious root formation, the base of cuttings was dipped for 10 secs in a 5000 mg/L solution of IAA (potassium salt) in water before striking (DUBOIS & DE VRIES, 1988). Cuttings were struck in flats, containing a mixture of sand and peat (vol : vol = 1 : 1), that were placed on benches under glass covers in the nursery glasshouse. In the nursery temperature was constant about 25°C, photoperiod was about 20 h (ØSTERBYE, 1970). Natural daylight was supplemented with HPI-T (Philips, 400 W) lamps, resulting in an irradiance of about 20 $Wm^{-2}$ during the whole rooting period. Cuttings were lifted and measured destructively after 23 days. At that time in most clones adventitious roots had occurred and broken axillary buds had grown into axillary sprouts.

### *Observations*

During the rooting period, the date of bud-break of the axillary bud of each cutting was recorded. After uprooting, the leaf area ($cm^2$) was measured with LI-COR area meter (model LI-3100). Length (mm) of the internode, the fresh root weight (cg), the length of the axillary sprout (mm) and the number of leaflets composing the leaf were recorded.

### *Methods*

The experiment was carried out in a randomized block design, in which the clone of each source plant was represented by 5 replicates of 3 cuttings. Analysis of variance was carried out for the morphological characters of each source plant:
- length of internode
- number of leaflets per leaf
- leaf area

and for the properties of their cuttings:
- days to axillary bud-break after striking
- axillary shoot length after 23 days
- root (fresh) weight after 23 days.

### 5.4.2. Experiment 2. Variation of the shoot yield of 'Sonia' as induced by clonal Edelcanina stocks of different vigour

Externally uniform *R.canina* 'Inermis' and 'Brögs Stachellose' seedling stocks, supposed to differ for vigour, were cloned by root grafting with 'Sonia'. The vigour of combination plants was studied in relation to the stocks used.

#### *Plant material*

One-season-old Edelcanina rootstocks were obtained from Rosaco, Veendam, The Netherlands, in November. Eight 'Inermis' and eight 'Brögs Stachellose' stocks in the grade 8-12 mm, were selected from batches of 100 stocks of each Edelcanina, on the basis of uniform, well-branched root systems. These two different Edelcaninas were chosen to create a probably *wider range of variation in induced vigour*. Fundamental differences between the two stocks as to performance were not expected to occur (Section 3.5.3.).

In the beginning of December each rootstock plant was cloned by root grafting (VAN DE POL, 1986; DUBOIS et al., 1990b) with 'Sonia' as a scion. Both the length and diameter of the pieces of root used were standardized. To enhance plant uniformity, 'Sonia' scions were only taken from the central part of flowering shoots. Grafted plants were raised in the nursery glasshouse under conditions similar to these described for cuttings in Experiment 1. Three weeks after grafting, when the scion and the stock had united, the primary shoot had emerged a few centimeters and the root segment showed new root growth, the young combination plants were transplanted into 'planttubes®' to stimulate geotropic root growth. In February, well-rooted combination plants were planted in the glasshouse in soil in two-row beds. Glasshouse conditions were: 16°C during the night and 19°C during day-time, with automatic ventilation starting at 22°C. Both basal and axillary bottom-breaks of 'Sonia' were soft-pinched (Chapter 2); shoots were harvested twice weekly. The experiment was continued for about 12 months, after which the plants were uprooted.

#### *Observations*

The date of pinching the bottom-breaks (at about 30-40 cm height) was recorded as 'date of emergence' (see also Chapter 4, Experiment 1). At that time, the diameter of a bottom-break was measured about 5 cm above its basis; diameter was classed as thin (≤ 6mm) or thick (> 6mm). The number of shoots harvested per plant was recorded. After uprooting, the (fresh) weight of the roots free of soil was determined.

### *Methods*

The experiment was carried out in a randomized block design. Each block, containing one combination plant of each of the sixteen rootstock clones, was replicated eight times, so that in all 8 x 16 = 128 plants were involved. Analysis of variance was carried out for the date of emergence of the first and second bottom-breaks, the bottom-break number and the number of harvested shoots of the 16 clones. Multiple linear regression analysis for yield was carried out with Genstat.

## 5.4.3. *Experiment 3.* Variation of the shoot yield of 'Sonia' as induced by pre-selected clonal Hybrid Tea stocks

Hybrid Tea (HT) rose seedlings were pre-selected for vigour on the basis of shoot yield during about 8 months. Subsequently their roots were used as a clonal stock for 'Sonia'. Growth and development of combination plants were studied in relation to the stocks used.

### *Plant material*

The HT-plant material was similar to that used for the experiments in Chapter 4. It consisted of 75 unselected, recurrent flowering seedlings (DE VRIES & DUBOIS, 1978), originating from a cross between the HT-cultivar 'Meiringa' and an unnamed seedling of a HT x (*R.multiflora nana* Hort. F1). The seedling plants were grown in the glasshouse in soil in two-row beds, from May until December. Glasshouse conditions were: 16°C during the night and 19°C during day-time, with automatic ventilation starting at 22°C. Seedling plants were treated like cut rose combination plants, viz. bottom-breaks were soft pinched and shoots were harvested twice weekly by cutting just above the third 5-leaf from below when in the flower bud the colour of the petals became visible between the sepals.

In January next year, from the HT-population two extreme categories of shoot yield (vigour) were selected: 8 seedlings with <8 shoots, and 8 with >24 shoots per plant (see also Fig. 5.7.). In both categories 15-25 plants were cloned by root grafting (VAN DE POL, 1986) with 'Sonia', and raised under conditions similar to those described for cuttings in Experiment 1. Uniformity of combination plants was enhanced by standardizing both the length and diameter of the pieces of root used, while 'Sonia' scions were taken only from the central part of a shoot that was about to flower. Four weeks after grafting, young combination plants of each rootstock clone were planted in the glasshouse under conditions similar to those of the seedlings in the previous year. In the glasshouse, both basal and axillary bottom-breaks of 'Sonia' combination plants were soft-pinched (Chapter 2); shoots were harvested twice weekly. Combination plants were grown for about 12 months, after which the plants were uprooted.

### *Observations*

Of each seedling of the HT-population, the times of seed germination and of anthesis (first flowering) of the seedling were recorded. 'Days to anthesis' was calculated as the number of days from seed germination to anthesis (DE VRIES, 1976a). The shoot yield of own-rooted seedlings was recorded from the time of planting the young seedlings in the glasshouse until the end of December (about 8 months). In 'Sonia' combination plants the dates of pinching the bottom-breaks ('date of emergence'), and the number of harvested shoots were recorded per plant; after uprooting the weight of the root system, free of soil, was recorded.

### *Methods*

The experiment was carried out in a randomized block design. Each block, containing one combination plant of each of the sixteen rootstock clones, was replicated eight times. Analysis of variance was carried out for the number of 'Sonia' shoots harvested on each rootstock clone.

## 5.5. Results

### 5.5.1. *Experiment 1.* Variation of plant characters and of the performance of softwood cuttings of uniform 'Inermis'

When lifted after 23 days, many cuttings had formed adventitious roots, and the initially quiescent axillary bud had often sprouted. In both rooted and unrooted cuttings, a relatively large lump of callus had formed at the proximal end. Adventious roots usually emerged from the bark of the internode just above the callus, but sometimes seemingly came from callus (Fig.5.1.). For about the first two centimeters, roots sometimes grew at a slightly upward angle.

*Between* the clones of the different source plants, for all characters very significant F-values ($p = 0.05$) were computed (Table 5.1.). Important genotypic variation occurred for the morphological characters: length of the internode, number of leaflets per leaf and the leaf area. As to the cuttings,

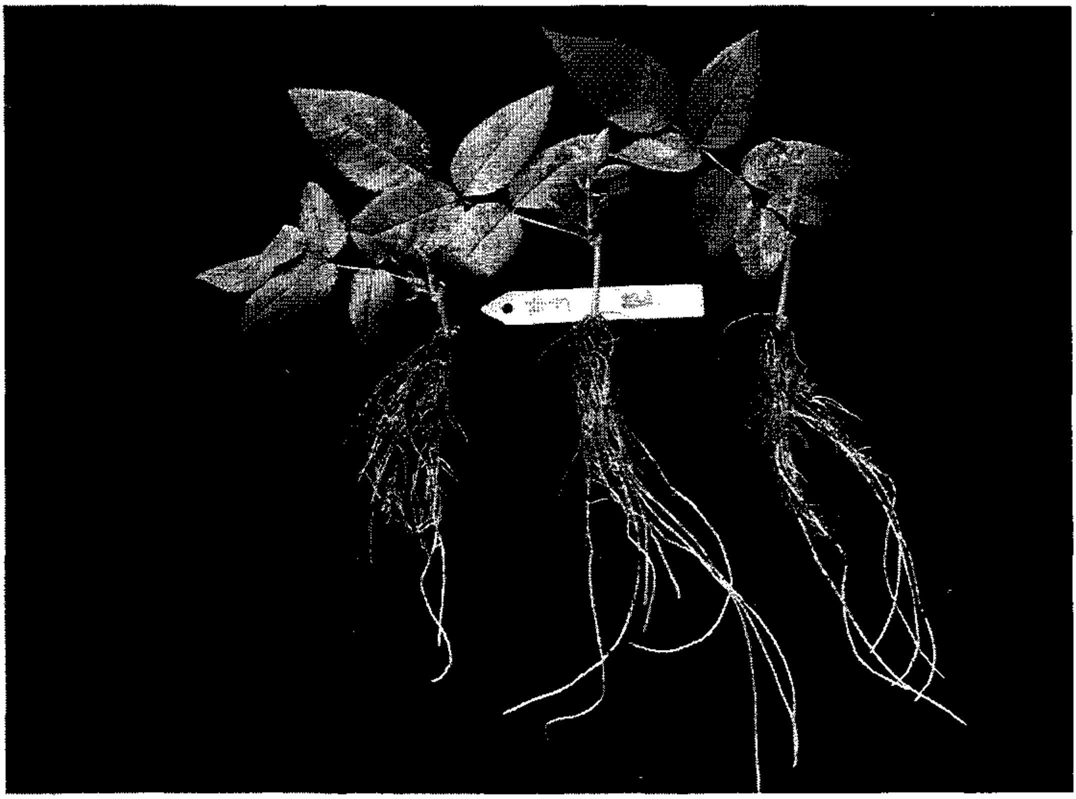

***Fig. 5.1.** Well-rooted and slightly sprouted 23-day-old softwood cuttings of R.canina 'Inermis' clone no. 11. Note root emergence from the bark above callus on proximal end.*

***Table 5.1. Mean per cutting, overall mean, coefficient of variance (CV), F-value from analysis of variance, and least significant difference (LSD, significant at p = 0.05), for characters of 30 R.canina 'Inermis' clones, and for their 23-day-old, single-node softwood cuttings.***

| Clone number | Internode length (mm) | Leaflets per leaf | Leaf area (cm$^2$) | Days to axillary bud-break | Axillary sprout length (mm) | Root fresh weight (cg) |
|---|---|---|---|---|---|---|
| *1* | *26.6* | *6.6* | *47.5* | *5.6* | *38.8* | *87.1* |
| *2* | *23.1* | *6.4* | *46.1* | *7.3* | *26.2* | *82.9* |
| *3* | *28.5* | *5.8* | *27.2* | *5.8* | *71.8* | *27.0* |
| *4* | *33.8* | *5.1* | *60.6* | *9.0* | *24.3* | *112.3* |
| *5* | *32.8* | *6.0* | *61.7* | *6.6* | *25.2* | *93.6* |
| *6* | *30.9* | *7.0* | *90.0* | *6.9* | *28.8* | *38.6* |
| *7* | *25.9* | *6.3* | *32.1* | *5.3* | *64.0* | *3.9* |
| *8* | *32.8* | *6.8* | *38.2* | *5.9* | *49.4* | *47.8* |
| *9* | *25.6* | *5.1* | *43.8* | *9.7* | *7.7* | *89.6* |
| *10* | *27.2* | *5.2* | *57.7* | *7.4* | *35.8* | *119.2* |
| *11* | *24.7* | *6.1* | *50.2* | *8.7* | *15.1* | *89.8* |
| *12* | *29.5* | *5.9* | *39.1* | *8.3* | *17.3* | *0.0* |
| *13* | *32.2* | *6.9* | *48.2* | *6.9* | *20.6* | *0.0* |
| *14* | *28.3* | *6.1* | *47.3* | *7.1* | *12.2* | *0.1* |
| *15* | *25.2* | *6.7* | *31.9* | *6.5* | *11.9* | *1.3* |
| *16* | *28.9* | *6.9* | *34.9* | *5.6* | *60.9* | *8.5* |
| *17* | *34.8* | *6.9* | *25.0* | *7.5* | *8.3* | *28.7* |
| *18* | *32.2* | *5.3* | *45.2* | *7.9* | *25.3* | *120.6* |
| *19* | *24.9* | *5.6* | *31.2* | *7.3* | *5.1* | *5.8* |
| *20* | *25.7* | *6.8* | *32.3* | *6.3* | *23.3* | *11.7* |
| *21* | *26.6* | *5.5* | *53.1* | *12.9* | *3.6* | *84.4* |
| *22* | *28.7* | *6.9* | *42.3* | *6.8* | *6.5* | *0.4* |
| *23* | *22.7* | *5.9* | *53.9* | *9.5* | *21.9* | *60.7* |
| *24* | *33.7* | *5.8* | *33.0* | *5.3* | *19.3* | *1.1* |
| *25* | *29.8* | *6.1* | *31.6* | *5.7* | *16.1* | *0.9* |
| *26* | *24.7* | *6.9* | *30.8* | *8.2* | *11.2* | *6.1* |
| *27* | *23.3* | *7.0* | *21.7* | *5.5* | *63.9* | *30.4* |
| *28* | *31.0* | *6.0* | *29.8* | *6.1* | *33.6* | *19.3* |
| *29* | *33.1* | *6.9* | *48.7* | *6.5* | *65.2* | *16.1* |
| *30* | *18.6* | *6.1* | *41.7* | *7.0* | *10.6* | *77.4* |
| *Mean* | *27.7±5.6* | *6.2±0.4* | *42.6±7.6* | *7.2±2.1* | *27.5±12.9* | *42.2±12.9* |
| *CV (%)* | *21* | *7* | *18* | *29* | *47* | *52* |
| *F-value* | *2.4* | *10.0* | *16.7* | *3.2* | *12.2* | *18.4* |
| *LSD* | *7.0* | *0.5* | *9.5* | *2.5* | *16.1* | *27.5* |

*Table 5.2. Interclonal correlations between characters of 30 R.canina 'Inermis' clones and their 23-day-old, single-node softwood cuttings (correlations significant at p = 0.01).*

| | (1) | (2) | (3) | (4) | (5) |
|---|---|---|---|---|---|
| *Internode length (1)* | - - | - - | - - | - - | - - |
| *Leaflets per leaf (2)* | *n.s.* | - - | - - | - - | - - |
| *Leaf area (3)* | *n.s.* | *n.s.* | - - | - - | - - |
| *Days to bud-break (4)* | *n.s.* | *-0.61* | *0.58* | - - | - - |
| *Sprout length (5)* | *n.s.* | *n.s.* | *n.s.* | *-0.63* | - - |
| *Root weight (6)* | *n.s.* | *-0.65* | *0.65* | *0.62* | *n.s.* |

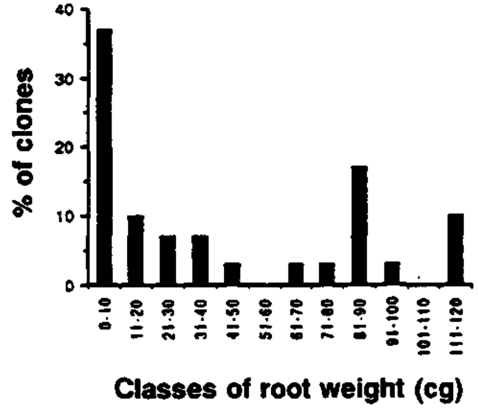

*Fig. 5.2. The distribution of 30 R.canina 'Inermis' clones over classes of root fresh weight of 23-day-old softwood cuttings (mean 42.2 ± 21.9 cg).*

genotypic variation occurred for the time of axillary bud-break after striking, and for the length of the axillary sprout and the fresh root weight after 23 days. Variation in the capacity of clones to form adventious roots is illustrated in Fig.5.2.. About 40% of the clones did not root at all or very poorly (root weight 0-10 cg), while the rooting of about only 15% was very good (root weight >90 cg).

