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YIELD, QUALITY AND VASE LIFE OF CUT ROSES
IN YEAR-ROUND GREENHOUSE PRODUCTION

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ACADEMIC DISSERTATION

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ORIGINAL PUBLICATIONS

ABSTRACT

Year-round greenhouse production of cut roses expanded rapidly in Finland in the 1990s. The use of supplemental lights increased substantially, and in terms of cultivation technique, the traditional upright growing technique was accompanied by the new shoot bending technique. These changes generated new challenges for growers, increasing their need of information about year-round cultivation.

The objective of this study was to improve the yield, quality and vase life of greenhouse cut roses in year-round production, with an emphasis on winter-time cultivation. Different growing conditions, growing techniques, cultivars and plant characteristics were studied as determinants of yield, quality and vase life.

The effects of different light intensities and daily durations of supplemental lighting on yield and quality were examined. Supplemental light at $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (photosynthetic photon flux) was insufficient for winter cultivation with a rest period in mid-winter, and correspondingly, $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF was insufficient for uninterrupted winter cultivation as far as the quantity and quality of yield are concerned. Lighting at $220 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for 20 h d^{-1} gave a high yield in dense plantation through all seasons. The efficiency of the duration of supplemental light was dependent on PPF and cultivar.

The duration of the rest period and rate of temperature raise at forcing interacted on the yield and quality of young 'Mercedes' plants. Two of the studied combinations resulted in high yields: a 6-week rest period followed by a rapid temperature raise at forcing, and a 2-week rest period followed by a slow temperature raise. These results suggest that physiological changes may take place in plants between the second and the sixth week of the cold period which subsequently affect the response to forcing temperature.

Pruning, which is usually done in traditional upright growing method, was compared with the shoot bending technique at the beginning of forcing after the rest period. Pruning leaves the plants almost or completely leafless, while bending retains the photosynthesizing leaves in the plants. In comparison with pruning, shoot bending increased yield quantity and shoot length in 'Mercedes' and 'Frisco'.

Blind shoot bending was also compared with shoot cutting after harvest. Bending increased the yield of 'Mercedes' but not that of 'Frisco', which is a more vigorous cultivar than 'Mercedes'. Length of the flowering shoots was, however, increased by bending in both cultivars. In the traditional growing technique, leaves remaining on the mother canes after harvest seemed to support good flower production in strongly growing cultivars. Hence, harvesting height is of importance.

Combined effects of various bending and harvesting heights on the yield quantity and quality were also investigated. High bending and high harvesting height at the beginning of cultivation resulted in an increased number of flowering shoots. This combination gave a crown with leaves and a high number of good quality bottom breaks, which are necessary for good flower production. Leafy plants did not need many bent shoots simultaneously; 1-3 shoots were enough. High harvesting height decreased the percentage of long flowering shoots compared with low height. Dense plantation in shoot bending growing technique ensured high production.

The growing technique had a minor effect on vase life. Cultivation conditions had varied effects on vase life. The duration of supplemental light affected vase life differently, depending on the cultivar. Daily light duration and different number of night-time breaks in lighting affected the vase life of 'Frisco'. Increased risk for short vase life seemed to be associated with high plant level variation within treatments. Estimation of plant specific hazards might provide us with new insights for understanding the flowers' behaviour in vase.

In year-round production, the vase life of 'Mercedes' was enhanced in the uninterrupted production, as compared with the production with a short rest period. Young and grafted plants had a higher risk for short vase life than older plants and cuttings. This may partly be explained by long stems and large leaf area which increased the risk for short vase life in 'Mercedes', but not in 'Frisco'. 'Mercedes' flowers tended to get bent neck, while 'Frisco' flowers usually senesced.

Differences in the carbohydrate content in the petals of rose flowers were observed between the cultivars. The content was higher in winter with supplemental light than in summer with natural light. Petal carbohydrate contents could not explain seasonal differences in the vase life, indicating that the effects of supplemental light may differ from those of natural light.

Based on the present results, an intensified cultivation method for roses is suggested.

LIST OF ORIGINAL PUBLICATIONS

The thesis consists of the following papers which are referred to by Roman numerals in the text.

- I Särkkä, L. and Rita, H. 1997. Significance of plant type and age, shoot characteristic and yield on the vase life of cut roses grown in winter. *Acta Agriculturae Scandinavica, Sect. B, Soil and Plant Science* 47: 118-123.
- II Särkkä, L. E. 2002. Effects of rest period length and forcing temperature on yield, quality and vase life of cv. Mercedes roses. *Acta Agriculturae Scandinavica, Sect. B, Soil and Plant Science* 52: 36-42.
- III Särkkä, L. E., Rita, H. J. and Ripatti, S. O. 2001. Cut rose flower longevity and its variation between plants of cv. Frisco grown in different lighting periods. *Acta Horticulturae* 547: 261-268.
- IV Särkkä, L. E. and Rita, H. J. 1999. Yield and quality of cut roses produced by pruning or bending down shoots. *Gartenbauwissenschaft* 64: 173-176.
- V Särkkä, L. E. and Eriksson, C. 2003. Effects of bending and harvesting height combinations on cut rose yield in a dense plantation with high intensity lighting. *Scientia Horticulturae* 98: 433-447.

Author's contribution

- I paper: Särkkä was responsible for the major part of this study. Rita carried out the data analyses.
- II paper: All stages of the work was done by Särkkä.
- III paper: Särkkä was responsible for the major part of this study. Rita and Ripatti analysed the data and were responsible for interpreting the corresponding results.
- IV paper: Särkkä was responsible for the major part of this study. Rita offered guidance during statistical analysis of the data.
- V paper: Särkkä was responsible for the major part of this study. Eriksson carried out the data analyses.

1 BACKGROUND

Rose (*Rosa hybrida* L.) is the most important cut flower in greenhouse production in Finland. In 2003, the growing area totalled 32 hectares (Anon 2004). This is 75% of the total cut flower growing area (bulb flowers excluded). Half of the rose growing area was in continuous year-round production with supplemental lighting and the mean cultivation time of the same plant stand in the year-round production was 5-6 years (Finnish Glasshouse Growers Association, personal communication).

In Finland, natural light conditions in October-February are an invariably limiting factor for good rose production in greenhouse. The use of supplementary lighting increased substantially in the 1990s. Growers wanted to improve the efficiency of the production, to respond to the increased international competition by strengthening domestic production, to develop their customer connections into year-round business and to ensure workplaces for employees over all seasons. The need for knowledge and research increased simultaneously with increased production. Economically sustainable lighting strategies were not known. Therefore, the starting point for this study was to carry out research to meet the growers' demands.

Two different cultivation practices are in use in the year-round cultivation of cut roses in Finland. Either a short rest period with interruption in lighting is applied in mid-winter during the darkest natural light conditions, or the plants are grown uninterruptedly throughout the year, using supplemental lighting. At the beginning of this research in 1992, the conventional light intensities at gardens were 65-100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (photosynthetic photon flux) with a daily duration of 15 to 20 hours. Towards the end of the 1990s, the continuous year-round cultivation became more common, together with higher light intensities. Today, high energy prices have again made the utilization of rest period topical.

Cultivation technique also underwent evolution in the 1990s. Shoot bending growing technique was gradually replacing the traditional upright growing technique, also internationally. This new technique posed new challenges to both cultivation and research.

2 INTRODUCTION

2.1 Rose plant and flower production

The greenhouse rose plant is self-inductive, i.e., flower initiation begins autonomously in extending shoots (Halevy 1972a). Flowering is not regulated by photoperiod or temperature, and rose is usually classified as day neutral plant. Flowering is recurrent and will continue throughout the year if the growing conditions are suitable (Zieslin and Moe 1985).

The essential factors affecting rose production are cultivation conditions and plant architecture, including the number of bottom breaks and their laterals and the number of harvestable flowers developed on the lateral branches. If the flower aborts during development, the shoot becomes blind. All growing conditions and techniques fundamentally aim at good sprouting of basal and axillary buds and to an undisturbed flower development.

2.1.1 Bottom breaks (renewal shoots)

Bottom breaks are juvenile-like, vigorous shoots growing from the base of the rose plant. These shoots form the basic structure of the plant. The basal shoots emerge mainly during the first year after vegetative propagation; thereafter their formation is rare. The basal bud breaks when the growth of the primary shoot is slowed down, for example, by bending. These buds are already present as secondary buds in the scale axils of the axillary bud before it develops into the primary shoot (Marcelis-van Acker 1993). Generally, the first two of the basal shoots are actual bottom breaks. The following shoots usually develop at the base of bottom breaks that have already grown (Marcelis-van Acker 1993). The quality of bottom breaks is important, because the number and quality of outgrowing laterals is positively correlated with shoot diameter (Kool and Van de Pol 1993).

2.1.2 Axillary buds, flower development and blind shoots

Transition from vegetative to reproductive phase (floral transition) is regulated by a complex genetic network that monitors the developmental stage of the plant and by environmental conditions, such as light and temperature (Araki 2001). Vegetative identity alters when the plant switches over from juvenile to adult phase. In *Arabidopsis* as a model plant, the vegetative meristem changes to inflorescence meristem which gives rise to bracts and associated flowers. If the inflorescence meristem undergoes a transition to floral meristem, the organs of the flower are produced (Battey and Tooke 2002). All these processes affect each other. The fundamentals of flowering control are assumed to be similar in annuals and

perennials, but perennials have the variety of ways in which their flowering and vegetative growth are coordinated (Battey and Tookey 2002).

A new shoot of a rose plant starts to grow from an axillary bud in the axil of a leaf underneath a harvested flowering shoot. During shoot development, several leaf primordia and leaves develop before the initiation of the flower. Leaf initiation starts already during the bud stage, and some of these leaf primordia become scales (Cockshull and Horridge 1977).

Flower development initiates, depending on the cultivar, at a shoot length of 2-4 cm (Zieslin and Moe 1985). In 'Mercedes', Maas et al. (1995) found the initiation to take place at the shoot length of approximately 2 cm. The morphology of flower bud development is well known, and Maas et al. (1995) divided flower morphogenesis into nine stages. For example, petals start to develop at stage 4 (Maas et al. 1995). Blind shoots develop as a result of deformation and abortion of flower bud, and this can occur at various stages of flower development. Deformation of the flower bud was observed in 'Mercedes' at 20 °C when the shoot length was approximately 11-15 cm, corresponding to stage 7 in flower development, i.e., the stage just before the visible initiation of stamen and pistils (Maas et al. 1995). This deformation was followed by flower abortion. In 'Frisco', necrosis of the primordium was already seen from the appearance of the petal primordia (Pien et al. 2000). The shoot length was at that time 8-10 cm (Van Labeke et al. 2000).

De Vries et al. (1981) described flower bud abortion in early or late stages of flower formation. In both cases, the flower differentiation did not proceed beyond stamen formation. In an early stage, the upper leaf could also be lost due to necrosis, explaining the low number of leaves in blind shoots. If abortion occurred in a later stage, usually after some flower stalk elongation, no necrosis of the upper leaf was observed. In addition, Nell and Rasmussen (1979) found no flower formation at all in consequence of the cessation of growth prior to the start of flower differentiation. Blind shoots have usually less leaves and are shorter and thinner than flowering shoots.

2.2 Growing conditions affecting yield and quality of flowering shoots

2.2.1 Light

Environmental factors (e.g. irradiance, photoperiod, temperature, water availability) are important for the purpose of controlling the transition to flowering in plants. These factors also interact with each other (Bernier et al. 1993). Light intensity is the most important climatic factor affecting rose plant growth and flowering (Zieslin and Mor 1990). Jiao et al.

(1991) reported that irradiance, CO₂ concentration and temperature accounted for 70, 20 and 5%, respectively, of the variance in whole-plant net photosynthesis of ‘Samantha’ roses. High light intensity increases photosynthesis and directs partitioning of assimilates to young shoots (Mor and Halevy 1984). This increased transport of assimilates to young shoots stimulates the growth and flower development (Mor and Halevy 1980). The import of assimilates to developing flower bud may be regulated by the level of endogenous growth substances in the flower (Halevy 1987).

Light is an important element in bud sprouting of roses. The lack of light causes both axillary and basal bud inhibition (Zieslin and Mor 1981). The effect of light coincides with the degree of inhibition along the stem. The buds higher up on the stem are least inhibited and also least affected by darkness (Zieslin and Khayat 1982). A prolonged period of darkness can almost completely inhibit the basal buds from sprouting (Zieslin and Khayat 1982).

Consequently, lighting increases yield by promoting bud break and decreasing flower abortion. Adequate lighting increases the number of bottom breaks and accelerates the development of the flowering shoot, thus reducing the time between flushes (Moe and Kristoffersen 1969, Carpenter and Anderson 1972, Zieslin and Mor 1981, Bredmose 1993).