*Within* the clones of source plants, variation for internode length, internode diameter, leaf area and leaflets per leaf was not significant (data not given), indicating the cuttings of one clone to be relatively homogeneous. Also regarding time of bud-break, axillary sprout length and root weight, cuttings within clones behaved uniformly.

Association of characters is presented in a correlation matrix (Table 5.2.).

Only *between* clones a number of very significant correlation coefficients occurred. Thus, days to bud-break and root weight were negatively correlated with the number of leaflets per leaf, and positively with the leaf area; days to bud-break were negatively correlated with sprout length, and positively with root weight. Other correlations were not significant. Correlations indicate that bud-break occurred sooner, and adventitious roots were heavier as source plants (genotypes) had more leaflets per leaf and their leaf area was larger. As was also found by DUBOIS & DE VRIES (1991) for Miniature roses, sprouts were longer and roots lighter, as bud-break of genotypes occurred sooner after striking.

### 5.5.2. *Experiment 2.* Variation of the shoot yield of 'Sonia' as induced by clonal Edelcanina stocks of different vigour

On each of the 16 clonal stocks, the growth and development of 'Sonia' scions followed the pattern as described for cut roses in general (Section 2.4.) and for 'Sonia' in particular (Section 3.4.3.). Judged outwardly, 'Inermis' and 'Brögs' clones performed similarly. In combination with each rootstock clone, 'Sonia' always developed a first and a second bottom-break, sometimes a third, and in exceptional cases a fourth one. The first differences between the 16 rootstock clones were visible in the time of emergence of the first and second bottom-breaks (Table 5.3.). Not included in Table 5.3. are the dates of the third (mean 217.7 ± 35 day, 11 clones), and of the fourth bottom-break (mean 276.0 ± 55 day, 2 clones). Significant variation between the rootstocks also occurred for the number of bottom-breaks and the number of shoots harvested from 'Sonia'.

*Table 5.3. F-values from analysis of variance (significant at p = 0.05), minimum, maximum and mean, for the dates of emergence of the 1st and 2nd bottom-break (Bb), the number of Bb's and the number of harvested shoots per plant in 12 months of the glasshouse rose 'Sonia', grafted on 16 Edelcanina rootstock clones.*

| | F-value | Minimum | Maximum | Mean (s.dev.) |
|---|---|---|---|---|
| *Date 1st Bb* | *20.6* | *82.3* | *112.5* | *94.5 ± 8.7* |
| *Date 2nd Bb* | *9.8* | *130.1* | *173.5* | *151.6 ± 17.0* |
| *Bb number* | *16.4* | *1.8* | *3.6* | *2.3 ± 0.5* |
| *Shoot number* | *4.5* | *22.8* | *33.6* | *27.4 ± 4.3* |

*Table 5.4. Correlations between the dates of emergence of the 1st or 2nd bottom-break (Bb), the number of bottom-breaks (Bb's), and the shoot production in 12 months of the glasshouse rose 'Sonia', grafted on 16 Edelcanina rootstock clones, ($p = 0.05$, $r > 0.48$; $p = 0.01$, $r > 0.61$).*

| | | (1) | (2) | (3) |
|---|---|---|---|---|
| *Date 1st Bb* | *(1)* | - - | - - | - - |
| *Date 2nd Bb* | *(2)* | *0.51* | - - | - - |
| *Number of Bb's* | *(3)* | *-0.68* | *-0.49* | - - |
| *Number of shoots* | *(4)* | *-0.77* | *-0.50* | *0.89* |

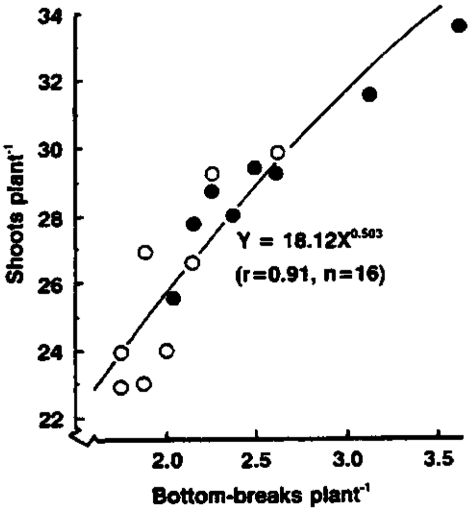

*Fig. 5.3. The relation between the number of bottom-breaks and the number of shoots harvested in 12 months from 'Sonia' cut rose plants, root grafted onto 8 'Inermis' (○) or 8 'Brögs Stachellose' (●) clones (d.f.= 15, r = 0.73). Correlations significant at p = 0.001.*

Times of emergence of the first and second bottom-break were correlated (Table 5.4.), indicating that as a rootstock clone induced a first bottom-break earlier, the second one emerged earlier as well. Rootstock clones that induced early emergence of the first bottom-break, induced both a higher number of bottom-breaks and of harvested shoots than did plants with a late first bottom-break. At a slightly lower level of correlation these relations were true for the second bottom-break as well. Finally, the more bottom-breaks were induced by a rootstock, the higher was the shoot production of 'Sonia'. Similar, just significant correlations with the times of emergence, occurred for the few clones that induced three or four bottom-breaks (data not given).

Fig.5.3. shows a very significant relationship between the number of bottom-breaks per 'Sonia' plant on each root stock clone, and the number of harvested 'Sonia' shoots. This indicates that the level of shoot production was largely determined by the number of bottom-breaks induced by the rootstock (Section 4.5.1.). Although the mean shoot yield of 'Sonia' was not significantly lower on 'Inermis' than on 'Brögs' stocks (25.7 vs. 28.3 shoots per plant, LSD 3.6, at $p = 0.05$), high shoot yield occurred more frequently on 'Brögs' than on 'Inermis' stocks. Comparison of the number of shoots shows a difference of 10.8 shoots (45%) between the least and highest yielding rootstock.

In order to test the association of the total shoot yield of 'Sonia', with the number of bottom-breaks and the dates of emergence of the first and second bottom-break, a multiple regression analysis was carried out. Three linear regressions were estimated:

1. $Y_1 = 0.68X_1 + 14.7$ ($r = 0.89$, $n = 16$)
2. $Y_2 = 0.54X_1 + 0.10X_2 - 8.9$ ($r = 0.93$, $n = 16$)
3. $Y_3 = 0.56X_1 + 0.12X_2 - 0.01X_3 - 8.6$ ($r = 0.94$, $n = 16$),

where $Y$= shoot yield, $X_1$= number of bottom-breaks per treatment, $X_2$= 365 days minus day in the year of 1st bottom-break, $X_3$= 365 days minus day in the year of 2nd bottom-break. The correlations, which in all three cases are significant at $p = 0.001$, indicate that shoot yield is mainly determined by the *number* of bottom-breaks and, as might be inferred from Table 5.4., to a lesser extent by the dates of the first, and particularly of the second bottom-break. Nevertheless, a multiple regression involving both the number of bottom-breaks and the time of emergence gives a better estimation of yield than in considering each parameter separately.

For each rootstock clone the percentage of thick (> 6mm) 'Sonia' bottom-breaks was calculated, which varied between 40 and 87%. A not significant correlation ($r < 0.01$) between the total number of 'Sonia' bottom-breaks per clone and the percentage of thick bottom-breaks per clone, indicates that the diameter of the bottom-breaks of a clone measured at the time of pinching, had no effect whatsoever on the vigour (yield) of the combination plant. Although 'Sonia' combination plants yielded more shoots as rootstock clones induced more bottom-breaks per plant (Fig.5.3.), the number of 'Sonia' shoots

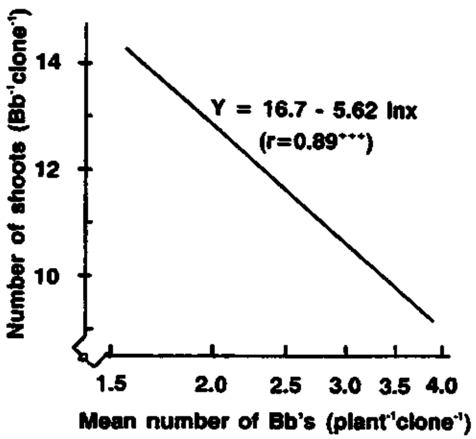

*Fig. 5.4. The relation between the mean number of bottom-breaks (log scale) of 'Sonia' cut rose plants grown on 16 clonal Edelcanina rootstocks, and the number of shoots harvested per bottom-break in 12 months.*
*Correlation significant at p = 0.01.*

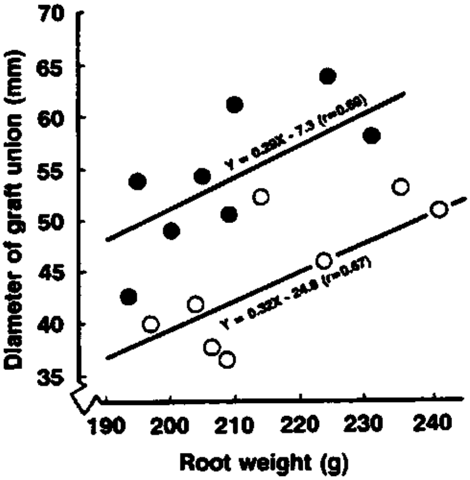

*Fig. 5.5. The relation between the (fresh) root weight and the diameter of the graft union of 12-months-old 'Sonia' cut rose plants, root grafted onto 8 'Inermis' (○) or 8 'Brögs Stachellose' (●) rootstock clones.*
*Correlations significant at p = 0.05.*

harvested per bottom-break significantly decreased as a rootstock clone had induced more bottom-breaks (Fig.5.4.).

The just significant correlations, shown in Fig.5.5., indicate that for each of the two Edelcanina stocks the diameter of the graft union increased with the root weight. Although at the same root weight 'Brögs' graft unions were generally thicker than those of 'Inermis', the slopes were remarkably similar.

### 5.5.3. *Experiment* 3. Variation of the shoot yield of 'Sonia' as induced by pre-selected clonal Hybrid Tea stocks

The Hybrid Tea (HT)-population showed marked variation for the number of days to anthesis (48 to 62 days). Days to anthesis were negatively correlated with the shoot production (Fig.5.6.), indicating that, as was also observed by DE VRIES (1976a; 1976b), seedling plants produced fewer shoots as first flowering had occurred later. The distribution of these HT-seedlings over classes of shoot production (Fig.5.7.) shows that the categories used for root grafting with 'Sonia' (<8 and >24 shoots), contained respectively 21% and 11% of the population.