In summer, temperature inside the greenhouse tends to rise too high, despite of ventilation, and the roofs are traditionally shaded with white paint to decrease the temperature. Shading, however, reduces irradiation and thereby decreases yield. More flowers abort and blind shoots develop (Moe and Kristoffersen 1969, Zieslin and Halevy 1975). Rose roots may also be damaged as a consequence of shading (Zieslin and Mor 1990). The negative impact of shading will be even more significant in cloudy days. Modern greenhouses are equipped with screens for shading control. Another effective method for temperature control is fog cooling. High pressure fogging systems are also effective for the purposes of humidity control. In Finland, fog systems have been more frequently used in greenhouse vegetable than flower production.

The yield follows seasonal fluctuations in global radiation, being lowest 1-2 months after the lowest radiation period (Cockshull 1975). In Finland, the natural global radiation in winter is not sufficient for rose production. The use of artificial lights together with higher temperatures and elevated CO₂ concentrations have minimized extreme fluctuations in yield, quality and harvest break times between different seasons. Supplementary lighting has increased the number of flowering shoots in all seasons, even in summer (Khosh-Khui and George 1977, Mortensen et al. 1992a, b, Bredmose 1993). Mortensen (1995) has shown, by measuring the photosynthesis, that light can be a limiting growth factor even on clear summer

days in the Nordic countries. Moe (1972) reports that high light intensity and long days promote flower initiation. The duration of supplemental lighting in Finland is usually 18-20 hours per day.

In a number of experiments, supplemental lights have had varied effects on the length and fresh weight of shoots (De Vries et al. 1982, Moe 1972, Carpenter and Anderson 1972, Tsujita and Dutton 1983, Zieslin and Tsujita 1990). This variation is connected with differences between cultivars and variation in plant management techniques between the experiments. Generally, the high light intensities used in the experiments conducted in the Nordic countries during winter have increased the quality of flowers, measured as quality grades and shoot fresh weight (Mortensen et al. 1992a, b, Bredmose, 1993).

Apart from irradiance, the quality of light is another important factor affecting bud sprouting. In general, red light (R) weakens the apical dominance while far red light (FR) strengthens it (Cline 1991). R light also promotes the sink activity of the flower bud more than blue or FR light, thus improving the growth and flower development (Mor et al. 1980). FR end-of-day light, compared with R, markedly reduced flowering of 'Mercedes' (Maas and Bakx 1995). This response indicates the involvement of the photoreceptor phytochrome. Maas and Bakx (1995) also showed that decreased proportion of blue light in PPF (photosynthetic photon flux) increased the shoot length of 'Mercedes' roses. Shaded plants experience a low R:FR ratio, which increases the plants' sensitivity to gibberellins, thus enhancing internodal length and inhibiting axillary bud growth (Hutchings and De Kroon 1994). In high pressure sodium (HPS) lamps, which are widely used as supplementary lights for roses, the R:FR ratio is approximately 3.6, while in natural light it is approx. 1.3 (Bredmose 1993).

2.2.2 Temperature

In mid-winter, low-temperature rest periods at approximately 2-5 °C have been commonly applied in Finland, because the natural light level is too low for growth. After the rest period, the plants are pruned and forcing is started by raising the temperature. For unlit rose plants, a rapid rise in temperature in January, immediately after the rest period, increased shoot blindness due to low global radiation, whereas later in the season, flower abortion was reduced when similar temperature treatment applied (Moe 1971). After two months' rest period, sprouting of buds was better when the rest period temperature was 2 °C, compared with 8-12 °C (Jensen 1979). When plants after pruning were exposed to a low temperature (4 °C) for short periods of time (1-2 weeks), the outgrowth of the basal buds remaining on the

crown was stimulated, while a longer cold period (3-5 weeks) resulted in partial inhibition of bud growth (Khayat and Zieslin 1982). Recurrent flowering of cut roses is controlled by a single recessive gene (De Vries and Dubois 1978). This gene probably affects the state of dormancy of the lateral buds by eliminating their need for low temperature to release the dormancy (Zieslin and Moe 1985). A short cold period, however, stimulated the outgrowth of the buds, particularly in the basal part of the plant. Khayat and Zieslin (1982) suggest that the response of basal buds to cold treatments after pruning may indicate residual dormancy in these buds. They also suggest that low temperature may activate the cytokinins accumulated in the basal part of the plant.

Marcelis-van Acker (1995) suggests that in axillary buds remaining higher up on the stem after cutting, the temperature effect on growth inhibition takes place inside the bud itself. A low-temperature treatment of intact shoots did not stimulate bud break, indicating an apical dominance effect (Khayat and Zieslin 1982), see section 2.3.1.

Increased diurnal mean temperature speeds up bud break, decreases the time to harvest, and shortens the stem length (Moe and Kristoffersen 1969, Moe 1972, De Vries et al. 1982). The number of leaf primordia in an axillary bud before the bud break was unaffected of temperature, but the total number of leaves preceding the flower decreased in elevated air temperature (Marcelis-van Acker 1995). Relatively high night temperatures, in comparison with day temperatures, promote bud break (Zieslin and Halevy 1975). Van den Berg (1987) reports a faster bud break in higher night than day temperature. Vogelesang et al. (2000) did not find any effect of temperature rise for 4 h at sunset on bud break or flower quality. The temperature treatment had no effect on the carbohydrate levels in plants. However, a higher night than day temperature reduced blindness (Zieslin and Halevy 1975, Van den Berg 1987). This effect could be seen already when the high temperature period was given at sunset for 2-4 h (Van den Berg 1987).

Low temperature (12-15 °C) increases shoot blindness until stamen and pistil primordia have been formed in the developing flower bud (Moe 1971). Decreasing the temperature after the flower bud was visible generally increased leaf area, stem length, stem diameter and flower dry weight (Shin et al. 2001). Further development of a newly sprouting bud is dependent on its ability to mobilize the assimilates from the leaves of the previous growth cycle. Lowered night temperatures decrease both CO₂ assimilation and respiration rates. Carbohydrate content is also reduced in young shoots and, in contrast, accumulated in older leaves (Khayat and Zieslin 1986). Low night temperature reduced the import of assimilates to the flower more than the export from the leaves (Khayat and Zieslin 1989), promoting

translocation towards the basal parts of the plant (Khayat and Zieslin 1986). Khayat and Zieslin (1987) found that the lowered night temperatures reduced the activity of some enzymes important in sucrose metabolism; i.e. sucrose phosphate synthase, which plays a major role in the regulation of sucrose synthesis in source leaves, and sucrose synthase, which is suggested to be an indication of sink strength in young shoots.

On the other hand, the light intensity interacts with low night temperature. When light intensity was a non-limiting factor, in 'Frisco' roses, the quality of flower stems was enhanced, the rate of flower abortion was decreased, and the carbohydrate content in the most mature leaf of the developing shoot was increased by low night temperature (Pien et al. 2000). If, however, the diurnal mean temperature was the same, the effect of different day/night temperatures had a minor effect in comparison with high light intensity (Van Labeke et al. 2001).

A lowered soil temperature promotes shoot blindness. This response may be a result from changes in the metabolic activity of the roots (Zieslin and Moe 1985). In addition, a lowered root temperature decreased shoot fresh weight and stem length (Mortensen and Gislørød 1996). Dieleman et al. (1998b) report considerable changes in root morphology with different root temperatures. At low air temperature, soil heating increased the number of bottom breaks (Brown and Ormrod 1980).

2.2.3 Carbon dioxide enrichment

Carbon dioxide is one of the main substrates for photosynthesis. Because photosynthesis is dependent on light and temperature, these factors cannot be separated from carbon dioxide enrichment in greenhouse. Results of positive effects of the CO₂ enrichment on growth and quality of plants have been reported and reviewed by Mortensen (1987). Problems with the external supply of CO₂ are related to too high a concentration due to an uncontrolled supply, and to air pollutants NO_x, CO, SO₂ and ethylene deriving from the burning gases of kerosene and propane (Mortensen 1987). These compounds cause plant injuries and impair their growth. Therefore the use of pure CO₂ gas is safer.

With a high CO₂ concentration in air, leaves export more assimilates than in ambient CO₂. However, the export rate is more sensitive than photosynthesis to very high temperatures (40 °C) (Jiao and Grodzinski 1998). Leaves are also capable of adapting to high CO₂ concentration. When plants grown in high CO₂ level were moved to ambient CO₂, their photosynthesis fell under the photosynthesis of the plants grown in ambient CO₂ (Jiao and

Grodzinski 1998). Transfer of plants from ambient CO₂ level to high CO₂ increased photosynthesis.

In the Nordic countries, CO₂ is supplied mostly during winter time, simultaneously with artificial lighting and closing of vents. The recommended concentrations are 600-900 ppm (Mortensen 1987). CO₂ enrichment in rose production is not as usual as in vegetable production in commercial greenhouses in Finland. During summer months, the CO₂ enrichment is usually interrupted because ventilation is necessary to control the temperature inside the greenhouse from rising too high. In our own observations, the indoor CO₂ concentration may diminish under the normal outside level of 350 ppm. The CO₂ deficit decreases photosynthesis and thus growth.

During periods of CO₂ enrichment, the ventilation temperature can be raised by 2-4 degrees to lengthen the enrichment time (Mortensen 1987). Elevated CO₂ concentration diminishes both light and dark respiration (Mortensen 1995, Jiao and Grodzinski 1998) and decreases transpiration through the effect on stomatal conductance (Jarvis and Morison 1981). High CO₂ concentration elevates the level of light intensity at which photosynthesis becomes saturated. For leaves of 'Samantha', the light requirement for photosynthesis was saturated at about 500 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF when the CO₂ level was 350 and 900 ppm, respectively (Jiao and Grodzinski, 1998). The maximum PPF inside the greenhouse was measured at 800-900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in a bright summer day in Norway (Mortensen 1995).

2.2.4 Air humidity

Air humidity affects the stomatal conductance, which controls transpiration and photosynthesis. Plant growth is usually normal in water vapour pressure deficit of 1.0-0.2 kPa, corresponding to relative humidity (RH) of 55-90% at 20 °C (Grange and Hand 1987). High humidity encourages diseases. In low air humidity, transpiration increases and can even lead to water stress in leaves, inducing closure of stomata and subsequent reduced transpiration and photosynthesis (Jarvis and Morison 1981).

It is a well known fact that in cut rose cultivation high (90%) relative humidity stimulates bud break, while low RH (<60%) delays it. Raising the air humidity increased leaf size and shoot weight and length in one rose cultivar, but had a minor effect in another cultivar (Mortensen and Gislerød 1997, 2000). Air humidity has an impact on the vase life of cut roses (Mortensen and Fjeld 1998, Mortensen and Gislerød 1999, Torre and Fjeld 2001; see section 2.4.3).

2.2.5 Irrigation

Reduced water availability during flower initiation has detrimental effects on the quality and quantity of crops (Halevy 1972b, Turner 1993). In rose plants, the stage of flower development affects the response to water stress (Chimonidou-Pavlidou 1996, 1999). If water supply was inadequate shortly after pruning, i.e., in the bud developing stage of leaf primordial initiation, flowering was delayed but the quality of the flowering shoot was unaffected. When water stress appeared at the stage prior to petal initiation, the flower quality decreased, with less well-formed petals and lowered height of the flower bud. Prior to stamen initiation, the water stress caused most damage to rose growth, resulting in up to 70% reduction of rose production and reduced stem length and fresh weight of the shoot. A few days' interruption in irrigation after the stamen formation and after the carpel formation had no negative effect on the quality or quantity of the rose flower (Chimonidou-Pavlidou 1996, 1999).

2.3 Growing techniques in flower production

2.3.1 Shoot branching and bud dormancy

Plant architecture is modified by the primary shoot apical meristem and by shoot branching from additional meristems. These characteristics are genetically determined to form species-specific forms but also influenced by environmental factors (Shimizu-Sato and Mori 2001). In shoot branching, the formation of axillary meristems in the leaf axils and the growth of axillary buds are necessary. It has been suggested that gibberellin has a role in controlling the formation of axillary meristem (Shimizu-Sato and Mori 2001). The primary shoot inhibits the growth of axillary meristems in many plant species. This phenomenon is called apical dominance. Although the growth of axillary buds is inhibited, these dormant buds are still metabolically equally active as growing buds, at least in peas (Stafstrom 1988).

Apical dominance appears to be controlled by a balance between cytokinin and auxin levels rather than the absolute levels of either hormone (Kapchina-Toteva et al. 2002). Auxin has an inhibitory effect on axillary bud growth, whereas cytokinin promotes the outgrowth of axillary buds (Shimizu-Sato and Mori 2001). Besides these two hormones, other factors and/or signals seem also to have important roles in controlling the axillary bud growth (Shimizu-Sato and Mori 2001).

Apical dominance can be released by decapitating the primary shoot and in some plants after the primary apical meristem has differentiated into the determinate organ, such as a

flower. Removal of the terminal bud rapidly promotes cell division in axillary buds (Martin 1987). In roses, at the time when the terminal flower bud is visible, the uppermost 2-4 axillary buds break (Dieleman et al. 1998a). These developing shoots take over the apical dominance by their auxin production and inhibit the buds further below from breaking. Zieslin et al. (1976) have also found that sprouting of buds in roses is inhibited to a higher extent at lower than at higher bud positions along the stem. The potential of axillary bud outgrowth is related to its position on the main axis and may be determined by a balance among several hormones (Shimizu-Sato and Mori 2001).

Apically derived auxin can suppress axillary bud outgrowth by acting in the xylem-associated or medullary cells, but it does not enter the bud itself (Booker et al. 2003). It is still uncertain how the effect of auxin on inhibition of axillary bud growth is mediated (Booker et al. 2003). Auxin may have a role in the regulation of cytokinin synthesis. Cytokinin is suggested to be synthesized in the stem, at least at the node after decapitation (Shimizu-Sato and Mori 2001). This cytokinin may play a role in the regulation of branching (Booker et al. 2003). Auxin-mediated regulation of root-derived cytokinin may not have a prominent role in the promotion of axillary bud outgrowth in the shoot (Booker et al. 2003). Dieleman et al. (1998a) report that in roses the cytokinin concentration in bleeding sap increased both before axillary and basal bud break and decreased thereafter. Buds that form bottom breaks seem to receive their cytokinin from the roots (Dieleman et al. 1997).

Abscisic acid (ABA) is suggested to be involved in the dormancy of axillary buds (Shimizu-Sato and Mori 2001). ABA level of dormant axillary bud was higher than that in growing axillary bud after decapitation (Gocal et al. 1991). ABA either promotes or maintains the dormancy in axillary buds (Shimizu-Sato and Mori 2001). However, Booker et al. (2003) suggest that although ABA and ethylene may regulate bud activity, they apparently are not involved in auxin-mediated apical dominance. Higher concentrations of ABA have been found in the lower part of the rose stem than higher up (Zieslin et al. 1976). After pruning the ABA level of roses was decreased in the stem parts close to both sprouting and non-sprouting buds, but accumulated ABA was found in subtending leaves of non-sprouting buds (Zieslin et al. 1978b). Zieslin and Khayat (1983) suggest that a balance between growth promoters, mainly cytokinins, and inhibitors, including ABA, contributes to the regulation of outgrowth of basal buds in rose plants.

In roses after harvest, it is usually the most terminal axillary bud that sprouts and shows the most vigorous growth. If the lower buds sprout, the terminal shoot still dominates over them and, in adverse growing conditions (e.g. low light level and low temperature), may even

arrest the growth of the lower buds, which elicits flower abortion (Van den Berg 1987). In the lower shoots, a reduced gibberellin activity and an increased ethylene production was found (Zieslin and Halevy 1976). The degree of bud growth repression is under genetic control (Tamas 1995), which explains some of the variation in bud sprouting between rose cultivars. ‘Madelon’ roses expressed stronger apical growth and fewer branches than ‘Motrea’ (Kapchina-Toteva et al. 2000). Kapchina-Toteva et al. (2002) suggested, that ‘Madelon’ has a greater auxin:cytokinin ratio than ‘Motrea’.

2.3.2 Plant management and structure

Fast rotation of plants and year-round cultivation have increased the use of cuttings instead of grafted plants. A good root system and flower quality are important advantages of rootstocks. The nodal position of a scion grafted onto a rootstock determined the harvestable flower yield (De Vries and Dubois 1992). For some cultivars, cuttings have produced more flowers than grafted plants (Tillge et al. 1974). Single-stemmed crop production with high plant density, where only one flowering stem per cutting is produced, is a new potential growing method for transportable bench systems and automatic harvesting (Bredmose 2000). In this type of production, the nodal position of a cutting affects the onset of axillary bud growth, stem length and biomass build-up of the stem (Bredmose et al. 2001). In conventional rose production, plants are commonly propagated by cuttings taken from different nodal positions.

A rest period in low temperature followed by pruning has been the traditional form of rose plant management practice in Finland during winter months when the global radiation is low. The use of supplemental lighting has shortened the rest time to a few weeks, or even turned the cultivation into year-round production. A short rest period can also be used for timing of flowering and during periods of oversupply of flowers in market. Moreover, harvesting in flushes is possible after a rest period followed by pruning.

After pruning, depending on the plant age and pruning height, plants are either totally or nearly leafless. Under low light conditions in winter, this results in an inadequate supply of carbohydrates during initial shoot growth, and a large portion of sprouting buds develop into blind shoots as the developing flowers abort (Zieslin et al. 1975). Pruning under these conditions may also result in root dying (Fuchs 1986).

Harvesting in flushes generates a large number of shoots to sprout simultaneously, like in pruning, increasing the competition for assimilates within plant and, in the case of shortage of assimilates, increasing shoot blindness (Kool et al. 1997). In flush harvest, the plant loses, during a very short period of time, plenty of its photosynthesizing capacity due to the removal

of leaves on the flowering shoots, which sometimes also causes root dying (Fuchs 1986, Kool 1996). In continuous harvesting system, where shoots of different developing stages are always present, the total yield during the production time may decrease (Kool 1996).

High greenhouse maintenance costs demand maximally effective use of the growing area. High plant density increases leaf area, yield per unit area, and stem length, but on the other hand, it decreases the fresh weight of the harvestable stems (Mortensen and Gislerød 1994, Kool 1997, Bredmose 1998, Dambre et al. 2000). Shading reduces irradiance and R:FR light ratio in dense canopies and in the continuous harvesting system it suppresses lateral bud outgrowth and branching (Mor and Halevy 1984, Kool 1996).

Plant structure is important in cut flower production. The number of second order laterals formed after cultivation for eight months had greater influence than the amount of basal shoots on the number of flowering shoots during the two following years of cultivation (Kool 1997). Harvesting height also affects the yield (Rathmell 1969). The flowering shoots have traditionally been harvested above two five-leaflet leaves, but many other heights, usually at a lower position on the stem, are nowadays common. If harvesting height is down to the scales, the sprouting buds abort more easily than those higher up (Zieslin 1981). Shoots at higher nodal positions remain shorter. The number of five-leaflet leaves left on the stem during harvest has a positive effect on the number of sprouting laterals (Zieslin 1981, Kool and Van de Pol 1996). Stem diameter is important because thick stems have heavier buds (Marcelis-Van Acker 1994), which form thick and heavy lateral shoots (Kool and Van de Pol 1993, Kool 1997). Buds of thick shoots break more readily and the developing time for flowering is diminished (Kool 1997). Thick shoots also translocate assimilates towards new developing shoots effectively (Lieth and Pasian 1991).

A new cultivation method, the bending technique, became common practice in greenhouse rose production during the 1990s. In this technique, several new outgrowing shoots from a cutting are bent at the base of the shoot to make a strong plant before the start of harvesting; later on, mainly the blind shoots are bent. This arching technique was introduced in Japan in the late 1980s (Ohkawa and Suematsu 1999). In the bending growing technique, the benches are mounted well above soil level, which improves air circulation in the vegetation and is more ergonomic for workers.

Bending has traditionally been used by pomologists to reduce growth and to produce early flowering in fruit trees. Bending horizontally has been used to improve the branching of young rose cuttings (Moe 1974). In horizontal position the buds sprout only on the upper side of the stem, while downwards oriented buds are highly inhibited to sprout (Zieslin and Halevy

1978). Bud inhibition is suggested to be related to redistribution of hormones in the bent shoot in response to gravity (Mullins 1965). A bud close to the bend on the proximal side of the stem achieves greater length than other shoots on the stem (Zieslin and Halevy 1978). As a whole, the shoot bending growing method has produced longer flowering shoots than the traditional method (Van Labeke et al. 2000, Lieth and Kim 2001).

Several bending operations have lengthened the time between new plantation and the first harvest by weeks, even months. Kool and Lenssen (1997) claim that the primary shoot should not be bent too early. They recommend bending at the time when, after removal of the visible flower bud, the leaf area index (LAI) in the canopy is 3. Delayed bending has generally promoted the rate of development and increased the diameter and weight of basal shoots (Kool and Lenssen 1997). A disadvantage of the bending technique is the lower plant density, owing to the extra space required for numerous bending operations during the cultivation. Bending blind shoots into the canopy has also reduced the overall bud break (Kool 1996). In some cases, yields have been lower with bending than with conventional growing techniques (Lieth and Kim 2001).

In flush harvesting the bending system is advantageous, because there are photosynthesizing leaves in the plants at all times. Warner and Erwin (2002) measured 28% higher whole plant net photosynthetic rate in plants grown with shoot bending than in those grown with traditional upright growing technique. The bent shoots also provide good hiding places for beneficial predators and parasites between the flushes, which is an advantage in the biological pest control of cut roses.

The number of bent shoots has been subject to studies. Higher number of bent shoots demands more space, and the numerous shoots shade each other, resulting in yellowing and dropping of the leaves of the lowest shoots and finally causing the death of the shoots. Pien et al. (2001) optimized the LAI for bent shoots between 1 and 3.5 by measuring leaf photosynthesis. Light interception determined the photosynthesizing capacity of leaves, and in the lower layers of bent shoots the carbon balance was negative. In vertical plant canopy, the photosynthetic capacity is higher in the leaves at the top of the canopy, compared with the leaves at the bottom of the plant (Gonzalez-Real and Baille 2000). The age of a leaf does not necessarily determine the photosynthetic capacity (Lieth and Pasian 1990). Photosynthesis in mature leaves increased after blooming and pruning when new shoots started to grow (Mor and Halevy 1979).

2.4 Vase life of roses

2.4.1 Carbohydrates and petal growth

Carbohydrates are involved in many growth processes in plants. Structural carbohydrates are necessary for the stability of tissues and non-structural carbohydrates are obligate in providing energy, i. e. respiration, and as carbon skeletons for the formation of other compounds. Certain carbohydrates are osmotically active and important for turgor pressure maintenance (Drüge 2000). Carbohydrates are essential to flowering of plants (Bernier et al. 1993) and an important energy source facilitating flower opening (Ho and Nichols 1977, Marissen and LaBrijn 1995). Increased concentration of sucrose in phloem exudates upon photoinduction of flowering in short- and long-day plants originates from reserve carbohydrates, not from increased photosynthesis (Van Nocker 2001). Structural, reserve and soluble carbohydrates are accumulated in flower (Ho and Nichols 1977). Starch is the main reserve carbohydrate in rose (Evans and Reid 1988).

Petal growth is the result of cell expansion which requires the influx of water and osmolytes into the vacuole (Evans and Reid 1988, Van Doorn 2001). Thus, petal area as well as fresh and dry weight increase when the opening of the flower takes place. Starch is hydrolysed during petal growth and it is important for the maintenance of cell size (Evans and Reid 1988). During rapid cell expansion starch content is decreased and soluble sugar content increased in the petals (Ho and Nichols 1977). Carbohydrates are substrates for the synthesis of cell wall components during petal cell enlargement (Mayak et al. 2001). Reducing sugars, such as glucose and fructose, are the main constituents of the sugars in mature petals (Kaltaler and Steponkus 1974). Fructose has been reported as a predominant carbohydrate during opening of flowers in roses and in *Campanula* (Marissen 1991, Ichimura et al. 1999, Vergauwen et al. 2000). The level of fructose and glucose increases rapidly in petals at the time of flower opening and continues to increase until the petals are about to drop (Van Doorn 2001). In *Freesia* florets the maximum amount of soluble sugars was detected at anthesis (Van Meeteren et al. 1995).

Soluble carbohydrates increase the osmotic pool and enhance the turgor pressure which is an essential component in the petal cell expansion processes (Halevy and Mayak 1974, Mayak et al. 2001). Starch is an osmotically inactive solute (Evans and Reid 1988). Ichimura et al. (1999) suggest that methyl glucoside is a carbohydrate also involved in flower opening of roses. It is transported into the vacuole of petal cells to lower the osmotic water potential and thus promotes flower opening. To utilize carbohydrates as osmolytes needs an active

transport system inside the cell (Ichimura et al. 1999). Sugars constitute approximately 55% of the osmotic pool in rose petals (Acock and Nichols 1979). Thus, solutes other than sugars account for a large portion of the osmotic potential of petal cells (Evans and Reid 1988). The role of another carbohydrate, *myo*-inositol, in petal growth of roses is uncertain, although exogenous *myo*-inositol at a high concentration may act as an extra-cellular osmolyte that inhibits water uptake and flower opening (Ichimura et al. 1999).

Sucrose is the main transport form of sugar to flower bud (Ho and Nichols 1977). Sugars are transported from leaves to flower bud in the phloem. Some of exogenously added sugars in vase solution are transported in the xylem and the stem may also have phloem loading capacity (Halevy and Mayak 1979, Marissen and La Brijn 1995). Carbohydrates in stem probably also contribute to flower opening. Flower diameter was larger in longer than in shorter rose stems (with leaves removed). This was also seen in *Freesia* florets (Van Meeteren et al. 1995). A good correlation was observed between the increase in petal fresh weight and the decrease in carbohydrate content in leafless rose stem (Ichimura et al. 1999). Cultivar differences in roses are seen in the transport capacity of sugars in vase. A cultivar with good flower opening was able to import more carbohydrates from the leaves and stem than a cultivar with poor flower opening (Marissen and La Brijn 1995).