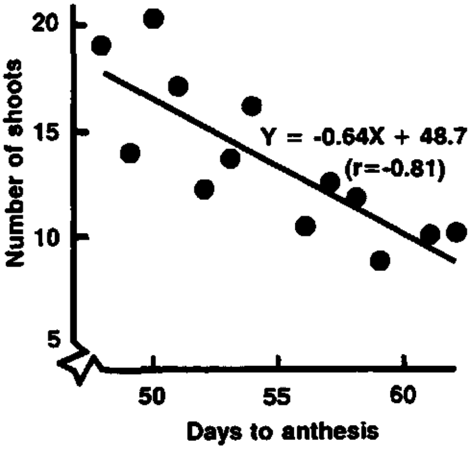

*Fig. 5.6. The relation between the number of days to anthesis (classes) and the number of shoots harvested in seedlings of the population 'Meiringa' x F1 (HT x R.multiflora nana Hort.) in 8 months.*
*Correlation significant at p = 0.001.*

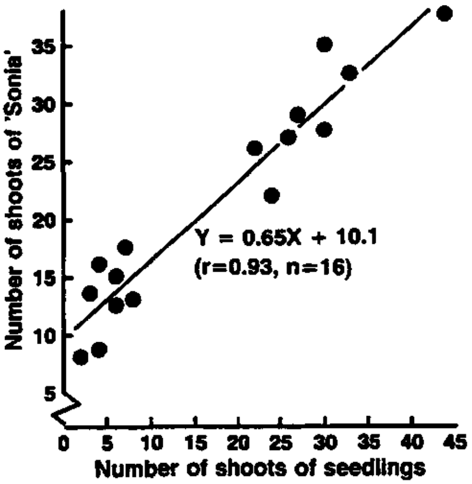

*Fig. 5.8. The relation between the number of shoots produced by own-rooted Hybrid Tea rose seedlings in 8 months, and those produced by 'Sonia' grafted onto the roots of these seedlings in 12 months. Correlation significant at p = 0.001.*

*Fig. 5.7. The distribution of the shoot production of 8-month-old HT-rose seedlings (n=75), in a population from the cross 'Meiringa' x F1 (HT x R.multiflora nana Hort.). Seedlings in the classes <8 or >24 shoots per plant (shaded areas), were root grafted with the scion variety 'Sonia' (see text).*

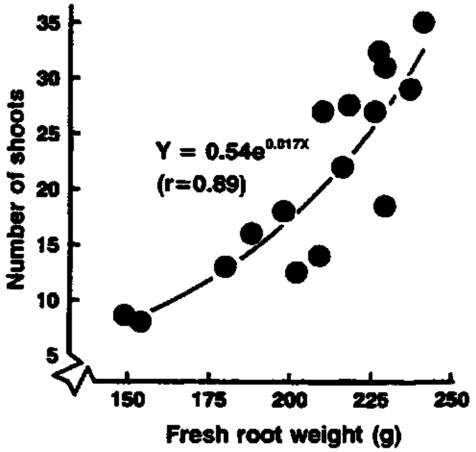

*Fig. 5.9. The relation between the fresh root weights of 'Sonia' plants grafted onto the root systems of various Hybrid Tea rose seedlings, and the number of 'Sonia' shoots produced on these stocks in 12 months. Correlation significant at p = 0.001.*

*Table 5.5. Analysis of variance (significant at p = 0.001) for the number of shoots harvested in 12 months of the glasshouse rose 'Sonia', grafted on root clones of 16 Hybrid Tea rose seedlings of different vigour.*

| | Mean (s.dev.) | Min. | Max. | d.f. | F-value | LSD |
|---|---|---|---|---|---|---|
| *Number of shoots* | *21.5 ± 9.6* | *6.6* | *37.6* | *15* | *70.6* | *3.6* |

The growth and development of the 'Sonia' combination plants followed a similar pattern as described in Experiment 2. The 16 HT-stocks differed significantly for the number of shoots induced in 'Sonia' in a 12-month period (Table 5.5.). Compared with the results of Experiment 2, that ran simultaneously in the same glasshouse, the mean shoot yield of 'Sonia' on HT-stocks was somewhat lower but more variable than on Edelcanina stocks (HT: mean 23.5 shoots, CV 41%; Edelcanina: 27.4 shoots, CV 16%).

Correlation between the time to anthesis of the seedlings and the shoot yield of 'Sonia' on HT-stocks was just not significant at p = 0.05. However, shoot yield of 'Sonia' on HT-rootstock clones over 12 months was significantly correlated with the shoot yield of the own-rooted HT-seedlings over about six months (Fig.5.8.). This indicates that as own-rooted seedlings had produced more shoots, the roots of those plants used as a stock for 'Sonia', induced a higher shoot yield in that cultivar as well. The mean fresh weight of the roots of the HT-clones after 12 months was significantly correlated with the number of harvested 'Sonia' shoots on these clones (Fig.5.9.), indicating that as the shoot yield of 'Sonia' on these clones increased, root weight of stocks had been correspondingly higher.

## 5.6. Discussion

### 5.6.1. Genotypic variation of Edelcanina

The results of Experiment 1 clearly demonstrate significant genotypic variation for both the morphology of leaves and internodes and the performance of softwood cuttings of randomly chosen *R.canina* 'Inermis' seedlings (Table 5.1.; Fig.5.2.). Most important, however, are the results of Experiment 2, demonstrating significant variation for the vigour (shoot yield) of clones of 'Inermis' and 'Brögs' rootstocks (Table 5.3.), of which the source plants had been selected for external uniformity. The results of the two experiments may confirm the presumption of hybridization, and show both 'Inermis' and 'Brögs' to be populations that are heterogeneous for vigour. There is no indication that the situation in other Edelcaninas used for the cut rose industry differs from that in 'Inermis' or 'Brögs'. These results show, that complaints about the lack of external (phenotypic) and internal (genotypic) uniformity of Edelcanina stocks are fully justified.

It may be concluded that from initially stable selections, current Edelcaninas have become segregating populations, and might even be considered as 'land races'. Nurserymen producing these stocks should be aware that this situation is likely to worsen with each new seed garden established, and that without severe measures, future Edelcaninas may be hardly distinguishable from each other and from *R.canina* L..

However detrimental genotypic variation in vigour of current Edelcanina stocks may be to cut rose cultivation, variation opens interesting possibilities for the selection of outstanding individuals in naturally segregating seedling populations (VAN DE POL, 1986). Providing Edelcaninas are maintained as stocks for the glasshouse, which in view of mediocre overall performance is a questionable proposition, selection may aim at genotypes to be used either as mother plants in seed gardens or, directly, as clonal rootstocks. Selection procedures for both seedling and clonal stocks are outlined in Chapter 6.

### 5.6.2. The size of the root system of combination plants

In Section 4.5.2., the influence of the vigour of various scion varieties on the size of the root system of one type of rootstock ('Inermis') was demonstrated. In those experiments the root weight of combination plants generally increased with the vigour of the scion variety and, as may assumed, with its shoot weight. In Experiments 2 and 3, the converse was also shown, that is, the vigour of one scion variety ('Sonia') was influenced by the genotype of the rootstock (Tables 5.3., 5.5.). Just like the root weight of 'Inermis' increased with the vigour of the scion variety (Section 4.5.3.), the weight of the root systems of clonal 'Inermis', 'Brögs' and HT-rootstocks generally increased with the vigour they induced in the scion (Fig.5.5.).

In the present experiments the shoot weight was not determined, but the root weights of combination plants that increased with scion vigour, again imply a certain equilibrium between shoot and root weight (Chapter 3). Because 'Brögs' root systems were always lighter than those of 'Inermis' at equivalent scion vigour, this equilibrium evidently is not the same for each scion-rootstock combination. It suggests a higher S/R ratio for combination plants on 'Brögs' than on 'Inermis' (Fig.5.5.). A similar performance of these two Edelcaninas was previously shown in Chapter 3, where stocks of various diameter were used for 'Sonia'. In that experiment also, 'Brögs' had consistently lighter roots than 'Inermis' and 'Pollmers', resulting in highest S/R (weight) ratio of 'Sonia' combination plants on 'Brögs' stocks (Fig.3.22.). However, not only in combination plants, also as ungrafted own-rooted seedling plants in the second year, 'Brögs' had highest S/R (weight) ratio in a series of different seedling stocks (WARNE & FOTHERGILL, 1942).

In regularly harvested 'Sonia' combination plants on the stock 'Inermis', an equilibrium between shoot and root growth was demonstrated by DE VRIES & DUBOIS (1993a). In those plants a more or less constant S/R (fresh) weight ratio of approximately 4, had established 5-6 months after planting in the glasshouse. Similar S/R (fresh) weight ratio for 'Sonia' on 'Inermis' was found in Section 3.5.3. of the present study. However, stocks apparently influence the S/R ratio of combination plants with the same scion variety. Considering the partitioning of dry matter in combination plants, stocks may be designated 'more efficient', if they induce a larger S/R weight ratio at the same yield level. From that point of view 'Brögs' would be a more efficient stock than 'Inermis' or 'Pollmers' (Fig.3.22.), and might as such deserve more attention either as a present-day stock for the culture in soil (SMIT, 1960; PESSALA, 1977), or as a segregating population for selection of clonal stocks.

Our results indicate that in breeding clonal rootstocks for cut roses, the possibility of selection for an efficient, relatively small root system may be taken into account. The behaviour of 'Brögs' stocks suggests that selection for high S/R (weight) ratio may be carried out already in ungrafted seedlings.

### 5.6.3. Mode of action of rose rootstocks

In addition to significant variation in the induction of vigour *between* different rootstock species and selections (DUBOIS et al., 1990a), the present results demonstrated significant variation for the vigour of 'Sonia', as induced by genotypes of 'Inermis', 'Brögs' and Hybrid Tea. These stock effects indicate that the 'vigour' of a scion variety can neither be considered independently of the genotype of the root system used nor, as was seen in Section 3.5.3., independently of the size of the root system used for grafting. From that point of view it might be recommended always to include self-rooted plants of the scion variety as a standard in rootstock experiments.

Concerning rootstock action in 'Sonia' combination plants, the first recorded differences in induced vigour occurred a few weeks after grafting as significant interclonal variation in the time of emergence and in the number of bottom-breaks. In subsequent stages of plant development, variation in the shoot yield of 'Sonia' occurred as well (Table 5.3.). Earliest possible differences, viz. those in time of axillary bud-break of 'Sonia' scions after bench grafting, were visually observed, but unfortunately not evaluated. From the correlations between time of emergence of bottom-breaks, number of bottom-breaks and shoot yield (Table 5.4.), it is clear that as rootstock vigour increased, axillary buds at the base of the primary shoot broke earlier and more profusely, resulting in more bottom-breaks at an earlier stage of plant development, and consequently in higher shoot yield.

It is remarkable that, in spite of variation in bottom-break diameter at the time of pinching (Experiment 2), clones with initially thick bottom-breaks did not yield higher than clones with thin ones (Section 5.5.2.). Absence of this relation may indicate that the larger diameter of high than of low yielding bottom-breaks after 12 months, as reported by VAN RIJSSEL (1982) and KOOL & VAN DE POL (1992), is the result of more harvested shoots per bottom-break, rather than a precondition of yield.

Merely owing to a sooner bottom-break emergence and a higher number of bottom-breaks per rootstock clone, combination plants on vigorous stocks would already have a marked lead in yield over those on weaker stocks. Although vigorous stocks induce early branching of the scion variety which, in turn, increases ultimate shoot yield, it has not yet been shown whether or not rootstocks affect later stages of plant development. If rootstock action is manifest at harvest level as well, this should be discernable in the branching capacity of the scion variety, viz. in variation in the time of axillary bud-break after harvest, and/or in the number of buds that break after harvest. The latter would be reflected in the number of shoots harvested per bottom-break over a 12-months period.

In the present experiments, the time of axillary bud-break was not recorded. As to the number of lateral 'Sonia' shoots per bottom-break, it was only seen that although vigorous rootstock clones induced more bottom-breaks and consequently more shoots (Fig.5.3.), the mean number of 'Sonia' shoots harvested per bottom-break decreased as clones were more vigorous (Fig.5.4.). However, within rootstock clones 'Sonia' plants differed as to the number of bottom-breaks formed. The mean number of shoots per bottom-break per rootstock clone, therefore, is a poor indication of the branching capacity induced at harvest level. Instead, the branching capacity induced by stocks of different vigour should be compared in equivalent combination plants, viz. those bearing the same number of bottom-breaks. Hence, if after each harvest vigorous stocks induce a larger number of broken axillary buds than weak stocks, this should be noticeable as more shoots per bottom-break. Observations on the number of shoots per bottom-break have been carried out in some detail in individual 'Sonia' plants on six clonal stocks by DE VRIES & DUBOIS (1993c). Analysis of variance demonstrated significant variation in the number of 'Sonia' shoots induced per stock. In Fig.5.10. these six stocks are arranged as to mean number of harvested 'Sonia' shoots. It can be seen that (i) as the number of bottom-breaks per plant increased, in each of the six rootstocks the number of shoots per bottom-break decreased (compare Fig.5.4.), and (ii) as rootstock vigour increased, plants with the same number of bottom-breaks generally had more shoots per bottom-break. These results clearly show rootstocks to be active as to number of broken buds at the harvest level, viz. *more* axillary buds broke after harvest as rootstock vigour increased. In addition to the *number* of buds broken, it was demonstrated that rootstocks induced different *time* of bud-break after shoot harvest (P.A. van de Pol, Agricultural University Wageningen, unpublished data). In an experiment

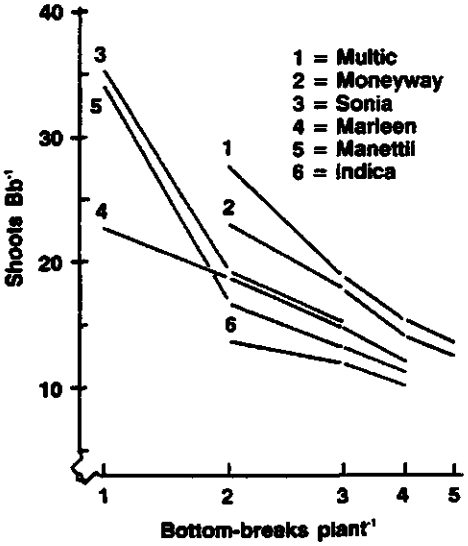

*Fig. 5.10. The relation between the number of bottom-breaks (Bb) per 'Sonia' plant grafted on six different rootstocks (log scale), and the number of shoots harvested per bottom-break in 12 months. (Figure after DE VRIES & DUBOIS, 1993c).*

with 'Motrea' grown on five rootstocks, significant differences in the number of days to sprouting of the upper axillary bud occurred.

Summarizing the foregoing, it is seen that rootstock action is independent of the stage of plant development and of plant height. It is thus concluded, that (i) major part of rootstock action is attributable to variation in the release from bud inhibition (branching capacity) at various stages of plant development, (ii) branching capacity of the scion variety increases with rootstock vigour.

In the HT-seedlings involved as rootstock clones in Experiment 3, the vigour was assessed as the shoot yield *(branching capacity)*, over an 8-month period. Differences in branching capacity remained operative when the original HT-seedling shoots were substituted by those of 'Sonia'. This demonstrates that, as in Poinsettia (STIMART, 1983) and tomato (WOOLLEY & BRENNER, 1981), degree of branching of the rootstock plant is graft-transmittable in roses. This conclusion is of importance for both rose rootstock breeding (Chapter 6) and for explaining the probable underlying mechanism of rootstock vigour on a hormonal base (Section 5.6.4.).

A primary effect of variation in branching capacity is a variation in leaf area per plant. As enunciated in Section 4.6.4., plants of vigorous scion varieties have a larger leaf area than weak ones. Likewise, scion varieties on vigorous stocks will have a larger leaf area than those on weak stocks. These observations agree with rootstock effects in citrus, where vigorous stocks induced a larger total leaf area and a higher dry matter production than weak ones in 'Satsuma' mandarins (MORINAGA & IKEDA, 1990). A higher rate of photosynthesis owing to higher stomata density should be verified in the rose.