2.4.2 Water stress and senescence in vase life of flowers

Inhibition of water shortage in the flowering shoot is of major importance in extending the vase life of cut roses. Water stress induces premature senescence, bent neck and wilting. In senescing petals respiration increases, membrane permeability changes and hydrolysis of cell components occurs (Halevy and Mayak 1979). The first respiration maximum coincides with the opening of flower bud. During flower maturation the respiration gradually declines, which is perhaps caused by insufficient supply of sugars for respiration. The sharp second peak in respiration occurs at the final senescence stage, after which respiration again declines (Halevy and Mayak 1979). Carbohydrates in petals have also a role in maintaining the membrane integrity, which delays senescence (Goszczyńska et al. 1990a). The blue discolouration of red roses seems to indicate that soluble carbohydrates are unavailable for respiration, which leads to depletion of amino acids and proteins. A small change in vacuolar pH generates the discolouration (Asen et al. 1971).

Growth regulators are involved in the process of senescence and they interact with each other and with other internal factors. Endogenous ethylene production has three distinct phases: in the first phase the production rate is low, in the second phase it increases rapidly,

and then declines in the third phase (Halevy and Mayak 1981). The rise in ethylene production occurs after flower opening in intact rose flowers and it is a sign for the terminal stage of senescence (Halevy and Mayak 1981, Van Doorn 1997). Mayak (1987) suggested the following events to take place during senescence of flower. At first, changes happen in membranes, including changes in microviscosity and phase-transition temperature. This is followed by a rise in ethylene production and subsequent loss of membrane permeability reflected in increased ion and water leakage. As a result of excessive water loss, the flower weight is reduced and wilting symptoms appear as the tissues desiccate. Water stress in plants may lead to increased ethylene production (Apelbaum and Yang 1981). In some ethylene-insensitive flowering plants, i.e. gerbera, daffodil and several cultivars of chrysanthemum, the endogenous ethylene does not regulate wilting of flowers in water stress (Van Doorn 1997).

There are cultivar differences in the level and action of hormones affecting the longevity of the flowers. In a short-lived rose cultivar the phase of accelerated rise in ethylene occurred earlier than in a long-lived cultivar (Mayak and Halevy 1972). Endogenous ABA content also increased in senescing petals and the level was higher in a short-lived than in a long-lived cultivar (Mayak and Halevy 1972). Cultivation conditions (e. g. light quality, duration of lighting and fertilization) affect the ABA content in petals (see section 2.4.3). The level of cytokinins in rose petals decreased as the flower aged and the level was lower in a short-lived than in a long-lived cultivar (Mayak and Halevy 1970). Cytokinins enhanced water uptake in cut roses (Mayak and Halevy 1974). The endogenous gibberellin content was lower in petals of a cultivar that had shorter vase life than a cultivar with a longer vase life (Agbaria et al. 2001).

As a result of partial water stress, flower petals fail to expand and the vase life may be shortened. It may take days from termination of water deficit until its effects are evident (Mayak 1987). To ensure a good vase life, water uptake at stem base and transport through the stem must be undisturbed, water loss must be controlled, and the capacity of the different organs of the flowering shoot to retain water must be maintained (Halevy 1972b, Zieslin 1989).

In roses, an abscission zone is a transition area at a junction of stem and peduncle where no xylem vessels are continuous from stem to peduncle, resulting in a high resistance to water flow (Darlington and Dixon 1991). The hydraulic conductance is also low in poorly vascularized peduncle, being the lowest at the base of the ovary. The abscission zone and the region of low conductance in the peduncle may co-operate in the control of growth and development of the rose plant (Darlington and Dixon 1991). The flower bud absorbs water,

which may in shortage of water lead to water deficit in peduncle region and contribute to the occurrence of bent neck (Zieslin et al. 1978a). In peduncle, cavitation-induced embolism may limit the water flow to the flower to protect the main stem (Darlington and Dixon 1991). High transpiration rate can induce water deficit in the neck tissue and cause bent neck, if the stomata in the leaves cannot close as response to the shortage of available water in the shoot (Mayak et al. 1974).

As the degree of maturity of the flower prolongs, the time required for abscission in the peduncle increases, suggesting that the structural strength of the peduncle affects the rate of abscission (Darlington and Dixon 1991). Parups and Voisey (1976) reported that the development of secondary thickening and lignification of the vascular elements in the peduncle region influence the occurrence of bent neck. Growth and rigidity of peduncles are affected by gibberellin and auxin (Zieslin et al. 1989). Thickening of vascular tissue takes place at a relatively late stage in flower development, showing variation between cultivars. Therefore, the harvesting stage should be adjusted to the cultivar to prevent the bent neck caused by too immature picking stage (Parups and Voisey 1976, Zieslin et al. 1978a).

2.4.3 Vase life and preharvest conditions

Preharvest conditions contribute to the postharvest keeping quality of the flowering shoots. Factors to be considered here are light, relative humidity, temperature, carbon dioxide enrichment and nutrition.

Cultivar differences in vase life length are seen in response to the supplemental lighting. High level of supplementary lighting does not necessarily prolong the vase life of cut roses (Fjeld et al. 1992, 1994). However, total light energy during the growth period influences the carbohydrate level in the flowering shoot, thus affecting the flower's longevity (Halevy and Mayak 1979).

Rose cultivars respond differently to light quality and daily duration of lighting. Orange light increases stomatal conductance (Blom-Zandstra et al. 1995). Blom-Zandstra et al. (1995) reported cultivar differences in nocturnal stomatal conductance in orange but not in blue or white light. High pressure sodium (HPS) lamps used as supplemental lights include mainly orange light. Quality of supplemental light has been reported to affect the level of ABA in petals but not in leaves of roses (Garello et al. 1995). The ABA content in petals at harvest was lower in plants grown under HPS lamps than in those grown under MH (metal halide) lamps. In vase, the ABA content in petals increased faster and the vase life was shorter for

flowers from MH-grown plants, compared with those cut from HPS-grown. The R:FR ratio in HPS lamps was 3.6 and in MH lamps 4.7 (Garello et al. 1995).

Supplementary lighting of 24 h per day has shortened the vase life of many cultivars, as compared with 18 and 16 h lighting regimes (Mortensen and Fjeld 1998, Mortensen and Gislerød 1999). Disturbances in stomatal closure in leaves of the flowering shoot after growing under supplemental lights for 20 h daily in winter seemed to explain early wilting and appearance of bent neck in vase for some rose cultivars (Slootweg and Van Meeteren 1991). The stomata closed only partly in darkness. Transpiration during the first two days in vase was doubled, compared with flowers grown without any supplemental light. Mayak et al. (1974) and Van Doorn et al. (1989) have also found a circadian rhythm of xylem flow in vase that was identical to intact plants in the greenhouse, which may contribute to the water balance in vase. Genetic variation in daily water consumption between the cultivars has been reported (Blom-Zandstra et al. 1995).

The hydraulic conductance of stem in rehydration after a short dry period following the harvest was lower in plants grown in supplemental than natural light (Slootweg 1997). The water transport capacity in vessel walls was suggested to differ due to the different light conditions during growth.

Air humidity is higher in greenhouses during the cultivation of roses than in postharvest conditions. Plants have a capacity to acclimate to humidity conditions and high air humidity during cultivation may shorten vase life length considerably in some sensitive cultivars (Mortensen and Fjeld 1998, Mortensen and Gislerød 1999). Leaf drying is a typical first sign of this problem. Relative humidities below 85% are usually recommended to ensure a good vase life (Mortensen and Gislerød 1999). Vase life of a sensitive cultivar was slightly reduced by increasing the humidity from 75 to 83% at 18 h lighting, but combined with 24 h lighting, the same increase in relative humidity strongly reduced vase life (Mortensen and Gislerød 1999). In cultivars which are sensitive to high air humidity the duration of a high humidity period should not exceed 12 h (Mortensen 2001). Already six hours' duration of high air humidity decreases the percentage of properly opened flowers.

No differences in the morphology and only small differences in lignin, hemicellulose and cellulose contents were observed between peduncles from flowering shoots grown in high (90%) and moderate (70%) relative humidity (Torre and Fjeld 2001). Darlington and Dixon (1991) have also reported that constant 77% compared to fluctuating 30-60% air humidities did not affect the anatomy of vascular system and hydraulic conductances in peduncles of several rose cultivars. Consequently, high transpiration rate and early wilting are considered

to be caused mainly by the malfunctioning stomata. Sallanon et al. (1993) found that rose plants grown *in vitro* in high air humidity developed structurally or physiologically malfunctioning stomata. Torre et al. (2003) found in roses a higher number of stomata which were open wider in high than moderate air humidity.

Petals of roses grown in high relative humidity contained less calcium than those grown in moderate humidity. Calcium is involved in the regulation of flower senescence. It influences cell wall and membrane structure and function (Halevy et al. 2001).

Both increasing and decreasing the temperature may reduce the vase life of roses (Moe 1975). Low temperature close to the harvest may also affect pigmentation of red roses seen as “blackening” or blueing of petals (Halevy and Zieslin 1969).

High carbon dioxide (CO₂) enrichment during cultivation has extended the vase life of some rose cultivars compared to ambient CO₂ level. High CO₂ concentration lowered cuticular transpiration and improved leaf water potential at complete stomatal closure, indicating a higher capacity of leaves to protect themselves against water losses by transpiration (Urban et al. 2002).

A high (21.4 mmol l⁻¹) compared to low (10.7 mmol l⁻¹) nitrogen fertilization during cultivation decreased the longevity of rose flowers ‘Royalty’ in vase (Menard et al. 1996). ABA level increased in both leaves and petals in high nitrogen supply. Both nitrogen levels led to nearly equivalent yields, indicating that cultivar ‘Royalty’ tolerates high nitrogen level, while the yield of another cultivar decreased at that high nitrogen level (Menard and Dansereau 1996). ABA levels in plants increase while levels of cytokinin, which delays the senescence, decrease in response to salt stress (Drüge 2000). Salt stress is an important factor in potted plant postharvest longevity.

2.4.4 Vase life and postharvest conditions

Storage, transport conditions and the conditions at the consumer’s home are essential for vase life. Storage in cold slows down transpiration and the growth of bacteria. Use of preservatives can prolong the flower longevity (Halevy and Mayak 1981).

During vase life the rate of transpiration declines but it tends to be higher than the water uptake. Even the rate of cuticular transpiration may exceed the water uptake rate (Van Doorn 1997). In general, stomata tend to close after harvest, but Mayak et al. (1974) showed that a short-lived cultivar had a lower ability to close stomata than a long-lived cultivar in response to water stress. Diminished water movement from vase to different parts of the flowering shoot may cause water stress, to be followed by bent neck, wilting and premature senescence.

Stem plugging is one of the main factors determining longevity of roses and can be caused by physiological occlusion due to plant itself, micro-organisms, or air embolism (Van Doorn 1989).

Amorphous plugs were found in rose stems 15-20 cm above the cut surface (Lineberger and Steponkus 1976). These plugs contain polysaccharides, lipids and protein-like material (Parups and Molnar 1972, Van Doorn 1989). Slime excreted by bacteria contains similar compounds (Van Doorn et al. 1991a). The origin of amorphous plugs is still tentative and their presence does not generally explain the resistance to water flow (Rasmussen and Carpenter 1974, Van Doorn 1989). Stem cutting at harvest also induces leaching of sugars, proteins and polyphenols from broken cells (Woltering 1987).

The highest hydraulic resistance in cut roses was found in the basal part of the stems. The number of bacteria in stems correlated with the development of blockage (Van Doorn 1989). The flowering shoot can readjust to restricted water uptake by partial closure of stomata, therefore the number of bacteria had to be very high before the loss of turgor (Van Doorn et al. 1986). The number of bacteria usually decreases on the way up to the stem (Put and Van der Meyden 1988). Put and Clerkx (1988) reported that yeast and filamentous fungi can also contribute to vascular blockage in rose and gerbera stem. Bleeksma and Van Doorn (2003) have shown that bacterial occlusion of the vascular system can cause a high rate of cavitation. Vessels filled with air bubbles restrict uptake and movement of water in the flowering shoots in vase.

Transient water stress during postharvest handling is common. When flowering shoots are held dry, the water transpired is replaced by air, which disrupts water column continuity and impedes water movement in consequence of the loss of turgor pressure (Mayak et al. 2001). This symptom when the water column in the vessels is disrupted with air is called air embolism. The volume of air taken up correlates with the volume of vessels that had been opened by cutting (Van Doorn 1989). The presence of air in the stem created no immediate barrier to the uptake of water after a few hours' dry storage of the flowering shoot. Disappearance of emboli is apparently due to dissolution of the gases in water. A prolonged exposure to air, however, resulted in occlusion of the lowermost part of the stem and inhibited water uptake (Van Doorn 1990). Recutting the stem under water is recommended to diminish the number of air-filled vessels after dry storage.

Preservative solutions are used to lengthen the vase life of cut roses. Some of the compounds slow down physiological processes, thus delaying senescence, while others enhance water uptake, reduce transpiration and/or diminish bacterial growth.