Different branching capacity of combination plants as induced by the stock, has important consequences for the methods of experimentation, as well as for rose growing. In order to economize on (i) the number of plants to be raised, (ii) the cultivated area in the glasshouse and (iii) labour, experiments are usually designed with a small number of plants per stock. In the present rootstock experiments, experimental units even consisted of one plant. Because vigorous stocks induce more bottom-breaks and better branching at harvest level than weak stocks, vigorous combination plants are broader than weak ones, and consequently tend to occupy a larger area than weak ones. Differences in plant habit may even be so large that combination plants of the same scion variety behave as different genotypes. Because at standard planting distance in the glasshouse, competition for room (light) occurs after the canopy has closed, a situation comparable to that in forestry occurs. Hence, in a competition situation differences among randomly distributed genotypes are likely to be obscured rather than magnified (CANNELL, 1983).

On the one hand, this may indicate that in subsequent monoculture, rootstock effects are larger than was estimated on the basis of experimental results. On the other hand, in the present experiments all plants were harvested at the same level, so that the broader habit of 'Sonia' on vigorous stocks may have reduced the vigour of combination plants on weak stocks. This would increase rather than decrease differences in performance.

The foregoing indicates that in rootstock trials (i) experimentation should be confined to one scion variety, (ii) planting distances should be well-considered, (iii) experimental units should preferably be larger than one plant.

In spite of showing generally a better start in the growth of young combination plants, in practice many promising new stocks are reported to fall short of expectations (VAN DE POL et al., 1988a). As disappointment concerns *quality* rather than *quantity* of the shoots harvested, it seems that growers do not fully exploit the advantages of vigorous new stocks, owing to the use of traditional (close) planting distances (KOOL & VAN DE POL, 1992).

### 5.6.4. Rootstock vigour and endogenous hormones

The probable role of endogenous hormone action in the vigour of rose plants was expounded in Section 2.6.. The variation in vigour of rose scion genotypes, resulting from variation in release from bud inhibition, was attributed to an antagonism between auxins synthesized in the shoot apex and cytokinins synthesized in the roots (Section 4.6.3.). In that concept, variation in branching capacity of the scion variety is owing to variation in the ratio auxin : cytokinin.

The present results show the performance of stocks of different vigour in one scion variety to be similar to that of scion varieties of different vigour on one stock, viz. vigour is reflected in the branching capacity of the scion. Consequently, the same concept about endogenous hormone action may be applied to explain rootstock effects. Hence, stocks of different vigour supposedly differ in cytokinin synthesis. In that concept, stocks with a relatively high cytokinin synthesis would be more vigorous than those with low synthesis. The results of Experiment 2 with Edelcanina clones and particularly those of Experiment 3 with root clones of HT-seedlings, do not contradict that concept.

Although the role of endogenous hormones in rose plants may ultimately be confirmed by analysis of cytokinins in xylem sap, as has been done in e.g. apple (TROMP & OVAA, 1990), and for auxins in axillary buds of other species (TAMAS et al., 1991), it is tentatively concluded that rose rootstocks, that vary in ability to release axillary buds of the cultivar from inhibition, vary for cytokinin synthesis (VERSTAPPEN, 1992). In this context it is noteworthy that improved branching of Poinsettia cultivars with strong apical dominance, after grafting on stocks with weak apical dominance, was likewise attributed to a balance between endogenous auxin and cytokinins (STIMART, 1983).

Obviously building on the model of the possible hormonal control of the growth and cropping in apple as proposed by LUCKWILL (1970), LOCKARD & SCHNEIDER (1981) hypothesized the mechanism of the vigour of apple rootstocks to be primarily based on endogenous hormonal action. In their concept, auxin synthesized in the shoot and in young apple leaves is considered *the* messenger to the roots. This auxin flows basipetally through the phloem and cambial cells of the scion variety to the roots. It is partly degraded in the (rootstock) bark, the degree of degradation depending on the amount of IAA oxidase, peroxidase, phenols and other compounds, and on the thickness of the bark. The level of these compounds as well as thickness of the bark, are genetically controlled and may vary among species and cultivars. The level of active auxin that reaches the roots controls root growth (branching) and metabolism, including the synthesis of hormones such as cytokinins. The lower the level of auxin that reaches the roots, the smaller is root growth and the lower the level of cytokinins synthesized. Cytokinins from the roots, arriving at the shoot tip would affect shoot growth which, in turn, influences auxin synthesis and its amount that reaches the roots. Via this feed-back system, genotypically different stocks are presumed to control the vigour of the grafted cultivar by their unequal inactivation of auxin. Although other hormones obviously play a role in plant growth, there is no indication that these compounds are utilized as signals to maintain root and shoot balance.

As was enunciated in Section 2.6., such a system of endogenous hormone action has not been proposed for the rose, although a situation similar to that in apple is not unlikely to be present (Section 5.6.5.). In this respect it should be remarked that 'weak' rose stocks showed much less root growth in e.g. nutrient solution than do 'vigorous' ones in the same period of time (D.P. de Vries, unpublished results), and that in spite of similar S/R ratio in established rose plants, total plant weights were smaller on weak than on vigorous rose stocks. The vigour of weak rose stocks might account for lower auxin supply to the roots and, owing to a feed-back mechanism, lower cytokinin synthesis. However, unlike apple, where shoots of trees of the same cultivar are actually shorter on 'weak' than on 'vigorous' stocks, in the rose shoot *number* rather than shoot *length* of the cultivar seems affected by rootstock vigour. If shoot length in the rose is affected, shoots even tend to be shorter on vigorous than on weak stocks (DE DOOD & RADEMAKER, 1991).

The inverse relationship between root bark percentage and the vigour of fruit rootstocks (BEAKBANE, 1961), which supports the auxin degrading theory, has not been investigated in the rose.

### 5.6.5. The vigour of rose combination plants. Proposed model

The vigour of combination plants is an essential part of commercial cut rose culture. With regard to further horticultural research as to influencing the yield level of glasshouse-grown rose plants, we tentatively present our concepts about plant vigour in a model (Fig.5.11.). It is realized that because the model is confined to the assumed action of endogenous auxin and cytokinins only, it necessarily represents a very simplified situation. Nutrition, water supply, temperature and light, which are supposed to be optimally employed in modern glasshouses, are not considered.

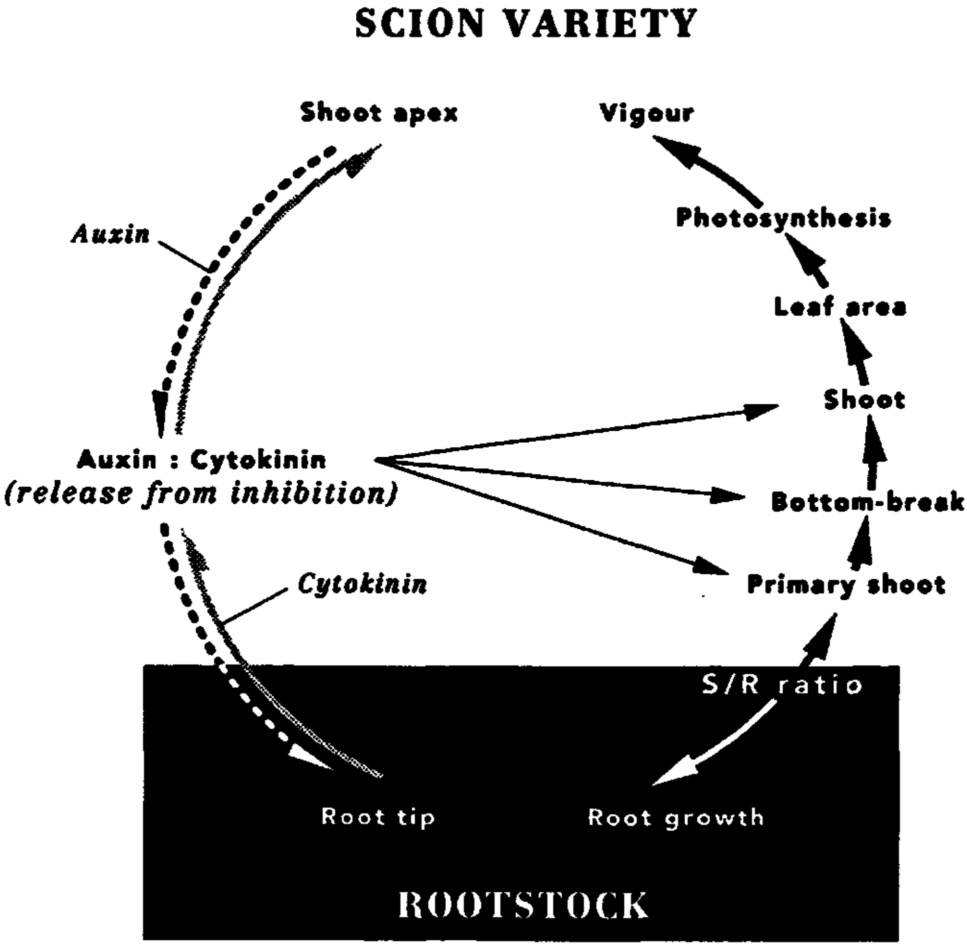

*Fig.5.11. A model of the vigour control of cut rose combination plants.*

In Fig.5.11., the upper part represents the scion variety, the lower part the rootstock. Additive vigour of scion variety and rootstock is assumed (Chapter 4.) The left-hand side covers action of the endogenous hormones auxin and cytokinin, whereas the right-hand side represents the main parameters of growth as affected by this action. In the shoot apex and young leaves of the growing combination plant, auxin is synthesized according to genotypically determined levels of the scion. Basipetally migrating auxin guarantees (initial) quiescense of axillary buds on the shoot (= correlative inhibition). When auxin reaches the rootstock, it is acropetally transported to the root tips where it stimulates new root growth. The quantity of auxin reaching the root tips may vary according to the degree in which it is degraded in the root bark. Relatively high auxin levels stimulate root growth more than do low ones. Cytokinins, which are synthesized in the root tips, are basipetally transported by the sap stream in the root xylem and, subsequently, acropetally in the scion variety. Both sensitivity to auxin and cytokinin synthesis, are genotypically determined characters of the stock used.

In the scion variety, cytokinins counteract auxin-controlled inhibition of axillary buds, resulting in the sprouting of these buds.

In the right-hand part of Fig.5.11., the consequences of endogenous hormone action are considered as to bud-break and subsequent growth. The sprouting of quiescent buds first concerns the axillary bud of the scion, of which the sprouting results in the primary shoot (see also Section 2.4.). Quiescence of the axillary buds of the primary shoot is initially controlled by correlative inhibition. However, when inhibition has released, its upper axillary buds may sprout and grow out into shootlets in which new systems of correlative inhibition are built up. Several weeks later, owing to toppling over or bending of the primary shoot, its lowest axillary buds sprout and grow out into the bottom-breaks. In subsequent stages of plant development, viz. after pinching the bottom-breaks and after successive shoot harvests, bud-break owing to cytokinin action concerns the time of sprouting as well as the number of axillary buds that sprout.

The time of sprouting and the number of buds that sprout, depend on the ratio of auxin : cytokinins, rather than on the absolute hormone levels. The actual ratio is determined by both the genotypes of the scion variety and the rootstock. The growth of combination plants is increasingly vigorous as the ratio auxins : cytokinins shifts towards cytokinins, or increasingly weak as the ratio shifts towards auxins. As combination plants grow more vigorously, the numbers of bottom-breaks and of lateral shoots increase. As a consequence of a larger number of shoots, the total leaf area is larger in vigorous than in weak combination plants, which effects an overall higher net-photosynthesis. This results in the increased growth of shoots and roots, ultimately measurable as shoot yield (vigour). In addition to the above factors, the length of shoots attained at flowering, and the daily shoot length increments are likely to increase variation in yield between (and within) cultivars. A more or less stable S/R ratio in regularly harvested combination plants might be established by constant (re)distribution of carbohydrates.

# Chapter 6

# Breeding improved rootstocks for cut roses

*'O King, the world exists only in your thought and feeling, and you experience joy or pain according to your own mind which is projected as the world. For him who harbours no poisonous thought and feeling there is no poison, while to the one who thinks poisonous thoughts, even nectar becomes poison'.*

*Yoga-Vasishtha. Transl. Hari Prasad Shastri. Shanti Sadan, London. p.137.*

# Chapter 6. Breeding improved rootstocks for cut roses

## 6.1. Introduction

**6.1.1. Breeding research in rose rootstocks. *Review***

**6.1.2. Principles of rootstock breeding in apple**

**6.1.3. Evaluation of breeding rose stocks**

## 6.2. New rootstocks for cut roses

**6.2.1. Requirements of modern stocks**

**6.2.2. Selection strategy of seedling stocks**

**6.2.3. Selection strategy of clonal stocks**

## 6.3. Current breeding research

## 6.1. Introduction

In the previous Chapters of our study, aspects of the vigour of scion varieties and rootstocks, and of scion-rootstock relationships with regard to the vigour of combination plants, have been investigated. In agreement with our objectives (Section 1.2.), some insight has been obtained into the possibilities of improving the uniformity of (seedling) Edelcaninas and the vigour of clonal rose stocks by breeding. In addition, our results have contributed to a more complete specification of requirements of rootstocks for cut roses adapted to current demands. Since aimed crosses between rootstocks were not carried out within the scope of this study, in this Chapter breeding is confined to considering various possibilities of selection. It should be realized, however, that rootstock breeding which takes many years of experimentation, should anticipate likely developments in the cut rose industry.

In the last decade, a number of important developments in rootstock nurseries, glasshouse culture and in horticultural research have run parallel. In the production fields of Edelcanina seedlings, application of pre-sowing chemical soil disinfection is being curbed (OLDENKAMP et al., 1992). This means that plant parasitic nematodes and *Agrobacterium tumefaciens* can be incompletely controlled only, so that there is an increased risk of planting infected young plants in clean glasshouse soil. Like in the nursery, in the glasshouse there is increasing criticism of the use of nematicides and pesticides (ANON., 1990b). Occurrence of soil-born diseases in the glasshouse may even have been a first argument for the use of artificial substrates in rose growing. In addition, the relatively low and variable yield of scion varieties on seedling Edelcaninas, has contributed to rapid expansion of the area covered with artificial substrates. Because young combination plants on seedling Edelcanina stocks are too large for most artificial substrates, growers have become increasingly interested in clonal stocks.

As a consequence of the above changes in growing practice, Dutch horticultural research takes the view that in the future, clonal rather than seedling stocks will be used in the glasshouse. Within that scope, new propagation methods for clonal stocks have been developed, and projects studying plant management on these stocks were initiated. Because the limit of yield of scion varieties obviously has been attained (DE VRIES & DUBOIS, 1987), further improvement of yield level is expected from the rootstock used, in combination with progressive plant management.