In shortage of water, the petal sugar content of 'Mercedes' roses increased (Mayak et al. 2001). Van Doorn (2001) suggests that the low sugar level in cytoplasm may decrease vase life although the concentration in vacuole is high. Preventing water stress, sugars in vacuole may become unavailable for respiration because they are needed for osmotic adjustment. The role of exogenous sugars for extending the vase life is well known. Sugar from vase solution accumulates in petal tissues, improving the osmotic potential and enhancing the carbohydrate pool for growth and respiration, which promotes flower opening and retards senescence (Van Doorn et al. 1991b, Kuiper et al. 1995). Exogenous sucrose reduced the age-induced increase in membrane lipid microviscosity (Goszczyńska et al. 1990a). Sugars in the vase solution accelerate the bacterial growth, which may lead to stomatal closure as a result of water deficit (Van Doorn 1997). Another reason for reduced transpiration may be a decline in water uptake due to slower flow rate of sucrose solution (Durkin 1979). Therefore, an antimicrobial compound is usually added to sugar solutions.

Calcium chloride (CaCl_2) in vase solution increased vase life (Torre et al. 1999); calcium promoted flower opening, enhanced initial fresh weight and delayed its reduction rate. Calcium treatment delayed the decrease in petal membrane proteins and phospholipids and slowed down the rate of electrolyte leakage from petals. It also suppressed ethylene production (Torre et al. 1999).

Gibberellin (GA_3) in vase solution enhanced the flower longevity of 'Mercedes', but not that of many other cultivars (Goszczyńska et al. 1990b). Petal gibberellin content was higher in 'Mercedes' than in 'Madelon' in which the gibberellin had no effect on vase life (Agbaria et al. 2001). Exogenously added ABA is effective in decreasing stomatal opening. Added ABA and sucrose in vase solution have opposing effects on cut rose flower senescence (Borochoy et al. 1976).

Antimicrobial compounds prevent and slow down the bacterial growth, ensure proper water uptake and delay senescence. These compounds are, for example, metal salts, quinoline compounds, ammonium compounds and compounds including chlorine (Van Doorn 1997). For instance, silver ion (e.g., AgNO_3) has a bactericidal character, promotes water uptake and has an inhibitory effect on ethylene action (Veen 1983). Treatment with an antimicrobial compound shortly after harvest is beneficial for several flower species.

3 AIMS OF THE STUDY

The main objective of the present study was to investigate factors contributing to improved yield, quality and vase life of greenhouse cut roses in year-round production with an emphasis on winter-time cultivation period. The effects of different growing conditions, growing techniques, cultivars and plant characteristics on yield, quality and vase life were studied. More specifically, the following aims were included:

- 1) to investigate if the increased supplemental light intensities and daily durations improve yield and quality in different growing conditions (I, II, IV, V);
- 2) to compare the effects of varying durations of winter-time rest periods and forcing temperatures on yield and quality (I, II, IV);
- 3) to determine if shoot bending, compared either to pruning after rest period or to blind shoot removal during cultivation, improves yield and quality (IV);
- 4) to analyse the combined effects of different shoot bending and harvesting heights on yield and quality (V);
- 5) to evaluate the impact of the different growing conditions, growing techniques and plant characteristics on the vase life of rose cultivars (I-V).

4 MATERIALS AND METHODS

An overview of the experimental part of the work is presented in the following. More detailed information is available in the original papers (I-V).

4.1 Plant material

Rosa hybrida L. cultivars 'Mercedes' (red, medium sized flowers) and 'Frisco' (yellow, medium-to-small fl.) were used in most of the trials. 'Mercedes' was the main cultivar used in cut rose production in Finland at the time this study began, and it had manifested problems in vase life in winter-time cultivation. 'Frisco' was chosen because, based on practical experiences, it is a cultivar with good vase life and good potential for production in winter. 'Sacha' (red), 'Indian Femma' (orange) and 'Dream' (pink) represented newer and 'Lorena' (pink) older medium sized flower cultivars (V).

Cuttings were used in all experiments. Grafted plants of different ages were included in (I). The ages at the beginning of forcing were 5.5 and 9.5 months for young and 17.5 and 21.5 months for old plants (I).

The harvesting stages for 'Mercedes' and 'Frisco' in winter and summer are shown in Figure 1. Petal carbohydrate contents (Figure 4) were analysed from the flower buds grown in the experimental year 1994 (I).

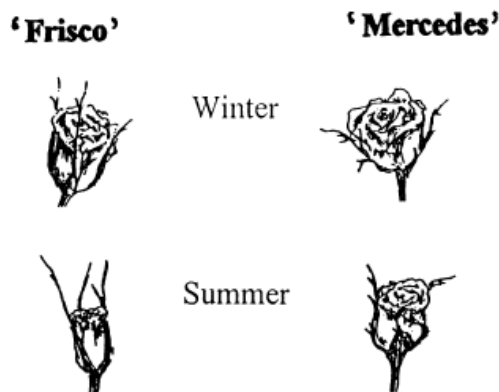


Figure 1. Stages of development at which the flowers of 'Frisco' and 'Mercedes' were harvested in winter and summer.

4.2 Growing conditions

4.2.1 Irradiance and duration of supplemental light (I-V)

Irradiance of supplemental light was measured by a quantum sensor, showing the photosynthetic photon flux (PPF) in $\mu\text{mol m}^{-2} \text{s}^{-1}$. PPF was usually measured at canopy level, i.e., at the height of the first and second youngest fully developed leaves on the flowering stem. Irradiances and daily durations in different supplemental light treatments are shown in Table 1.

Supplemental lights were either continuously on (II, V) or they were turned off during the mid-winter rest period (I-IV). Experimental lighting was terminated in spring (I-IV).

Table 1. Irradiance levels (PPF) and daily durations in the supplemental light treatments reported in the original Papers I-V.

	Duration, h d ⁻¹	PPF, $\mu\text{mol m}^{-2} \text{s}^{-1}$		Duration, h d ⁻¹	PPF, $\mu\text{mol m}^{-2} \text{s}^{-1}$
Paper I	15	63	Paper III	20/15	100
	20	63		20	100
	15	100		18	100
	20	100	Paper IV	20	100
	20/15	100			
	18	100			
Paper II	20	65	Paper V	20	165-180
	20	100		20	220

4.2.2 Other growing conditions and plant density (I-V)

Growing substrates were *Sphagnum* peat or rockwool. Peat was in the form of 20 cm thick beds (I, III), 10 litre containers with two-thirds of perlite (II), or as peat slabs (V). Rockwool was in sheets (IV). Plant density was in the traditional growing method 14.2 or 11.1 plants per net square meter (I, III, IV). For roses grown in containers, the density was 4.7 plants per gross square meter (II). In dense plantation the plant density was 31.25 per net square meter (V).

Setpoints were usually 16-20 °C for daytime temperature and 60-80% for relative humidity. Relative humidities in January-March in 1993 and 1994 (I) are shown in Figure 2. Carbon dioxide enrichment was applied at 350 ppm (I, IV) or 800 ppm (V) of pure gas when the vents were closed. The plants received completely soluble nutrient solution at 1.5-2.0 mS cm⁻¹.

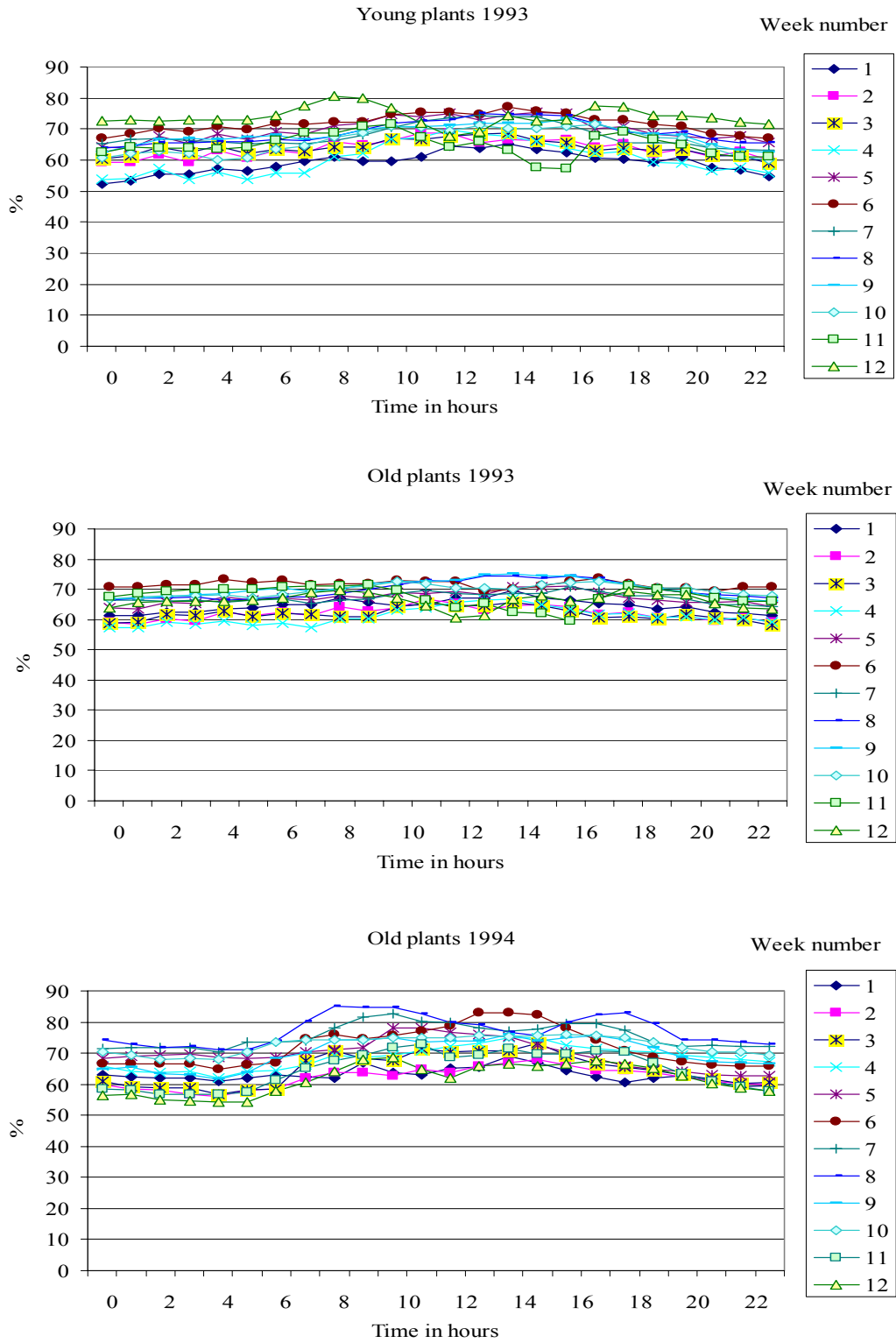


Figure 2. Relative humidities in greenhouse compartments in January-March 1993 and 1994 (I).

4.2.3 Rest period lengths and forcing temperatures (I-IV)

In November-December, rest periods of two different lengths were applied (II): 2 weeks and 6 weeks. Plants were in cold storage (2 °C) during the rest period. Forcing in the greenhouse started at the beginning of January. Two temperature schedules were used: fast (20 °C) and slow (8/13/20 °C). The growing temperature was achieved in week 3 and in week 4, respectively. During cold storage the plants received $1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF incandescent light 8 hours per day to avoid leaf drop.

In (I, III, IV) the rest period was accomplished in the greenhouse at the temperature about 4 °C. At forcing, the temperature was usually raised directly to 19-20 °C.

4.2.4 Vase life test conditions (I-V)

After harvest the flowering shoots were cold stored for 1-2 days at 4 °C in dark in deionised water. In the vase life testing room the conditions were the following: 10 or 12 (V) hours photoperiod, 10 or 23 (V) $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF provided by fluorescent tubes, air temperature 20-22 °C and relative humidity approximately 40%. Vase water was changed once a week.

4.3 Growing techniques

4.3.1 Shoot bending and pruning in the traditional upright growing technique (I-IV)

At the beginning of forcing the plants were either pruned (I-IV) or the shoots were bent below horizontal position (IV). No leaves, or only a few, were left on the pruned plants. The bent stems were leafy. Most of the stems broke on the upper side of the stem at bending, because the wood was hard (IV). Blind shoots were either removed (I-IV) or bent (IV).

4.3.2 Bending and harvesting height combinations in the shoot bending growing technique (V)

In the new growing system part of the shoots, usually blind, are bent throughout the whole cultivation period. At the beginning of cultivation, three bending heights of the primary shoot were chosen: at base, above three buds and above five buds. Harvesting heights were dependent on bending heights. Heights were above 1, 3, 3/2 (first time above 3 buds, thereafter above 2 buds), 5/1, 5/2 or 5/3 buds (V Table 1). New bottom breaks were in their first harvest cut at the bending height. Cultivation time varied from 5 to 17 months.

4.4 Measurements

The number of flowering and blind shoots (II, IV, V), the number of bottom breaks (V), and the proportions of cuttings that rooted and the proportions of sprouted axillary buds were counted (V). For quality assessment, the flowers were classified into grades extra and 1 to 4 (II, IV, V). In addition to visual quality, the minimum stem lengths required for these quality grades are 40 (extra), 35, 30, 25 and 20 cm (1-4) for 'Frisco' and, correspondingly, 50, 40, 35, 25 and 20 cm for 'Mercedes', 'Sacha', 'Indian Femma', 'Dream' and 'Lorena' (Ristimäki 1988). The length classes were measured from 20 cm upwards at 10 cm intervals: roses with stem length less than 30 cm long were classified as bunch roses.

The number of leaves (I, II) and the length of the flowering shoot (I, II, V) in vase were measured. The fresh weight of the flowering shoot was also measured (II). Leaf areas were measured from 10-21 randomly selected flowering shoots (I). The average area of one leaflet was used to estimate the leaf area of the flowering shoot in vase.

The vase life was recorded on the basis of daily observations, until bent neck or loss of decorative value due to senescence or wilting occurred (I-V). In petal carbohydrate measurements, the flower buds were collected at both harvesting stages (Figure 1) in February and July. Data presented cover only the development stage that was used in summer harvest.

4.4.1 Enzymatic determination of soluble sugars and starch

Two flower buds per block were collected and assayed for soluble sugar and starch contents. The results are means of 2x3 flower buds. Immediately after harvest the petals were ground to powder in liquid nitrogen and stored at -70 °C before extraction. Petal powder (1.0 g) was homogenized in double distilled water. Glucose, fructose and sucrose were extracted using a shaking water bath at 60 °C for 2 h. After cooling, the 40 ml extract was vacuum filtered to remove the insoluble material. The volume was then adjusted to 50 ml with double distilled water and the samples were stored at -20 °C before assay. The enzymatic assays were carried out with the assay kit supplied by Boehringer Mannheim GmbH, Germany.

For extraction of starch, 2.5 ml of 8 M HCl and 10 ml of DMSO were added to 1 g of petal powder, and the extraction was carried out as for sugars. After rapid cooling, 2.5 ml of 8 M NaOH and 35 ml of Na-citrate buffer (0.112 M, pH 4) were added. Following vacuum filtration, the assay was immediately performed in accordance with the instructions of the enzyme supplier, Boehringer Mannheim GmbH, Germany.

4.5 Statistical methods

One- and two-factor treatment structures, together with randomized block designs, were used in all experiments. The majority of the quantitative variables, including counts (e.g. log-transformed number of shoots) were analysed by using ANOVA (I, II, IV). Poisson distribution was exploited explicitly in the analysis of counts in (V).

Proportions were used to characterize the behaviour of variables measured on nominal (e.g. occurrence of bent neck) and ordinal (e.g. quality grade) scales. The analysis was based on binomial distribution and logit models were used (I, II, IV, V).

Mean values were used to characterize vase life duration (I-IV), although differences in variation of vase life may be masked. As the distribution of vase life tends to be skewed, medians were used as well (V). When senescence is monitored as a cause for lost ornamental value, the actual length of a flower's vase life sometimes remains unknown. This takes place when a flower has to be removed for other reasons than senescence, e.g. bent neck or dried leaves; such a phenomenon is called censoring. Survival analysis allows, however, comparison of treatments with respect to vase life duration even with censored data (I, III). For the comparison, the treatments are characterized by their hazard functions. The hazard $h(t)$ is the risk of ceased ornamental value of an individual flower due to senescence after t time units in vase. An elaboration of survival models (Ripatti and Palmgren 2000) allows estimation of plant level hazards of ceased ornamental value (III).

5 RESULTS AND DISCUSSION

5.1 Yield and quality in different growing conditions and techniques

5.1.1 Irradiance and duration of supplemental light (I, II, IV, V)

The yields of both ‘Mercedes’ and ‘Frisco’ increased as the total amount of supplemental light increased (Table 2 and II Table 1). Lighting increases yield by promoting bud break and decreasing flower abortion, and furthermore, it improves the quality, increases the number of bottom breaks and accelerates the development of the flowering shoot so that less time is needed between flushes than in conditions with no supplemental lighting (Moe and Kristoffersen 1969, Carpenter and Andersson 1972, Zieslin and Mor 1981, Bredmose 1993). In winter cultivation with a rest period, irradiance of $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF was insufficient for obtaining a good yield in terms of quantity and quality (Table 2; II Tables 1 and 2). Lighting at $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for 20 h d^{-1} seemed to be insufficient for uninterrupted cultivation in winter months: ‘Mercedes’ did not give higher yield when compared with plants which received a rest period. In continuous cultivation of ‘Mercedes’ there was a harvest break, which could have been shorter with higher irradiance. ‘Frisco’ yielded better in continuous cultivation than with a rest period (Särkkä unpublished). Cultivar differences are, thus, obvious. Mortensen et al. (1992a) also reported high yields in winter with supplementary lighting in excess of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF.

The yield of the second flush was lower than that of the first flush both for ‘Mercedes’ and ‘Frisco’ (Table 2). This difference was not seen in another experiment (IV Table 1). In the first experiment (I) lighting was discontinued in spring at the end of March, which was before the start of the second flush, but in the later experiment (IV) the lights were on until the end of April. Thus, supplementary lighting should not be terminated too early in the spring. High supplemental irradiance, even in summer, may increase yield (Mortensen et al. 1992a, b, Bredmose 1993). Zieslin and Halevy (1975) reported reduction in flowering in the second flush as a cumulative effect of low irradiance.

Cultivars differ in their response to long light durations. At low PPF ($63 \mu\text{mol m}^{-2} \text{s}^{-1}$), long daily photoperiod (20 h d^{-1}) seemed to have a more negative effect on yield than shorter photoperiod (15 h d^{-1}) (Table 2). Hendriks and Ludolph (1987) have also reported negative results for ‘Mercedes’ with long light duration and low PPF. The long light duration promoted bud sprouting, but in absence of sufficient light energy, the incidence of blindness increased (Tables 2 and 3). ‘Frisco’ utilized supplemental light more efficiently than ‘Mercedes’.

Continuous lighting, compared with 16 h d⁻¹, at 145 μmol m⁻² s⁻¹ PPF in winter months considerably increased the yield of ‘Frisco’, while in ‘Sacha’ the response was variable (Särkkä unpublished). According to Bredmose (1993), ‘Frisco’ is a cultivar with a good ability to exploit supplemental light.

Table 2. Mean number of flowering shoots per plant in three successive flushes for ‘Mercedes’ and ‘Frisco’, reported in Paper I. Supplementary lighting ceased in week 13 and the main harvest of flush 2 started in week 16.

Year	Duration h d ⁻¹	PPF ¹⁾ μmolm ⁻² s ⁻¹	PPF molm ⁻² d ⁻¹	‘Mercedes’			‘Frisco’		
				Flush 1	Flush 2	Flush 3	Flush 1	Flush 2	Flush 3
				shoot per plant			shoot per plant		
1992									
	15	63	3.4	2.2a	2.2	3.4	3.5	2.6	5.0
	20	63	4.5	1.9a	2.5	3.8	3.5	2.9	5.8
	15	100	5.4	3.2b	1.9	3.7	5.6	3.1	4.9
	20	100	7.2	4.0b	2.7	3.8	5.1	3.7	5.6
				p-values			p-values		
PPF				<0.01	ns	ns	<0.01	<0.01	ns
Duration				ns	ns	ns	ns	ns	ns
Duration*PPF				<0.05	ns	ns	ns	ns	ns
1993									
	15	63	3.4	2.3a	2.1	3.4	2.3	2.6	5.4
	20	63	4.5	2.6a	1.8	4.0	3.8	2.7	5.4
	15	100	5.4	2.7a	2.2	3.7	3.8	3.5	6.0
	20	100	7.2	5.2b	2.7	3.1	6.0	4.8	6.1
				p-values			p-values		
PPF				<0.01	ns	ns	<0.01	<0.01	ns
Duration				<0.01	ns	ns	<0.01	ns	ns
Duration*PPF				<0.05	ns	ns	ns	ns	ns

¹⁾ PPF value used in the analyses

Significance level p<0.05, ns= non-significant

Values tagged with different letters differ significantly from each other (Tukey’s HSD test).

Towards the end of the 1990s, the growers increased the supplementary irradiation level on the basis of the results of earlier experiments. A high irradiance of 220 μmol m⁻² s⁻¹ PPF for 20 h d⁻¹ (15.8 mol d⁻¹) throughout the year gave high yields in all seasons and cultivars (V Table 2). No difference in the number of flowering shoots was seen between winter and summer. The time between flushes was short, which also enhanced the total yield of the cultivation period.

Table 3. The proportion of blind shoots of all shoots in flush 1 of the year 1992 for ‘Mercedes’ and ‘Frisco’, reported in Paper I.

Duration h d ⁻¹	PPF μmolm ⁻² s ⁻¹	Blind shoots	
		‘Mercedes’ %	‘Frisco’ %
15	63	63	54
20	63	71	57
15	100	50	32
20	100	44	46

Plant density affects the amount of light that penetrates to the plant canopy. In this respect, flush harvesting has an advantage in comparison with continuous harvesting: better light interception during axillary bud break thanks to reduced shading by developing stems. On the other hand, continuous harvesting benefits from the less dense canopy structure during flower stem development, owing to different stem heights of the growing shoots. The lower number of shoots diminishes intra-plant competition for assimilates. A young growing shoot is dependent on assimilates from the parent plant until it reaches the development stage when the flower bud is visible (Mor and Halevy 1979, Jiao et al. 1989). In ‘Frisco’ the proportions of blind shoots in plants with bent shoots were in average 22% in two of the studies (IV and V), although the PPF level was much higher in one (V, 11.9-13 mol m⁻² d⁻¹) than in the other (IV, 7.2 mol m⁻² d⁻¹). Plant density also differed considerably between these two experiments. With high plant density the irradiance level should also be high. However, the increase in the number of blind shoots does not always correlate with the decrease in the number of flowering shoots (Zieslin and Halevy 1975).

Installation height of the lamps has an impact on cultivation conditions. With high plant density, lamps installed close to the vegetation will warm the plants and improve air circulation, thus having a drying effect on the vegetation, which in turn diminishes incidence of plant diseases caused by high humidity (V). Lamps also reduce the warming costs of the greenhouse in cold climates, such as in Finland during winter months.

In high supplementary lighting, high level of CO₂ enrichment is obligatory in order to ensure a good growth (V). The yield of cut roses increased considerably with CO₂ enrichment of 700 ppm, in comparison with no CO₂ supply (Outa and Särkkä 2004). Mortensen (1987) has reported on the significance of sufficient CO₂ level on yield and quality of rose flowers. In our calculations, the CO₂ enrichment at 800 ppm accounted for as little as 2% of total costs

in production with high plant density and high supplementary lighting (V, Särkkä et al. 2001). In addition to the yield (output), the economically optimized supplementary lighting depends on the energy costs (input).

The quality of the first flush after the rest period was lower with low than with high PPF. Results of Mortensen et al. (1992b) support our findings, although contradictory results have also been reported, e.g., Carpenter and Andersson (1972), Armitage and Tsujita (1979).

5.1.2 Rest period and forcing temperature (II)

Rest period of 2 or 6 weeks in mid-winter did not reduce the yield of young ‘Mercedes’ plants, as compared with continuous growing with supplemental lights at $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for 20 h d^{-1} , where the yield was calculated at the beginning of January (II Table 1). Average fresh weight of flowering shoots was higher in uninterrupted production than in most of the rest period treatments. The effect of light should be kept in mind when discussing the effects of the duration of the rest period and forcing temperature.

An interaction between rest period length and forcing temperature was observed. Both yield and quality were poorer with a long rest period combined with slow forcing than in the other treatments (II Tables 1 and 2). A low temperature is known to increase flower bud atrophy (Zieslin and Halevy 1975). When rest period was two weeks, slow forcing was beneficial, but after a rest period of six weeks, fast forcing gave the best yield (II). At low temperature the physiological stage of the buds and plants changes, including changes in hormone levels and carbohydrate balance (Van der Berg 1987, Crabbe and Barnola 1996). Khayat and Zieslin (1982) reported that a short cooling period of 1-2 weeks after pruning stimulated bud break, while a longer period of 3-5 weeks resulted in partial inhibition in bud break. Apparently, significant changes take place in the plants between the second and the sixth week in cold.

Temperature raise from 17 to 21 °C during axillary bud sprouting decreased the number of leaves on a flowering shoot (Marcelis-van Acker 1995). In the present study, slow temperature raise at forcing after a long rest period decreased the number of leaves and the stem length, when compared with fast temperature raise (II Table 3). Asaoka and Heins (1982) reported, for another cultivar, shorter stems after storage at 2 °C for six than for two weeks. They also found that the forcing time to flowering was prolonged when cold storage was followed by a high cultivation temperature. In the present trial, slow temperature raise at forcing delayed flowering by one week, but the time from the onset of the 20 °C temperature to flowering was one week shorter than in fast forcing. Long rest period lengthened the main

harvesting period, indicating partial inhibition in bud break. As the development of roses is temperature sensitive, it can thus be controlled by choosing different temperature strategies.

High energy costs have made the issue of rest period topical in Finnish gardens. If the cultivar response to supplemental light at a given PPF in mid-winter is not very good and the market price for flowers is low, it may be economically justified to give the plants a rest period and save energy.