Major developments, expected before the turn of the century include: (i) new legislation that will make the production of Edelcanina seedlings increasingly difficult (ANON., 1990c), (ii) rose culture in soil in the glasshouse to be replaced by culture on artificial substrates (PEELEN, 1991). As a consequence, the important role of seedling Edelcanina stocks for cut roses is likely to be diminished, so that the demand for improved clonal stocks is urgent.

In the light of the above developments and expectations, the main part of this chapter is dedicated to rootstock breeding. It is my opinion that apart from their excellent manageability, only clonal rootstocks may guarantee the rare combination of desirable characters that is needed for future glasshouse culture. The use of (seedling) Edelcaninas will probably be restricted to outdoor roses, rather than to Dutch glasshouse culture. If (seedling) Edelcaninas are yet to be improved, no time should be lost.

In the present chapter, the current knowledge about breeding research in rose rootstocks is reviewed first. Apple rootstock breeding in England, as one of the finest examples of a consistently carried out programme, is then considered. Agreements and differences between breeding apple and rose stocks are evaluated. In the proposed strategies, 'breeding' is restricted to the selection for desirable individuals in existing plant material. For the Edelcaninas this may consist of seedling populations in which, owing to hybridization (Chapter 5), segregation of characters occurs. For clonal stocks, plant material is likely to consist of segregating populations resulting from directed cross-breeding, and/or of populations that have arisen from genetic modification. In the last section, aspects of current breeding research are considered.

### 6.1.1. Breeding research in rose rootstocks. *Review*

Initially, for the cut rose culture seedling and clonal stocks were used alternatively, but in course of time preference for either type has developed in different geographical regions. Seedling stocks of mainly the Edelcanina type

***Table 6.1. Species that have been involved as seedlings or clones in rootstock research. Classification of species and sections of the Subgenera Eurosa and PLatyrhodon according to REHDER (1960).***

| Section | Species |
|---|---|
| Subg.II | |
| *Eurosa:* | |
| *Gallicanae:* | *R.alba, R.francofurtana,* |
| *Caninae:* | *R.canina, R.coriifolia, R.corimbifera, R.dumetorum, R.micrantha, R.rubiginosa, R.rubrifolia, R.villosa,* |
| *Cinnamomeae:* | *R.acicularis, R.blanda, R.cinnamomea,R.laxa, R.lheritieana, R.nutkana, R.rugosa,* |
| *Synstylae:* | *R.helenae, R.maximowicziana, R.moschata, R.multiflora, R.sempervirens, R.setigera, R.watsonia* |
| *Chinenses:* | *R.borboniana, R.chinensis, R.noisettiana, R.odorata* |
| *Banksianae:* | *R.fortuneana* |
| *Laevigatae:* | *R.laevigata* |
| Subg.III | |
| *Platyrhodon:* | *R.roxburghii hirtula* |

nowadays form a majority in N.W.Europe and Japan, while clonal stocks like 'Manettii', *R.indica* 'Major' and sometimes *R.multiflora* are used in countries around the Mediterranean and in The United States of America.

Prior to about the year 1880, when exchange of characters by means of crossing was not yet understood by horticulturists, new rose cultivars originated from 'open pollination' or from sporting. At that time seedling rootstocks were still taken from the wild, and clonal stocks chosen among vigorous, readily rooting, non-recurrent flowering cultivars (KRÜSSMANN, 1986). But even when breeders had been engaged in large-scale programmes for new cut rose cultivars for several decades, rootstocks remained untouched. On the one hand, this is astonishing, because many more species seem qualified for breeding rootstocks than for breeding scion varieties. On the other hand, rootstock breeding is predictably laborious and time-consuming because of lack of selection criteria. Nonetheless, in course of time either seedlings or clonal plants of numerous rose species (Table 6.1.) have been appraised as a rootstock (BUCK, 1951; EDWARDS, 1955; KRÜSSMANN, 1962;

LOTHIAN, 1953; MANEY, 1938; McFADDEN, 1962). However, particularly for the glasshouse culture, very few of the species that initially seemed promising stood the hard test of practice. It is unclear why so many other species available in the *Eurosa*-sections of Table 6.1. have been excluded sofar. Neither species of the Eurosa-sections: *Pimpinellifoliae, Carolinae, Bracteatae*, nor those of the Subgenera *Hulthemia* or *Hesperhodes* (REHDER, 1960) have been used.

Two species have been more involved in research, and contributed more to current stocks than others, viz. *R.canina* L. and *R.multiflora* Thunb..

In naturally segregating populations of *R.canina*, the Dog Rose, which is endemic in Europe and Central Asia (KRüSSMANN, 1986), the important Edelcaninas have arisen from selection (Section 3.2.2.), rather than from directed crosses. Clever European nurserymen have attached their name to dozens of Edelcaninas at the beginning of the 20th century (SCHMID, 1956). Edelcaninas have traditionally been propagated by seeds. Despite incidental successes in rooting (CANT, 1929; DE DOOD, 1989a; SYTSEMA, 1991), these stocks generally are recalcitrant to vegetative propagation (Section 5.5.1.). Large-scale selection of clonal Edelcanina was not undertaken before 1986. With the aim to preserve the renown 'Inermis' for the glasshouse culture, in that year the Dutch growers organization STUR (Stichting Uitgangsmateriaal (Kas) Rozen) started selection for superiorly yielding clones with more than 550 different genotypes (DE DOOD & RADEMAKER, 1987; DE VRIES & DUBOIS, 1990). Sofar three clones have been introduced, viz. 'Sturun', 'Sturdu' and 'Sturtri' (ANON., 1990a), which should be propagated by cutting-grafting. Another clonal 'Inermis', 'Spektaculair', which was randomly selected from 8-12 mm seedlings in 1989, is to be propagated exclusively by root grafting.

In spite of important observations, research has not led to major advances in the development of seedling or clonal Caninas. Hence, investigations of cytologists in gamete formation of the pentaploid ($2n=5x=35$) *Caninae* (TäCKHOLM, 1920; 1922; HURST, 1931; FAGERLIND, 1940), did not give rise to breeding improved (seedling) Edelcaninas. Later studies, showing possibilities of hybridizing Edelcaninas with other rose species (ZEILINGA, 1969; KROON & ZEILINGA, 1974), have likewise failed to stimulate breeders. To our best knowledge, Edelcaninas with reduced seed dormancy, selected by KRICKL (1958), have not been introduced in practice. Inheritance of resistance to powdery mildew (*Sphaerotheca pannosa* var. *rosae* Lév.) in Edelcanina was studied by PERSIEL (1974), but unfortunately her encouraging results did not find application in breeding.

Probably owing to ease of propagation, good bud-take, high vigour, large genetic variability, and general cross-compatibility, only the diploid (2n=2x=14) species *R.multiflora* Thunb., the Blackberry Rose of Japan, has been actively used in breeding both seedling and clonal rootstocks. In about 1936, Iowa Agricultural Experiment Station started a project of breeding and testing stocks that were hardy, thornless and adapted to growing various forms of roses, in which *R.multiflora* was extensively used as a progenitor (MANEY, 1938). Although results of that experiment are unknown today, I.T.9 and I.T.18 clonal stocks which were introduced by Iowa State University around 1978, may have resulted from that programme. These stocks were raised after several generations, using *R.multiflora cathayensis* Rehder & Wilson, *R.helenae* Rehder & Wilson, *R.odorata* (Andrews) Sweet and common *R.multiflora* as breeding partners (BUCK, 1978). To my best knowledge both stocks are unknown in N.W.Europe. Another stock, introduced as Iowa 60-5 in 1965, resulted from the cross (*R.maximowiciana* Regel x 'Tausendschön') x 'Burr's Multiflora'.

In Denmark, STOUGAARD (1984) successfully analysed variation in seedling populations of *R.multiflora*. Selection resulted in mother bushes that produced offspring with improved root collar length, which is an important character in grafting. In France, Dr. Goujon at INRA-Fréjus (GOUJON & BARRADE, 1975) selected the clone 'Fredica' from the cross *R.multiflora x R.indica* 'Major' which, unfortunately, has not become the expected break-through in clonal stocks.

With the probable exception of Stougaard, aims in rootstock breeding were poorly defined, while variation of characters within populations was left unstudied. This means that with regard to vigour, neither criteria of selection of seedling or clonal stocks, nor breeding strategies have been developed. Nevertheless, nurserymen evidently have preferred vigorous, and as much as possible thornless genotypes for (clonal) rootstocks. This choice, of which the results have not been unsuccessful sofar, agrees with our concept of vigour (Chapter 5).

### 6.1.2. Principles of rootstock breeding in apple

Ever since seedlings began to give way to clonal stocks, first interest of horticulturists has lain in predictably influencing the vigour of combination trees. In the breeding history of clonal apple stocks in England, two eras may be distinguished: (i) selection in existing clones of different provenance, and (ii) cross-breeding and selection in seedling populations.

In the selection phase, hundreds of clonal apple stocks in use in Great Britain and on the Continent were collected by East Malling Research Station as early as the year 1912 (FERREE & CARLSON, 1987). From these, the sixteen famous 'Malling' stocks were selected on the basis of (i) difference in morphological characters, (ii) capacity to form rooted layers after stooling, (iii) graft-compatibility, (iv) tree vigour and (v) fruiting capacity, using 'Lane's Prince Albert' as a scion variety (HATTON, 1917; 1920). The use of 'Lane's Prince Albert' as the primary scion variety in all (successive) experiments, illustrates presumed absence of scion-rootstock interaction as to vigour (Section 4.2.2.). Reviewing more than 20 apple rootstock breeding programmes, CUMMINS & ALDWINCLE (1983) still supported a similar approach in which (i) the propagability of various genotypes was established, (ii) selection for vigour control was given highest priority. Validity of this procedure, however, is not general but restricted to 'adult' genotypes. It has been demonstrated in woody plants that when phase change from juvenile to adult occurs, the propagability of the same genotypes may gradually decrease (STOLLE, 1962; SPETHMANN, 1986; HACKETT, 1987). The above mentioned clones, that probably had been used as a stock for ages, presumably were 'adult' or 'mature' (PIERIK, 1990).

Procedures of selection in seedling populations, aiming at apple stocks that were of different vigour, precocious and resistant to woolly apple aphid (*Erisoma lanigerum* Hausmn.), were initiated in joint programmes of East Malling Research Station and John Innes Horticultural Institution. The result of these programmes was a series of rootstocks known as Malling-Merton (MM) clones. In spite of initial contradictions, a useful correlation between the vigour of own-rooted rootstock seedlings and that of the grafted combination trees was demonstrated (TYDEMAN, 1933; 1937a; HUTCHISON, 1967), indicating rootstock vigour in apple to be graft-transmittable. Furthermore, it was shown that selection for vigour within (rootstock) seedling populations can be carried out on the basis of field observations on total shoot length and root collar diameter in 2-6 year old plants.

Selection for vigour in combination with precocity, however, has consistently troubled rootstock breeders. In this context, the term 'precocity' is used as synonymous to 'earliness' and as such indicating genotypes with a short juvenile period. In nursery and fruit growing practice, 'precocity' is also used to indicate the earliness of blossoming of scion varieties. TYDEMAN (1937b) demonstrated an inverse relation between the vigour of 'Lane's Prince Albert' trees on different easy-propagating stocks and their blossom production. This was taken to indicate that precocity decreased as rootstock vigour increased. At face value such a relationship would indicate that precocity would only occur in weak stocks, thus opposing large-scale introduction of precocious stocks of high vigour. This apparently negative relationship between vigour and precocity based on the limited range of East Malling stocks, has led to the incorrect conclusion that "weak = precocious".

Thanks to the findings of breeders of apple scion varieties, the relationship between vigour and precocity was clarified only several decades later. Seedling populations raised to improve apple *cultivars* are usually grown in the nursery for two years and subsequently transplanted to the orchard. Once in the orchard, the trees that had been tallest in the nursery flowered early (short juvenile period), those that had been shortest flowered late (long juvenile period), thus indicating precocious genotypes to be on average the most vigorous (VISSER, 1964). In addition, in both own-rooted seedlings and in combination trees, precocious genotypes also had the best fruit bearing capacity (VISSER et al., 1976). Owing to early fruiting, initially tall trees subsequently grew slower than late flowering ones. Consequently, the late flowering genotypes were ultimately taller than the early ones. Although being very significant, the negative correlations between tree size and precocity leave room for the selection for vigour within the same category of precocity or, conversely, for precocity within the same vigour category. Similar relationships between precocity and vigour have been described in pear (VISSER, 1967; VISSER & DE VRIES, 1970) and indicate that they may occur generally in woody crops (HEYBROEK & VISSER, 1976).

For fruit rootstock breeding aimed at precocious stocks of different vigour, the relationships found in cultivar breeding indicate the possibility of selection for vigour in groups of genotypes of the same precocity, without laborious grafting with a cultivar and testing complete populations in the orchard. Determination of vigour at first flowering of the seedling trees has the additional advantage that propagability may be assessed when the trees have become adult. It is unclear, whether or not the relationship between vigour and precocity is widely appreciated and applied in modern rootstock breeding. The foregoing indicates that in apple, and probably generally in rootstock (seedling) populations of woody crops where adventitious rooting is not *the* major problem, the number of rootstock plants to be tested in combination with a scion variety may be effectively reduced prior to actual grafting.

### 6.1.3. Evaluation of breeding rose stocks

Considering the possibilities of improving rose stocks by breeding, two categories of stocks are distinguished in this study, viz. (seedling) Edelcanina and clonal stocks in general. Breeding in Edelcaninas starts from the principle that these stocks particularly lack external and internal uniformity. The external (phenotypic) uniformity which is primarily affected by environment, may be improved by cultural measures (Section 3.6.3.). Improvement of the genotypic uniformity may be attained by breeding.

Unlike in clonal Hybrid Tea stocks, in this study the induction of vigour by seedling Edelcaninas has not been investigated in relation to the original seedling plants (Section 5.5.3.). Because it is likely that the notoriously mediocre vigour of the Edelcaninas is an inherent property of *R.canina* L., improvement as to vigour is hardly expected without cross-breeding with other species.

In view of the above reasoning, in this Chapter the improvement of the internal (genotypic) uniformity of vigour of Edelcaninas is considered. Improvement aims at few genotypes with superior uniform seedling offspring to be used as mother bushes, that may be selected via numerous seedling populations. It cannot be excluded, however, that the same parameters of vigour that may be used in the selection of clonal stocks apply to seedling Edelcanina as well.