5.1.3 Shoot bending compared to pruning or blind shoot removal (IV)

If the rest period strategy is chosen, the cultivation technique at the beginning of forcing should also be carefully considered. In traditional upright growing technique the plants are pruned before forcing. After pruning, depending on the age and pruning height, the plants are either totally or nearly leafless. A drastic defoliation caused by pruning results in decreased root growth and mass (Fuchs 1986). Shoot bending, on the other hand, leaves the plants leafy. Bending the shoots instead of pruning in a 1.5 years old vegetation increased the yield of the first flush to the level of the third flush, which received more global radiation during growth than the first flush did (IV Table 1). The proportion of blind shoots was lower in bent than in pruned plants (IV Table 1). The assimilate supply of the bent shoots to growing laterals may have played an important role in diminishing the flower bud abortion in low-light conditions in winter. The functioning roots in bent plants might also transport stored carbohydrates to young shoots before these became self-sufficient in assimilation.

The flowering shoots were longer, but the proportion of first grade blooms was not higher in the bent plants, as compared with the pruned plants. Zieslin and Halevy (1978) reported that, in a horizontally bent rose stem, the shoot from a bud close to the bend on the proximal side of the stem achieves greater length than the other shoots on the stem.

Pruning usually promotes bud break, but in our study the difference in comparison with the bending practice was minimal. Bending the shoots below horizontal level did not prevent sprouting of buds, and the apical dominance was thus removed as it is in pruned plants. Indeed, the number of all shoots was slightly higher in bent than in pruned plants (IV Table 1). This is in accordance with findings of Faust (1989) with fruit trees where apical dominance was effectively removed by bending below horizontal position. Based on our study, bending of shoots in traditional upright growing technique is recommended instead of pruning after a rest period in mid-winter for both ‘Mercedes’ and ‘Frisco’.

The blind shoot bending during cultivation was performed in 1.5 years old plants grown with traditional upright growing technique. Bending the blind shoots instead of cutting them

off resulted in an increased number of flowering shoots in ‘Mercedes’ but not in ‘Frisco’ (IV Table 1). Blind shoot cutting in ‘Frisco’ enhanced the number of sprouting shoots, but simultaneously increased the proportion of blind shoots. This equalized the yield to the same level as with bending. Kool (1996) has also reported reduced overall bud break in blind shoot bending.

In the present study, the harvesting height was above one or two leaves. The harvesting height is known to influence the yield (Rathmell 1969). The number of outgrowing laterals is positively affected by the number of 5-leaflet leaves remaining on the mother cane (Zieslin 1981, Kool 1997). Photosynthesis increases in mature leaves after blooming and pruning when new shoots start to grow from lateral buds (Mor and Halevy 1979). However, Aikin and Hanan (1975) reported that the assimilation capacity of green leaves remaining on a rose stem after harvest was less than half of the maximum. The outgrowth of a bud to a flowering shoot is influenced by the assimilate supply. A higher number of leaves remaining on the parent shoot resulted in a higher assimilate production for the outgrowth of the buds (Marcelis-van Acker 1994). In ‘Mercedes’, bending the shoots had a positive effect on shoot growth. ‘Mercedes’ has a weaker root system than ‘Frisco’ and may suffer more from shoot cutting and transport less carbohydrates to new shoots than ‘Frisco’. The assimilation capacity of the older leaves may also be lower in ‘Mercedes’ than in ‘Frisco’. In ‘Frisco’ the leafy parent plants could supply energy to the same amount of new shoots as the plants with bent shoots. In cultivar Kardinal, Warner and Erwin (2002) measured, at the same plant density, a 28% higher whole plant net photosynthetic rate in plants grown with shoot bending than in plants in the traditional upright growing system. Bending the blind shoots in the traditional cultivation technique is recommended for cultivars like ‘Mercedes’ which are not as strongly growing cultivars as ‘Frisco’. However, blind shoot bending results in long flowering stems in both cultivars.

5.1.4 Shoot bending and harvesting height combinations (V)

In the shoot bending growing technique the primary shoot has usually been bent down at its base. This stimulates the outgrowth of the two most basal buds (Kool and Lensen 1997). However, bending above five buds with various harvesting heights (Method 5B), as compared with bending at base with harvesting above one bud (Method B), resulted in higher yields in eight of nine trials (V Table 2). In six of nine trials, various harvesting heights combined with bending the primary shoot above five buds yielded better than when bending above three buds. Bending above three buds with various harvesting heights (Method 3B) yielded more in

five out of nine trials than bending at base with harvesting above one bud. It was essential, however, that new bottom breaks were harvested for the first time at bending height. Building of a crown on a high height was substantial. At base bending and harvesting above one bud no crown was built.

In Method B, the total number of sprouting shoots was lower than in the other growing methods. Harvesting above one bud from the beginning of cultivation impaired the formation of basal shoots, the number of which is positively correlated with flower production (Zieslin et al. 1976, De Vries and Dubois 1983). Buds towards the base of the shoot are more inhibited to sprout, and bud sprouting may also be reduced by a lack of leaves at the base of the plant (Zieslin et al. 1976).

In ‘Sacha’ grown for ten months, a larger yield was obtained when the harvesting height after high bending was higher than above one bud (V). This was not yet visible after eight months’ cultivation. At higher harvesting height in ‘First Red’, Dambre et al. (2000) received 10% more flowering stems after six months’ cultivation, increasing gradually up to 34% after two years of cultivation. Kool (1997) showed that the number of second order laterals formed after eight months’ cultivation had a greater influence than the number of basal shoots on the number of flowering shoots during the following two years.

De Vries and Dubois (1984) found a good correlation between the number of bottom breaks and the number of harvestable shoots. The quality of the bottom breaks is important because thick shoots increase the number and quality of outgrowing laterals (Byrne and Doss 1981, Kool and Van de Pol 1993). In our study, making the crown at a higher height seemed to have a positive effect on the number of good bottom breaks (V Table 4). The assimilate supply from the leaves left in the plant at the high harvesting height may also have been a contributing factor.

High plant density in the shoot bending growing system increased the number of flowering shoots substantially, with great differences between the growing methods (e.g. for ‘Sacha’ 13, Method B: 847 fl. per m² and Method 5B: 2039 fl. per m²). Cultivar differences were notable. The planned cultivation time with high plant density was some months, but the production continued profitable at least for one year (Särkkä et al. 2001). The longest growing periods were 17 months for ‘Sacha 13’ and 16 months for ‘Dream 12’ (V Figure 2). Dambre et al. (2000) reported significantly increased flower production even with a small increase in plant density, from 6 to 8 plants per m², using shoot bending growing technique. Warner and Erwin (2002) obtained a lower yield in shoot bending than in traditional upright growing technique with the same plant density.

High plant density increases leaf area, the yield per growing area and stem length, but it decreases the weight of harvestable stems (Mortensen and Gislerød 1994, Kool and Van de Pol 1996, Kool 1997, Bredmose 1998). Moreover, shoots at higher nodal positions remain shorter. In view of this, the proportions of bunch roses (<30 cm) produced under our growing and harvesting conditions were surprisingly low. Cultivar differences were observed though. The higher harvesting height lowered the quality of flowers, expressed as proportions of various grades (V Figure 3), in agreement with the studies referred to above, but the number of high grade flowers was greater owing to the higher total yield. The quality of flowers in the first flush was lower in summer plantings, especially with Method 5 B. In high greenhouse air temperature in summer the stem length remained shorter (IV).

In the shoot bending growing technique, where shoots are bent through the whole cultivation cycle, the number of bent shoots depends on the leafiness of the plants and on the cultivar. In cultivation system with harvesting in flushes, we bended only a few shoots, approximately 1-3 bent shoots were simultaneously kept in each plant. Growers have applied the bending technique with a higher number of bent shoots, but it has led to leaf yellowing and shoot dying of the lower bent stems in shortage of light. Pien et al. (2001) have optimized the LAI (leaf area index) for bent shoots to be between 1 and 3.5. In continuous harvesting, the role of bent shoots may be more important for the hormone balance to form long stems than for the assimilate supply.

Kool and Lenssen (1997) concluded that the primary shoot should not be bent too early, not until the LAI in the canopy is 3 or more. ‘Madelon’, which they used in their trials, is considered a big flowered cultivar in Finland. If bending of the primary shoot takes place at too late a stage, the stem becomes woody and breaks off easily. This loss of the shoot retards growth. An advantage of bending higher up is that the plant does not become leafless if the stem breaks off. In our trials, bending before the stem was too wooden also shortened the time to harvest. The growing capacity of young plants was enormous. Cultivar differences are, however, possible. Our latest trial with a big flowered cultivar ‘Amadeus’ indicates that bending twice may be reasonable when cultivation time has been planned to be some years, but the harvesting height is important for maximal flower production (Särkkä 2004).

5.2 Vase life and the effects of growing conditions and techniques (I-V)

The selected cultivation technique, traditional upright or shoot bending, and the cutting position on the mother stem had a minor effect on vase life of cut rose flowers from the

conventional cultivation point-of-view (IV, V). In conclusion of our experiments, the vase life of 'Mercedes' was increased in high global radiation, in year-round uninterrupted cultivation, in rest period treatment with old plants originating from cuttings, and when the flowering stems were short and had less leaves (I, II, IV). The vase life of 'Frisco' was in average good, although some variation was observed (I, III-V). Global radiation, supplemental lighting, temperature treatments during rest and forcing, and air humidity are discussed, as well as the quality of the flowering shoot in relation to the vase life (I-V). The main causes for the end of vase life were bent neck for 'Mercedes' and senescence for 'Frisco', suggesting water stress soon after harvest for 'Mercedes' and a late water stress and/or species-specific senescence for 'Frisco'.

The different monthly global radiation levels could explain some of the variation in the vase life (I, IV). For instance, in the year 1994 both the vase life was longest and global radiation level highest compared to years 1992 and 1993 (I), and the vase life usually increased towards the spring (IV). In the year 1993, when natural light conditions were equal for the young plants on own roots and the old grafted plants, the difference in vase life length between the plants was small for 'Frisco' while in 'Mercedes' it was bigger, indicating other factors to be involved (I). Natural light has a lower R:FR ratio than the HPS lamps have. ABA content in petals, which enhances senescence, was increased in higher than in lower R:FR ratio (Garello et al. 1995). The quality of light could influence the vase life length through e. g. plant hormones. Light quality also affects the behaviour of stomatal conductance (Blom-Zandstra et al. 1995). In orange light and in darkness after orange light the stomatal conductance was higher than in white or blue light.

The higher supplemental lighting did not increase the vase life of the first flush after the rest period (I, II). Fjeld et al. (1992) reported an increased vase life for 'Frisco' and a decreased vase life for 'Mercedes' with an increased PPF, but the light increment they used was higher than in our experiments. In high intensity lighting ($220 \mu\text{mol m}^{-2} \text{s}^{-1}$) the vase life of many cultivars was good (V). Continuous lighting (24 h) has resulted in shorter vase life in many rose cultivars, as compared with 16 and 18 hours (Mortensen and Fjeld 1998, Mortensen and Gislerød 1999). Vase life of 'Sacha' decreased dramatically in 24 h lighting, and with a duration of 20 h, as many as 30% of flowers had bent neck (V). Optimal light duration varies between the cultivars. Slootweg and Van Meeteren (1991) have reported incomplete stomatal closure of rose leaves grown under supplemental light, causing increased transpiration. Long daily duration of supplemental lighting seems to have a negative influence

on stomatal closure and, as a consequence, increased water loss from leaves (Mortensen and Gislerød 1999).

Lighting periods affected the vase life of 'Frisco' (III). Although the mean differences between various treatments were small, the treatments were different with respect to risks (hazards) of ceased ornamental value. These risks were higher in treatments with one lighting break in the night-time (one night break) than in treatments with two lighting breaks in the night (two night breaks) (III). In the most hazardous light treatments, 20 h d⁻¹ and 20/15 h d⁻¹, both with one night break, the risk for short vase life was 40% and 29%, respectively, higher than in the treatment with 20 h d⁻¹ and two night breaks. The last mentioned light treatment (20 h d⁻¹, two night breaks) yielded a considerably higher proportion of survived cuts between 9 and 13 days than the other treatments (III Figure 1). In the 20 h d⁻¹ treatments the different number of night-time breaks may have affected stomatal functioning in 'Frisco' leaves.

Variation of vase life hazards was also studied at plant level. Assessment of plant specific hazards provides us with new insights for understanding the flowers' behaviour in vase. Increased risk for short vase life seemed to be associated with high plant level variation within treatments (III Figure 2). This variation may reflect individual differences between plants, growing conditions around each plant, inter-plant competition, or plant specific characters including vitality and appearance. Nell and Rasmussen (1979) and Zieslin and Tsujita (1990) have argued that high light intensity is especially important after decapitation to ensure good bud sprouting and to avoid flower abortion. The decrease in the amount of light in the treatment with 20/15 h d⁻¹ and one night break, due to abbreviated light duration after flower initiation, may have contributed to the high plant level variation of this treatment. This decrease may have led to impaired competitiveness in assimilation in less vigour plants.