Unlike the Edelcaninas, the breeding of clonal stocks should focus on the improvement of scion vigour (yield). Vegetative propagation of selected genotypes guarantees preservation of the same combination of characters. The selection of clonal stocks is primarily directed towards the few genotypes of outstanding vigour that may occur among numerous individuals in (seedling) populations. Since the proposed selection strategy of clonal rose stocks with improved vigour appears to have much in common with that of rose scion varieties (Section 5.5.3.), some backgrounds of the latter procedure are considered first. In recurrent flowering Hybrid Tea rose seedling populations, relationships between plant characters, similar to those in apple (Section 6.1.2.) occurred. Hence, in a seedling population, in groups of individuals of the same age, the plants that flowered for the first time, were always longer than those that did not yet flower. However, like in apple, comparing the length of all individuals measured at flowering, plants were generally shorter as their juvenile period had been shorter (DE VRIES, 1976a). Very effective to the selection of vigorous (high yielding) cut rose cultivars, is a negative correlation between the *juvenile period* (days from seed germination to first flower) and *shoot yield* (vigour), occurring between the seedlings of a population (DE VRIES, 1976b; Section 5.5.3.). The level of significance of this correlation does not rule out the selection of infrequently occurring genotypes that combine short juvenile period ('earliness' or 'precocity') and long shoots, which are reflected in the clonal stage in high yield and long lateral branches (DUBOIS & DE VRIES, 1987). In agreement with the findings of Chapter 4, genotypes with a short juvenile period evidently have a better 'branching capacity' than those with a long juvenile period, indicating precocity likely to be associated with correlative inhibition.

Comparing the selection criteria of clonal apple rootstocks (Section 6.1.2.) with those proposed for the rose, both contrasts and agreements occur. As discussed in Chapter 2, in cut rose culture a range of stocks of different vigour is less required than in apple; for most rose cultivars high rootstock vigour even seems a prerequisite. Like in apple, selection for vigour in rose stocks can be carried out in individual, ungrafted rootstock plants of a population. The basis of selection is that (i) vigorous genotypes are recognized as plants with many (long) shoots and (ii) vigour is graft-transmittable to the scion variety (Chapter 5). Precocity of rootstocks, which in apple is important for early fruiting, seems to have two aspects in the rose. On the one hand induction of precocity is not an issue because flower bud initiation is determined by the scion variety (Section 2.3.). On the other hand, selection for that character cannot be omitted in rootstocks, since selection for the most vigorous part of the population inevitably contains the most precocious genotypes as well. Propagability of clonal stocks is of equal importance in the rose and in apple. As rose cuttings generally form adventitious roots readily, selection for propagability may be carried out after selection for vigour. Ironically, the renown seedling Edelcaninas are recalcitrant to adventitious rooting, indicating that in selection for e.g. clonal 'Inermis', propagability should have priority over vigour, a sequence that unfortunately has not been recognized in the STUR-programme (DE VRIES & DUBOIS, 1990; DE DOOD & RADEMAKER, 1991; Section 6.1.1.).

It is noteworthy that in initially juvenile genotypes of woody plants a decreased readiness to form adventitious roots may occur in course of time (HACKETT, 1987; PIERIK, 1990). Because after re-invigoration by in vitro culture, the rootability of several mature rose rootstock clones increased (DE VRIES & DUBOIS, 1992), a general decrease in the ability to form adventitious roots when plants mature may be expected. Decrease of rootability, however, is likely to occur sooner in populations from originally recalcitrant progenitors than from readily rooting ones.

## 6.2. New rootstocks for cut roses

### 6.2.1. Requirements of modern stocks

In focussing breeding in Edelcaninas on uniformity and of clonal stocks on vigour, it should be kept in mind that in addition to these major characters, modern stocks for the glasshouse should meet a range of additional requirements. Notwithstanding the importance of the quality of rootstocks for the commerce, criteria have been formulated arbitrarily only. To fill up that void, a number of requirements have been specified that are partly based on nurserymen's customs, partly on the results of present study. Distinction is made between (1) general requirements of stocks for cut roses, and those specific for (2) Edelcanina seedling rootstocks or (3) clonal rootstocks, as well as for (4) stocks in combination with a scion variety.

*1. General*

- uniformity, both phenotypic and genotypic
- long root collar
- fibrous root system
- few thorns
- broad graft-compatibility
- freedom from virus
- resistance to specific diseases

*2. Edelcanina seedling stocks*

- high percentage of 8-12 mm root collar diameter
- minimum root collar length of 20 mm

*3. Clonal stocks*

- long, non-flowering shoots
- many quiescent axillary buds
- shoots consisting of many internodes of the same diameter
- internodes preferably longer than 50 mm
- readily adventitious rooting in cuttage or cutting-grafting
- adaptation to various culture media

*4. In combination plants*

- non-suckering

*The ability to induce:*

- uniform plants
- high and early branching capacity
- high shoot yield
- long shoots (quality)
- high shoot/root ratio
- resistance to continuous harvesting
- winter-activity
- not paling or blueing the flower color
- insensitivity to blind shoot formation
- insensitivity to flower malformation
- longevity

Once culture in artificial substrates was introduced, characters which strongly held for outdoor cultivated (seedling) Edelcaninas, like nematode resistance, winterhardiness, anchorage in soil or readily parting of the rind for budding, have for the greater part lost significance, since cutting-grafting can be carried out year-round with glasshouse-grown cultivars and stocks. However, nematodes may reproduce in rockwool (AMSING, 1990), while the occurrence of 'new' diseases like Black rot during propagation (YPEMA et al., 1987), or *Gnomonia* (VAN DER MEIJ & VERMEULEN, 1991) and *Phytophthora* (AMSING & KERSSIES, 1991) in that substrate indicate that the above requirements should be continuously revised.

### 6.2.2. Selection strategy of seedling stocks

As outlined by DUBOIS (1989), in the selection of seed-propagated Edelcaninas with improved uniformity, two operations which do not exclude each other, are proposed:

- *in the short-term* (3-5 years), a moderately severe selection that may contribute to stabilization of existing genotypic variation,
- *in the long-term* (10-15 years), a severe selection that may improve external and internal uniformity, as well as yield.

In both options, after selection for uniformity, the vigour of selected rootstock plants should be tested in combination with a scion variety.

In the *short-term selection*, variation may be curbed by establishing new seed gardens with mono-clonal mother bushes. This policy has already been successfully pursued on a small scale by progressive Dutch nurserymen, planting seed gardens in France. Although the basis on which the mother bushes were selected is unclear, indispensable properties like trueness-to-type, good seed set after self-pollination, high seed germination and, most important: uniform offspring, must have been taken into account. In view of auspicious results obtained sofar, this rather simple selection may have been adequate to meet current demands.

The *long-term* selection provides for large-scale selection of superiorly performing mother bushes, in combination with uniform and vigorous progeny. Relations between the habit of mother bushes and the performance of their progeny was emphasized by LEEMANS (1967). Likewise aiming at mono-clonal mother gardens, high seed set of mother bushes after self-pollination is a prerequisite. The success of such an operation depends on having the disposal of a large genepool which, in e.g. the Dutch province of Groningen, is amply available.

Five consecutive steps of selection are broadly outlined. In the *first* step 'good looking' mother bushes are selected on the basis of fruit and seed set after controlled self-pollination. In the *second* step, viability and germination percentage of seeds of these bushes is tested over a range of years. In the *third* step uniformity and individual vigour of the progeny of the remaining mother bushes is tested by sowing, followed by thinning to attain equal plant distance, or by planting at fixed distance after pre-germination in the glasshouse, to circumvent main effects of plant density (Section 3.4.2.). The most important, laborious, costly, but indispensable *fourth* step of selection consists of testing the vigour (shoot yield) of the most uniform seedling progenies in combination with a standard scion cultivar in the glasshouse. The *fifth* and last step in this procedure is the establishment of new mono-clonal seed gardens with few superior mother bushes, either own-rooted or grafted on a identifiable rootstock.

Because the above selection procedure may take at least 10-15 years, its results are expected to be of significance to outdoor roses, rather than to cut roses in the glasshouse.

### 6.2.3. Selection strategy of clonal stocks

According to our reasoning in Section 6.1.3., in the selection procedure of high yielding clonal rootstocks from recurrent flowering populations, a *first* step may consist of retaining the individuals that combine a short juvenile period, a large number of early emerging bottom-breaks, a high shoot yield (shoot weight) and, in addition, long shoots. In that way selection is carried out for both precocity and vigour. Obviously, desirable traits as enumerated in Section 6.2.1., should be taken into account.

However effective this selection may be in *recurrent* flowering populations, rootstock populations are likely to result from crosses with at least one *non-recurrent* flowering progenitor or from genetic modification of non-recurrent clones. Non-recurrent flowering being dominant over recurrent flowering (SEMENIUK, 1971a; 1971b; DE VRIES & DUBOIS, 1978), this means that the F1-population is non-recurrent flowering. Hence, the above concept about selection for vigour and precocity, must be 'translated' from recurrent into non-recurrent flowering genotypes.

Although the growth pattern of plants of both categories is basically the same (Section 3.6.1.), most non-recurrent seedlings do not flower until the second year, and then in spring only. This means that the number of harvested shoots is an impractical parameter of vigour. Fortunately, when left unpruned in the first year, non-recurrent, presumably juvenile genotypes vary for time of emergence and number of bottom-breaks as well as for the number of their lateral shoots. In addition, both bottom-breaks and their laterals largely differ in length (DE VRIES & DUBOIS, 1978). This indicates that after the first growth season, approximately like in apple (Section 6.1.2.), the individual vigour of non-recurrent genotypes may be assessed on the basis of (i) time of emergence of bottom-breaks, (ii) number of bottom-breaks, and (iii) number of lateral shoots per bottom-break. These data may be supplemented with total shoot length and plant weight as additional parameters of growth. Although selection is preferably carried out in the glasshouse, it is reassuring that the branching capacity of seedlings is independent of the temperature regime in which the plants are grown (DE VRIES et al., 1986), indicating that the most area consuming part of selection may be carried out in the field.

The *second* step in selection should consist of rigorously comparing the propagability of the retained vigorous and otherwise desirable genotypes with standard stocks. Regarding that procedure, it is notable that adventitious rooting of softwood cuttings of stocks agrees with success in cutting-grafting (Section 2.2.). Results of Section 5.5.1. show softwood cuttings of large-leaved 'Inermis' genotypes to root more readily than small-leaved ones, a relation that was also found in various dwarf rose genotypes (DUBOIS & DE VRIES, 1991). This might indicate the internode of large-leaved genotypes to form adventious roots more readily than internodes of small leaved ones. It appeared, however, that the root mass of softwood cuttings formed in a certain period after striking, is directly related to the leaf area of the cuttings, rather than to genotypic variation in the ability of shoot segments to form adventitious roots (DUBOIS & DE VRIES, 1985). This indicates that testing the rooting of softwood cuttings of prospective stocks is useful to discard shy rooters, but that rooting should be verified in cutting-grafting with a standard scion variety, in comparison with a standard stock.

Depending on the number of rootstock genotypes to be selected in combination with a scion variety, decision has to be made whether cutting-grafted combination plants first are tested (on a relatively small area in 3-4 weeks) for vigour of root growth and preliminary shoot development in e.g. nutrient solution (D.P.de Vries, unpublished results), or directly cultivated in the glasshouse.

In the *third* step, the actual yield in the glasshouse of a standard cultivar grafted on selected stock-genotypes is compared with a standard stock. Owing to significant correlation between the first and second year's yield (DE VRIES & DUBOIS, 1987), combination plants of all selected stocks may be grown for about one year, allowing a first selection for vigour. If there are many stock-genotypes to be tested, uprooting after about 12 months might be considered, in order to start a subsequent experiment with a reduced number of stocks, but of superior vigour. This trial should be continued for at least two years so that, in addition to vigour, other properties of combination plants (Section

6.2.1.) may be assessed. Since the time of sprouting of the scion in roses is an early parameter of (scion) vigour (Section 4.5.2.), it would be of interest to selection to investigate if, and to what extent, sprouting of the scion after grafting is affected by stocks of different vigour.

The *fourth* and last step of selection consists of establishing hedges of source plants of superior genotypes which, depending on degree of winter hardiness, may be planted in the open or in moderately heated glasshouses.

## 6.3. Current breeding research

Our study has contributed to an improved understanding of the mode of vigour control of combination plants by the rootstock. In turn, improved understanding of rootstock action has shown the way to improvement by breeding. Actual sexual hybridization, however, is not yet undertaken. In fact, rootstock research as a whole has only just started.

Considering the possibilities of sexual hybridization, it is not much to say that genotypic variation for vigour, precocity, propagability, thornlessness or disease resistance within the genus *Eurosa* (Section 6.1.1.) has been hardly exploited. Taking also into account cross-incompatibility not to be a major problem, this would indicate a bright future of improvement by sexual hybridization. However, the financial costs for the realization of large-scale programmes over a range of years are predictably high. In addition, inconsistent results with present new stocks hardly stimulate rootstock breeding by crossing on a commercial scale. Future progress, therefore, is expected from funded research carried out at horticultural institutions, rather than from efforts of private breeders.

In the present situation funded research follows two courses of action, (i) genetic modification of clonal stocks by introduction of bacterial genes via *Agrobacterium* (WEISING et al., 1988), and (ii) unravelling the physiological basis of scion-rootstock relationships. In genetic modification, the action of *rol* A, B and C genes (GELVIN, 1990), separately or in various combination, on the growth and morphogenesis of roots is being studied. In addition to their expected practical application in rose culture, transformants of well-known clonal stocks with increased sensitivity to and/or synthesis of endogenous auxin or cytokinin may further elucidate knowledge of the mode of rootstock action.

Determination and quantification of cytokinins in the xylem sap of clonal rootstocks, may elucidate the role of these hormones in the branching of scion varieties and, hence, in vigour control by stocks.

In view of increasing critisism of environmentalists on the use of plant protecting chemicals in floriculture in general, and on chrysanthemum and rose in particular (ANON., 1990b), new techniques of introducing genes that code for resistance to specific pests and/or diseases should be investigated, also with regard to rootstocks. In addition, recent possibilities of the fusion of somatic cells in woody crops (OCHATT et al., 1989), may enable to combine Rose species that are difficult to cross, as well as roses with other Rosaceous species.

# Chapter 7

# Practical consequences

> *“……. That's why the Papalagi (white men) trot through life like a flung stone. While going, almost all keep their eyes focussed on the ground before them, and they swing their arms far away from their bodies to make their way faster. When somebody stops them, they exclaim spitefully: "Why do you disturb me, I have no time. You better put your own time to good use". They behave as if a man who runs through life is more valuable than one who goes slowly.*
>
> *Tuiavii. The Papalagi.*

# Chapter 7. Practical consequences

## 7.1. Stocks and plant management

## 7.2. Is there a future without stocks ?

## 7.1. Stocks and plant management

It should be realized that the introduction of stocks with improved vigour necessarily includes specific plant management. As indicated in Section 5.6.3., improved branching capacity, which is the essence of vigorous stocks, creates combination plants that grow broader than those on traditional stocks. This indicates that the vigour of stocks is only optimally expressed in the quantity and quality of the shoots harvested, when plants have sufficient room. Thus, planting cultivars on vigorous stocks has consequences for the plant-to-plant distance in the glasshouse, as well as for plant management. Without detailing in exact figures, it may be put forward that only at somewhat wider plant-to-plant distances the advantages of vigorous stocks are fully exploited and that, conversely, when planted at traditional distances, vigorous stocks hardly have an advantage over common ones. Because growers usually seem to be unfamiliar with this kind of information, they insufficiently recover the promised high yields of new stocks and tend to turn to well-known, cheaper, be it only mediocrily yielding stocks.

In addition, the general acceptance of vigorous stocks seems to be hampered by a signalled inverse relation between shoot quantity (yield) and shoot quality (stem length) of the same variety on different stocks (DE DOOD & RADEMAKER, 1991). Disposal of that phenomenon, however, as just "a disadvantage of potentially high yielding stocks" (KROMWIJK & VAN MOURIK, 1991), demonstrates lack of understanding rootstock action in growing practice. This might even lead to the incorrect conclusion that only the least vigorous stocks would yield highest flower quality. However, because at the flower auctions long shoots, particularly of large-flowered cultivars, yield higher prices than short ones, growers are inclined to go for 'quality' rather than for 'quantity' rootstocks.

The foregoing demonstrates the necessity for carrying out experiments in which the plant-to-plant distance of various scion-rootstock combinations is a major variable. In such experiments the number of laterals occurring after harvest should be controlled. But instead of being removed, shoots that are considered too weak, too late, or superfluous, should be bent in order to exploit their contribution to total photosynthesis.

The above concepts are presently being investigated in the Horticultural Department of the Agricultural University Wageningen. With the aim to control plant uniformity and optimal shoot density via the plant-to-plant distance and the number of bottom-breaks per plant, KOOL & VAN DE POL (1993) grew various cultivars under controlled light and temperature regimes. Their experiments already indicate excellent possibilities to combine high yield and stem quality, by fully exploiting branching capacity and leaf area in improved planting and plant management systems.

## 7.2. Is there a future without stocks ?

For the past seventy years, Dutch cut rose culture in soil has been dominated by Edelcanina seedling stocks. In current artificial substrates, however, seedlings give way to clonal stocks. Owing to research and improved nursery conditions, cutting-grafting of clonal stocks has become a generally accepted method. As a consequence, possibilities to produce self-rooted cultivars have improved simultaneously. Today there is even a tendency to grow cultivars on their own roots in artificial substrates, thus returning to the 'pre-stock era' of the 17th century. For that trend there are several grounds:

- *Firstly*, scion varieties of the Hybrid Tea type generally produce higher percentages of good plants in cuttage than in cutting-grafting. In addition, new, highly praised 'Inermis' clones like 'Sturdu' are recalcitrant rooters in cutting-grafting.
- *Secondly*, the method of cuttage is easier and cheaper than that of cutting-grafting. Treatment of only the scion variety requires considerably less time and effort than cleaning, grading, cutting and grafting of stocks.
- *Thirdly*, self-rooted plants are not only cheaper owing to better success in propagation and less labour, but royalties of present stocks considerably increase the price of combination plants that consist of a patented scion as well.

In this situation, the grower should continuously weigh the pros and cons of promising new, vigorous, be it expensive combination plants on the one hand, and of cheaper self-rooted plants of which the vigour has been insufficiently tested, on the other. Matters are further complicated by progressive (Dutch) breeders who, foreseeing a future in soilless rose culture, have successfully developed new methods for culture and selection, completely based on self-rooted plants. Irrespective of the price of the plants, however, it should be asked whether this trend is conducive to the cut rose industry or to the plant producers. Although there is no single answer to that question, our view is that the shoot yield (vigour) of self-rooted cultivars should at least equal and preferably exceed that of the same cultivars on a rootstock. This means that cultivars suitable for self-rooted culture should have both scion and rootstock properties. Making use of our results presented in Section 5.5.3., there are good chances that high yielding scion genotypes have vigorous roots as well. This means that before self-rooting can be recommended, the vigour of cultivars should be thoroughly determined. In the breeding procedure for scion varieties (Section 4.6.1.), however, selection for (seedling) vigour is usually omitted. Consequently, (i) the cultivars available for the cut rose culture range from weak to vigorous, and (ii) if information about their vigour is available, it is the result of growing them on 'Inermis'. A well-founded judgement of the vigour of scion varieties, that might be obtained afterwards by systematically comparing self-rooted and grafted plants, is neither pursued. Because most newly-introduced cultivars are short-lived only (OPREL, 1988), the chances that such comparisons will ever be made are negligible. Hence, the recommendation and culture of self-rooted plants is mainly based on trial and error. This conclusion agrees with the results of numerous experiments, showing self-rooted cultivars to yield generally inferior and at best equal to combination plants (DUBOIS et al., 1990a). An important objection as to the use of self-rooted cultivars, therefore, is based on uncertainty about plant vigour.

Besides the requirement of high vigour, the success of growing self-rooted cultivars may be determined by the root architecture, and possibly the performance of the root system. It is a well-established fact that seedling roots and adventitious roots of the same genotype do not follow the same growth pattern. Whereas seedling roots usually grow positively geotropic, adventitious roots tend to grow plagiotropic. In addition, even among scion varieties that are vigorous on a stock, cuttings differ in the formation of adventitious roots, viz. as to root number, root length and root weight attained in a certain lapse of time (DUBOIS & DE VRIES, 1992). These differences, which have only been investigated in softwood cuttings, may have significance in the subsequent development of the plants, and therefore in yield. Apart from these differences, several self-rooted cultivars are known to show chlorosis, decreasing shoot quality, and increased percentage of blind shoots in winter. This indicates that adventitious roots of these cultivars may be less adapted to stress conditions than those of qualified stocks. Another objection to the use of self-rooted cultivars, therefore, is based on uncertainty about performance of the (adventitious) root system.

The foregoing indicates that, however well-balanced the co-operation of root and shoot in one undivided genotype may seem, growing self-rooted scion varieties may have serious drawbacks. These arguments seemingly oppose the use of clonal rootstocks, which grow on adventitious roots as well. It is noteworthy, however, that clonal stocks which are intendedly selected for vigour and adventitious root formation, rarely show similar drawbacks as self-rooted cultivars. This difference may be ascribed to the fact that, unlike cultivars, most clonal stocks have been tested for performance over a range of years, under a range of environmental conditions, with a range of cultivars.

Although breeding scion varieties with efficient root systems is not impossible, it should be kept in mind that current cultivar breeding has increasingly become a play of large quantities. Today, only about 1 out of 1.000.000 seedlings raised may be a commercial success when grown on a rootstock (DUBOIS & DE VRIES, 1987). Even if self-rooted cultivars are aimed at, primary selection in the recurrent flowering seedling populations is necessarily aimed at properties of scion varieties. In spite of the fact that 'vigour' is displayed in both the shoot and the roots of genotypes, our considerations about self-rooted plants show that next to vigour, other properties play a role as well. This indicates that the number of seedlings that combine cut rose and rootstock properties, must be a manyfold of one million and as such be rare. In addition, it is likely that 'good' stocks contain genes for vigour that are not available in the gene pool from which scion genotypes are chosen. Incorporating 'rootstock' genes in the 'scion' pool, may not favour the scion varieties.

Summarizing the foregoing, it is my opinion that for the time being, breeding vigorous cultivars and vigorous rootstocks in separate programmes is more conducive to cut rose culture than seeking for a compromise in one genotype.

In spite of the above arguments in favour of the use of rootstocks, current confusing opinions among cut rose propagators, growers and horticultural advisory services about the merits of different (clonal) stocks, may predict future expansion of self-rooted cultivars in the Dutch cut rose industry. In order to fully exploit the possibilities of self-rooted cultivars, the custom of planting young plants in the glasshouse in beds may be reconsidered. An alternative to that system is offered by growing self-rooted cultivars raised from single-node cuttings, at densities of 60-100 plants per m$^2$ on transportable benches (FOUGHT & ANDERSON, 1990). This method, that was developed in The Netherlands by DE VRIES et al. (1977; 1978) was named 'strivetten'. Considered in the light of the present study, an important advantage of this method is that the number of axillary buds that break after harvest does not play a role at all, while retarded bud-break may be met in the nursery rather than in the glasshouse. Given suitable cultivars, this method seems to allow a high number of shoots of medium length per unit area, to be harvested in consecutive short cultivation cycles.

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# Samenvatting

## De groeikracht van kasrozen

*Ent-onderstam relaties; fenotypische en genotypische variatie.*

Snijrozen voor de kas zijn gewoonlijk combinatieplanten die bestaan uit een entras en een onderstam van verschillend genotype. In deze studie is een aantal milieu- en genotypische factoren onderzocht die de groeikracht van individuele onderstammen en entrassen, alsmede van combinatieplanten in de kas beïnvloeden.

In een één seizoen oud veldgewas van Edelcanina onderstamplanten, kwam significante variatie voor ten aanzien van alle waargenomen planteigenschappen. Onderstamkwekers maskeren deze variatie gedeeltelijk door onderstamplanten na het oprooien te sorteren in standaardklassen van wortelhalsdiameter. Niettegenstaande bossen *R.canina* 'Inermis' van verschillende herkomst waren gesorteerd in dezelfde diameterklasse (8-12 mm), kwam er zowel tussen als binnen deze bossen significante variatie vóór ten aanzien van de vertakking van het wortelstelsel, het aantal takken, het aantal grondscheuten en de wortelhalsdiameter.

Het effect van de plantdichtheid, als mogelijke bron van variatie, werd bestudeerd door 'Inermis' zaailingonderstammen te telen bij negen plantdichtheden tussen 30 en 190 planten per m$^2$. Naarmate de plantdichtheid toenam, werd de wortelhalsdiameter van deze één seizoen oude onderstammen kleiner, verschoof de verdeling van de planten over diameterklassen van een meerderheid dikke (>10 mm) naar een meerderheid dunne (≤6 mm), nam de variatie van de wortelhalsdiameter toe, en nam tot 170 planten per m$^2$ de biomassa toe. De plantdichtheid had een significant effect op de expressie van planteigenschappen. Wanneer de plantdichtheid toenam, hadden planten minder takken, waren deze langer en lichter in gewicht, werden de wortels lichter en vertakten minder, en nam de scheut/wortel (vers) gewicht ratio af; het percentage planten met een kromme wortelhals werd niet beïnvloed.

Fenotypische variatie van 'Inermis' wordt voornamelijk toegeschreven aan verschillen in leeftijd van de planten en aan plant-tot-plant afstand in het zaailingveld.

De wortelhalsdiameter van de onderstam bij enting had een significant effect op de groei van 'Sonia' combinatieplanten in de kas. Naarmate de wortelhalsdiameter van de Edelcanina's 'Inermis', 'Brögs Stachellose' en 'Pollmers' toenam van 3 tot circa 15 mm, was de primaire scheut van 'Sonia' langer, verschenen grondscheuten vroeger, en nam de takproductie, uitgedrukt hetzij als aantal, gewicht of lengte van de tak, toe. Na 12 maanden was het absolute versgewicht van aanvankelijk dikke onderstammen weliswaar het grootste, maar de gewichtstoename van dunne onderstammen was veel groter (ca. 20 x) dan die van dikke (2-5 x). De scheut/wortel (vers) gewicht ratio van 12 maanden oude planten werd niet beïnvloed door de aanvankelijke wortelhalsdiameter, maar 'Brögs Stachellose' induceerde hogere ratio's dan 'Inermis' of 'Pollmers'.

Ent-onderstamrelaties werden onderzocht door de groei en ontwikkeling van Theehybride rozenzaailingen op eigen wortel in het eerste jaar, te vergelijken met die van hun klonen geënt op 'Inermis' in het volgende jaar. Rekening houdende met verschillen in niveau van de groei en ontwikkeling, kwam de expressie van eigenschappen van zaailingen overeen met die van hun klonen. De aantallen grondscheuten en geoogste takken van zaailingen en klonen werden niet beïnvloed door ent-onderstam interacties. Naarmate de groeikracht van snijroosgenotypen toenam, liep het slapende oog van griffels sneller uit na het enten, verschenen er meer grondscheuten in een vroeger stadium, was de takproductie in 12 maanden hoger en nam het wortelgewicht van de onderstam toe. De waarde die in de teeltpraktijk wordt toegekend aan een groot aantal grondscheuten als basis voor een hoge takproductie, werd bevestigd. Om het productieniveau van toekomstige snijrooscultivars te verbeteren, wordt veredelaars aangeraden vóór te selecteren op aantallen grondscheuten en takken van zaailingen op eigen wortel.

In klonen van zwakgroeiende Theehybride snijroos zaailingen bevorderde de onderstam 'Inermis' de groeikracht van combinatieplanten, maar naarmate de zaailing op eigen wortel groeikrachtiger was, nam de groeikracht van combinatieplanten minder sterk toe. In combinatieplanten van verschillende entrassen geënt op één type onderstam, werd de groeikracht meer bepaald door het entras dan door de onderstam. De grote waarde die door de praktijk aan 'Inermis' wordt toegekend, lijkt niet gerechtvaardigd.

Een belangrijke component van groeikracht van entrassen wordt gevormd door hun relatieve vertakkingsgraad. Omdat vertakkingsgraad berust op de mate van correlatieve remming, wordt verondersteld dat de verhouding van auxinen (geproduceerd in de scheut) en cytokininen (geproduceerd in de wortel), het bepalende mechanisme van knopuitloop is. De voorsprong van groeikrachtige op zwakke genotypen, is waarschijnlijk te danken aan een groter bladoppervlak per plant tengevolge van een snellere uitloop van meer knoppen na enten en na elke oogst.

Teneinde de mogelijke (ongewenste) bastaardering van Edelcanina onderstammen aan te tonen, werd eerst de genotypische variatie van 'Inermis' ten aanzien van planteigenschappen en adventieve wortelvorming van zomerstekken bestudeerd. Na zes maanden in de kas te zijn geteeld bleken aanvankelijk uniforme (8-12 mm) 'Inermis' genotypen te verschillen ten aanzien van internodiumlengte, aantal blaadjes per blad en de bladoppervlakte. Bij 23 dagen oude zomerstekken, trad tussen de verschillende genotypen significante variatie op in de tijd van axillaire knopuitloop, axillaire spruitlengte en gewicht van de adventieve wortels. Tussen 'Inermis' klonen waren aantallen blaadjes per blad, bladoppervlakte en tijd tot knopuitloop gecorreleerd. Vervolgens werd genotypische variatie bestudeerd in *R.canina* 'Inermis' en 'Brögs Stachellose', ten aanzien van de groei en ontwikkeling van 'Sonia' geënt op klonen van deze onderstammen. Ten gevolge van verschillende inductie van groeikracht, verschilden 'Sonia' combinatieplanten in de data van verschijnen van de 1e en 2e grondscheut, het aantal grondscheuten en de takproductie over 12 maanden. Zowel bij 'Inermis' als 'Brögs' kwamen significante correlaties voor tussen het wortelgewicht en de diameter van de entplaats na 12 maanden. Bij eenzelfde wortelgewicht had 'Brögs' de dikste entplaats. Genotypische variatie van Edelcanina's wordt toegeschreven aan bastaardering met andere Edelcanina's of rozensoorten.

Als laatste werd het effect onderzocht van op groeikracht vóór-geselecteerde Theehybride onderstammen, op de groei en ontwikkeling van 'Sonia' combinatieplanten. Daartoe werd een Theehybride zaailingpopulatie bestudeerd. In deze populatie was de takproductie van zaailingen na 8 maanden, negatief gecorreleerd met het aantal dagen van zaadkieming tot anthese. De takproductie over 12 maanden, van 'Sonia' geënt op klonen van laag- en hoogproducerende Theehybride zaailingen, was positief gecorreleerd met zowel de takproductie van de oorspronkelijke zaailing, als met het wortelgewicht van de combinatieplanten.

In alle proeven was de takproductie van 'Sonia' positief gecorreleerd met het aantal grondscheuten per plant per onderstam. In het algemeen gold dat, indien een onderstamkloon de 1e grondscheut vroeger induceerde, de 2e grondscheut navenant vroeger verscheen; 'vroege' klonen induceerden meer grondscheuten en een hogere takproductie dan 'late' klonen. De diameter van 'Sonia' grondscheuten bij toppen, en het aantal per onderstamkloon geproduceerde takken, waren niet-significant gecorreleerd. De groeikracht van rozengenotypen bleek een inherente eigenschap te zijn, die zowel in de bovengrondse als de ondergrondse plantedelen tot expressie kwam. In combinatieplanten wordt de groeikracht van het onderstam-genotype overgedragen aan het entras.

Een belangrijk effect van sterke onderstammen is de inductie van een grotere vertakkingsgraad bij het entras, die zichtbaar is als snellere uitloop van meer axillaire knoppen in elk stadium van plantontwikkeling. Tengevolge van de inductie van een grotere vertakkingsgraad, hebben cultivars op sterke onderstammen reeds in een vroeg stadium van plantontwikkeling, een groter fotosynthetiserend bladoppervlak dan op zwakke onderstammen, en daardoor een voorsprong in groei. Belangrijke verschillen in de inductie van groeikracht door onderstammen worden toegeschreven aan endogene hormoonwerking, waarin onderstammen worden verondersteld te verschillen in cytokininesynthese. Een model voor de groeikracht van combinatieplanten, gebaseerd op additieve groeikracht van entras en cultivar, alsmede op de waarschijnlijke endogene hormoonwerking, wordt voorgesteld.

Edelcanina's induceren in het algemeen een matige groeikracht en vertonen genotypische variatie voor productie; bovendien zijn hun wortelstelsels te groot voor de meeste kunstmatige substraten. Edelcanina's zijn in 't algemeen niet geschikt als klonale onderstam omdat ze zeer recalcitrant blijken te zijn in vegetatieve vermeerdering. Mede doordat Edelcanina planten alleen na chemische grondontsmetting van de akker goed kunnen worden geteeld, lijkt de belangrijke rol van deze onderstammen voor de kasroosteelt voorbij te zijn. Wanneer niettegenstaande de nadelen, Edelcanina's toch door veredeling moeten worden verbeterd, kan op redelijk korte termijn de bestaande genotypische variatie worden gestabiliseerd door de selectie van 'goed-ogende' zaadstruiken, en het aanleggen daarmede van monoklonale zaadtuinen. Op de lange termijn kan verbetering worden bewerkstelligd door van grote aantallen moederstruiken eerst de (generatieve) nakomelingen grondig te beoordelen. Met de beste moederplanten kunnen dan eveneens monoklonale zaadtuinen worden aangelegd.

In de moderne snijroosteelt op substraat moet de voorkeur worden gegeven aan klonale onderstammen boven zaailingen. Voor de selectie van klonale onderstammen komen populaties in aanmerking die het resultaat kunnen zijn van kruising of genetische modificatie. Wat betreft de parameter 'groeikracht', kan eerste selectie plaats vinden op basis van het aantal takken en/of scheutlengte per plant na één seizoen. Groeikrachtige onderstam-genotypen komen waarschijnlijk het meest veelvuldig vóór onder individuen met een korte jeugdperiode. Het is gewenst te selecteren op onderstamgenotypen die, bij dezelfde groeikracht van de combinatieplant, een hoge scheut/wortel ratio induceren.

Het omgaan met combinatieplanten op sterke onderstammen wordt besproken. Bij een afweging van de voor- en nadelen van het gebruik van snijrooscultivars op eigen wortel en die op een sterke onderstam, wordt de voorkeur gegeven aan de laatste.

# Nawoord

De roos is ongetwijfeld het leukste siergewas om in te werken. Wellicht dat om die reden rond de roos een aantal practische en wetenschappelijke rosomanen loopt. Hun bezetenheid werd misschien het beste vertolkt door de geestelijke vader van 'The Rose Maffia', mijn vriend Naftali Zieslin, toen hij uitriep: "to be a rose for just one minute, might make me understand....."!

Hoe intrigerend rozen ook zijn, ik had niet gedacht toen ik in 1971 aan veredelingsonderzoek begon, er ooit een proefschrift over te schrijven, zeker niet één over onderstammen. Nou ja, wel gemijmerd natuurlijk over de mogelijke voordelen vandien, maar promoveren kon wettelijk niet eens. Ook nog niet toen Tijs Visser daar omstreeks 1983 naar informeerde. Des te dankbaarder ben ik Peter van de Pol die mij op het juiste ogenblik in de juiste richting, die van Professor Dr.J.Tromp, duwde.

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Peter van de Pol, jouw enthousiasme heeft bijgedragen tot een opwaardering van het nationale en internationale rozenonderzoek. Direct, als initiator van dit onderzoek, maar ook indirect, door uitwisseling van ideeën, heeft dat zelfde enthousiasme veel aan dit proefschrift bijgedragen.

Lidwien Dubois, wel beschouwd promoveer jij ook. Van het begin af aan heb je in dit onderstammenonderzoek, waar we eigenlijk niet zoveel zin in hadden, als gelijkwaardige partner meegedacht en meegewerkt. Daardoor werd je mede-auteur van alle artikelen die de basis voor dit proefschrift hebben gevormd. Je hebt bij vrijwel alle bespreek-sessies van het proefschrift gezeten en, in de weinige vrije tijd die je had naast je rechtenstudie, ook bijgedragen aan de uiteindelijke indeling. Ik ben je geweldig dankbaar voor je niet aflatende inzet, en kan rustig zeggen dat het zonder jouw hulp nooit wat was geworden.

Een belangrijke stimulans gaat uit van de omgeving waarin je onderzoek doet. Die wordt zeker niet in de laatste plaats door de leiding van een instelling bepaald. De heren O.Banga, C.Dorsman en N.G.Hogenboom ben ik er dankbaar voor dat ze hebben begrepen dat alleen in volledige vrijheid van handelen het beste onderzoek wordt gedaan.

Nic Hogenboom, ik denk soms dat ik mensen ken, maar ik was even sprakeloos toen jij zo enthousiast reageerde op mijn voornemen een proefschrift te schrijven.

Tini Colijn, ik dank je voor de stimulerende klopjes op de rug 'onderweg'. Sectorchefs werden destijds niet aangesteld om te managen, maar om senioronderzoekers wat beter te kunnen bezoldigen.

Tijs Visser, je was mijn eerste Sectorchef, en je bent ook de beste gebleven. Je was niet alleen een onderzoeker met duizend-en-één ideeën, je was ook handig. Bovendien, de vrijheid die je zelf nodig had, gunde je ook aan je medewerkers. Ik heb verschrikkelijk veel van je geleerd en aan je te danken.

Hein van Holsteijn, de roos is de enige snijbloem met stekels; dat was wel even wennen. Ik dank je voor de 'relatieve rust' die je me gunde.

Om de teelt van onze veredelingsproducten op 'Aalsmeers Peil' te brengen hebben we jarenlang geworsteld met de zandgrond in de kassen van het IVT. Het is vooral aan het voortdurend meedenken van onze veel te vroeg overleden vriend Jos Vierboom te danken geweest dat dit gelukt is. Het latere tuin-team bestond uit Jan Matijsen en Bert van Haren, naderhand vervangen door Paulien van de Poel. Zij waren jarenlang verantwoordelijk voor de goede opkweek en de teelt van het plantmateriaal en voor een belangrijk deel van de oogstwaarnemingen. Onze boomkweker-in-hart-en-nieren Teus van de Woerd, ben ik niet alleen dankbaar voor zijn waakzaam oog tijdens de vermeerdering, maar ook om zijn aparte kijk op 'de gang van zaken'.

Het rozenonderstammen-team op het CPRO-DLO heeft, zoals alles wat beweegt, steeds een ander gezicht gekregen. Hans Dons, Arie van Dijk, Lot

Hänisch ten Cate, Theo van der Salm en Caroline van der Toorn vormen de noodzakelijke, moderne aanvulling op de klassieke veredeling.

Een proefschrift schrijven doe je dan misschien wel in je eentje, maar al schrijvende realiseer je je pas hoe afhankelijk je bent geweest van anderen die je persoonlijk of wellicht alleen uit de literatuur kent. Direct of indirect hebben Guus van den Berg, Josee de Dood, Co Groenwold, Steven Groot, Ep Heuvelink, Hans (wiskunde) Jansen, Martin Joustra, Eli Khayat, Geert-Jan de Klerk, Michael Kool, Bert Kroon, Daan Kuiper, Harry van de Laar, Hans Lambers, Christianne Marcelis, Yoram Mor, Meine van Noordwijk, Rob den Outer, Roy Pollock, Michael Raviv, Jo Roggemans, Bert Smit, Cees Spitters, Wietse Sytsema, Hendrik-Jan van Telgen, Bob Veen, Francel Verstappen, Cor Vonk Noordegraaf, Naftali Zieslin en Sierd Zijlstra hun bijdragen geleverd.

An exeptional contribution has been made by my friend Andy Roberts. He took the trouble to positively critisize the complete text, as well as to embellish my 'german-like' english.

Aan de practische basis van dit onderzoek stonden de mensen van ROSACO (C.S.de Vries en G.J.Nienhuis), Adri Akkerman, Joop Alkemade, Rob Bogaards, Wil de Bresser, Louis van Diepen, Joop Dreise, Cees Groenewegen, Rob Leemhuis, Ad van Marrewijk, Adri Mulder, Jan Rademaker en Henny Verschuren.

Weliswaar trek je grafieken tegenwoordig zó uit de laserprinter (dank je Sies Toxopeus), maar een groot gedeelte van de gepresenteerde is nog ambachtelijk getekend door de heren Beekhof, Karel Ham en Grades Post. De dames van de 'typekamer', Jannie Kramp en Gea Jonker hebben me al in een vroeg stadium bijgestaan door reeds verschenen teksten in WP51 over te zetten.

Jan-Paul, de genetica verloochent zich niet: je bent nu al bijna zo eigenwijs, en zeker zo eigenzinnig als ik ! En al is originaliteit onbetaalbaar, toch...... Je hebt van de lay-out van dit boekje iets buitengewoons weten te maken.

Pieter, jammer dat er weinig juridische kanten aan het geheel zitten; je weet echter nooit of het muisje nog een staartje heeft. Bedankt voor je opgewekt humeur in gezinsverband.

Goekje, het is al niet eenvoudig naast een rozengek te leven, maar ik realiseer me dat de laatste twee jaren erger waren dan ooit. De effecten werden meer tastbaar naarmate de vivo-rozen in de vaas werden vervangen door 'kompüter-versies'. Ik kan niet beloven dat het na dit werkje echt beter wordt, maar hele weekeinden werken lijkt me sterk overdreven. Ik dank je voor je voortdurende steun.

Tenslotte dit. Als iemand denkt me nog even goed te moeten irriteren, moet-ie vooral zeggen: "leuk om je carrière mee af te sluiten, zo'n proefschrift.....!"

# Curriculum vitae

Dirk Paulus de Vries werd op 1 februari 1930 te Amsterdam geboren. Hij bezocht het Nieuwe Lyceum te Hilversum en vervolgens de Kweekschool voor de Zeevaart te Amsterdam. In 1950 trad hij in dienst bij de N.V.Stoomvaart Maatschappij 'Nederland' te Amsterdam, en voer daar achtereenvolgens in de rangen Stuurmansleerling, 4e- en 3e Stuurman. In 1952 behaalde hij het diploma 3e Stuurman G.H.V.. Van 1954-1955 vervulde hij de dienstplicht bij de Koninklijke Marine, laatstelijk als Luitenant ter Zee der 3e klasse KMR.

Van 1957-1959 bezocht hij de Rijks Hogere School voor de Tropische Landbouw te Deventer. In 1959 trad hij in dienst bij het IVT te Wageningen. In 1969 werd hij ingeschreven in het Ing.-register.

Het veredelingsonderzoek op het IVT betrof tot 1966 steenfruit, tot 1972 zure kers en peer, en tot heden rozen.

Vanaf 1974 publiceerde hij, individueel of met andere auteurs, 48 wetenschappelijke en 35 voorlichtende publicaties over rozenveredeling.