Estimation of plant specific hazards allowed identification of the frailest and the most reliable plants in the canopy (III). High frailty values explain increased risk for short vase life. In the 20/15 h d⁻¹ / one night break treatment, the edge plants in a bed were frailer than plants in the middle of the bed (Figure 3). Location of the plants had a minor influence in the other treatments. In the 20/15 h d⁻¹ / one night break treatment, the long dark period in the night and the plastic curtains used in the corridors to separate the treatments from each other over night may have affected the growing conditions of the edge plants differently from those in the middle. The air humidity in the plant canopy may have increased more during the long (9 h) than the short (4 and 2 h) dark periods (III). High air humidity has been shown to considerably decrease the vase life of some rose cultivars as a consequence of high transpiration in vase (Mortensen and Fjeld 1998, Mortensen and Gislerød 1999, Torre and

Fjeld 2001); this is usually expressed as dried leaves and bent neck. For ‘Frisco’, however, senescence was the most common determinant of the end of vase life, indicating either that ‘Frisco’ tolerates well higher humidity or that other factors were involved. Results of Mortensen and Gislerød (1999) showed that ‘Frisco’ is not a sensitive cultivar to high air humidity.

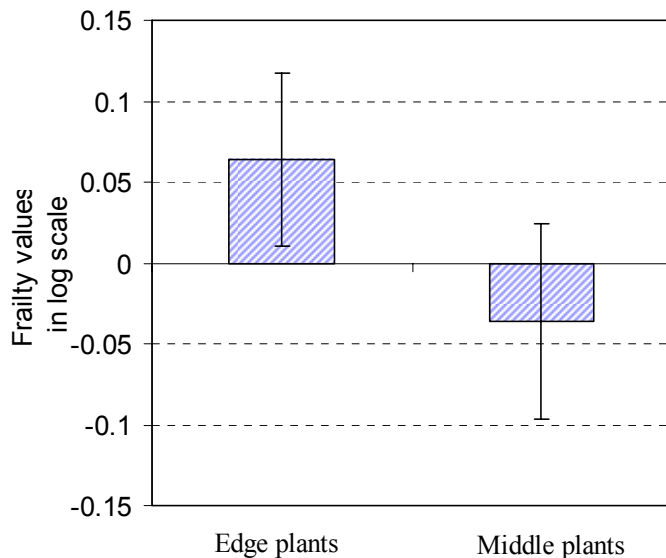


Figure 3. Mean frailty values \pm SE of ‘Frisco’ plants grown either in the middle (N=29) or in the edge (N=27) of the beds in the supplementary light treatment with a photoperiod of 20/15 hours and one night-time break, see section 5.2 for details.

Both plant type and plant age seemed to affect the vase life of ‘Mercedes’ and ‘Frisco’ after a rest period and pruning in the first flush (I). Air humidity did not seem to play an essential role for vase life length, at least not in two of the three experimental years (Figure 2). In high (90%) relative humidity the higher number of stomata which also were wider open than when grown in moderate (70%) air humidity caused high loss of water in plants, thus decreasing flower longevity (Torre et al. 2003).

Grafted plants seemed to be at a higher risk for ceased ornamental value than plants on own roots (cuttings) of both plant ages, except between the young plants of ‘Mercedes’ (I Figures 1 and 2). Hyttinen (1998) reported that, when grown with supplemental lighting, flowers from old cutting plants of ‘Mercedes’ had a longer vase life than those from grafted plants. Rootstocks should provide a good and strong root system which would be favourable in stressful conditions, such as after pruning in low light conditions, and produce high-quality flowers. In ‘Mercedes’, the grafted plants produced longer flowering stems than the cuttings

did, but the long stems had shorter vase life (I). This was not seen in ‘Frisco’. Hazendonk and Van der Wurff (1995) observed only small differences in the effects of various plant types on vase life from July to October.

Vase life was longer in older plants of both grafted plants and cuttings than in younger plants of the corresponding plant types (I Figures 1 and 2). The effect of plant age was greater than that of plant type. The yield per plant did not affect the vase life duration (I), suggesting that there were enough metabolites for flower formation. However, this did not explain the quality of the flowering shoot. In young ‘Mercedes’ plants, the rest period treatments seemed to influence the vase life considerably (I, II). In year-round uninterrupted cultivation, ‘Mercedes’ had less flowers with very short vase life than after the rest period treatments (II). Even the rest period length seemed to affect the flower longevity. The proportion of flowers with less than six days’ vase life was higher after six than after two weeks’ rest period (II Figure 2). The physiological stage of the whole plant changes during low temperature storage, including changes in hormone levels and carbohydrate balance (Crabbe and Barnola 1996). Such changes may affect the responses to forcing conditions, and even the genetic background of ‘Mercedes’ to winter rest may be involved. Such background is lacking for ‘Frisco’ (von Drathen, Kordes’ Söhne, personal communication). Temperature is known to determine the number of leaves on the stem (Marcelis-van Acker 1995) and in our studies the stem length, leaf area and fresh weight were affected (I, II). Therefore, even the inner structure of the flowering shoot may have been affected, resulting in a slower flow rate of water in stem and peduncle and the less lignified peduncle at harvest, which subsequently promoted bent neck in high transpiration.

We studied stem length and leaf area as possible explanations for the short vase life. In ‘Mercedes’, the necks of long stems tended to bend more easily than those of short stems, and increased leaf area also increased the sensitivity to bent neck (I Table 4). Long stems appeared in the young plants of both cultivars and in grafted plants in ‘Mercedes’ (I). This could explain some of the variation between the plant ages and plant types in ‘Mercedes’. Slootweg (1997) has reported a low hydraulic conductance for rose stems grown in supplemental light, and easily wilted flowers had lower water uptake ability than non-wilted flowers (Zieslin et al. 1978a). In our experiment the fresh weight of ‘Mercedes’ decreased towards the end of vase life, while in ‘Frisco’ it slightly increased through the period in vase, indicating a better water movement in vascular elements for transpiration in ‘Frisco’ than in ‘Mercedes’. The increase in the number of leaves caused an increased neck droop in ‘Samantha’ and ‘Cara Mia’ roses (Zieslin et al. 1978a). Removal of leaves is reported to

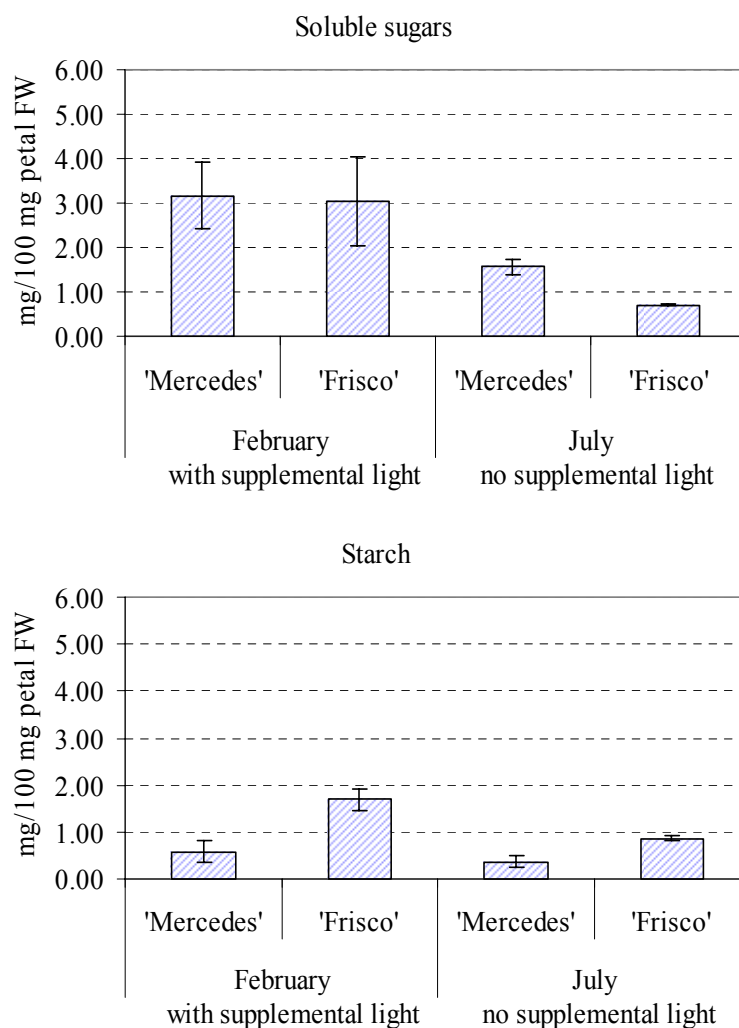
decrease water loss (Carpenter and Rasmussen 1974). High transpiration from leaves causes water stress when water flow through the stem is limited. Neither stem length nor leaf area affected the vase life of 'Frisco' (I). The leaves of 'Frisco' also have low cuticular transpiration (Urban et al. 2002).

Zieslin et al. (1978a) reported that the flower itself also transpires and its ability to absorb water from other parts of the shoot affects the sensitivity to bent neck. Carbohydrates accumulated in flowers increase their osmotic concentration and improve their water-absorbing capacity (Halevy and Mayak 1974). Van Doorn et al. (1991b) showed that opening of flowers in cut roses was related to their initial carbohydrate status. The starch and total carbohydrate (starch + soluble sugars) contents in petals of 'Frisco' were in winter significantly higher than in 'Mercedes' (Figure 4), indicating the better ability for 'Frisco' to ensure water movement to flower bud. This offers an explanation for the practical experience that flower buds of 'Frisco' can be harvested in winter in an earlier developmental stage than those of 'Mercedes' to ensure proper flower opening.

Auge et al. (1990) reported that leaves of 'Samantha' roses had higher osmotic potential (less negative) at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF than at 400-500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF. In our experiment, the carbohydrate content in the petals of 'Frisco' and 'Mercedes' roses was lower in natural light in summer than with supplemental lights in winter (Figure 4). This could be related to seasonal, cultivar specific variations in carbohydrate contents in genus *Rosa* (Brandon 1939). On the other hand, Marissen (2001) showed that in winter the carbohydrate content in petals of some rose cultivars grown in supplemental light was higher than in natural light conditions. The high accumulation rate of carbohydrates in petals may also be a sign of osmotic adjustment for competition of the available water in a plant. The water transport capacity of vessel walls of flower stems in vase was lower in stems grown in supplemental light than in stems grown in natural light (Slootweg 1997). After cutting, the petal sugar content in 'Mercedes' was increased as a response to transient shortage of water (Mayak et al. 2001). These sugars were transported from leaves. Because the vase life is usually better in summer than in winter, the carbohydrate content cannot be considered a good indicator of vase life, which was also concluded by Marissen (2001).

We did not use any preservatives in our studies, because they could have masked the effects of growing conditions and techniques on vase life. However, in conventional cultivation these substances should be used as they improve the vase life and give a possibility to grow even cultivars that seem to be sensitive for cultivation conditions, such as artificial lighting, and develop flowering shoots with low keeping quality. The short vase life

is usually associated with the high demand of water for transpiration and water transport problems which can, at least to a great extent, be overcome by using preservatives.



	Soluble sugars p-value	Starch p-value	Total p-value
Flush*cultivar	<0.01	<0.01	<0.01
Contrasts			
February: 'Mercedes' vs. 'Frisco'	ns	<0.01	<0.01
July: 'Mercedes' vs. 'Frisco'	<0.01	<0.01	ns
'Mercedes': February vs. July	<0.01	ns	<0.01
'Frisco': February vs. July	<0.01	<0.01	<0.01

Significance level $p < 0.05$, ns= non-significant

Figure 4. Mean \pm SD petal carbohydrate contents in 'Mercedes' and 'Frisco' in February, with supplementary lighting for 20 h d⁻¹ at 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, and in July, without supplemental lights. In table the p-values of F-tests and contrasts.

6 CONCLUSIONS

Supplemental light intensities should be sufficiently high in order to ensure high yield and good quality of cut roses. The PPF level should be higher in year-round uninterrupted cultivation than in cultivation with a rest period during the darkest natural light conditions. Optimal duration of supplemental lighting is dependent on the PPF level and the cultivar. Irradiation at $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF was insufficient for winter cultivation with a short rest period, and correspondingly, $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for uninterrupted winter cultivation. Irradiation at $220 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF for 20 h d^{-1} gave a high yield in a dense plantation through all seasons.

The duration of the rest period and the rate of temperature raise at forcing interacted on the yield and quality of flowers from young ‘Mercedes’ plants. The results indicated that physiological changes take place in the plants between the second and the sixth week in cold, and these changes contribute to varied responses to forcing temperature.

For growth and production it is important that a plant has plenty of leaves. In the traditional growing technique this may be a problem, because in pruning and harvest most of the leaves disappear. For good flower production, shoot bending instead of pruning is recommended in the traditional upright growing technique after a rest period. Benefits from bending of blind shoots after harvest in the traditional growing technique were, however, dependent on cultivar and harvesting height. The results from different shoot bending and harvesting height combinations indicate that plant architecture at the beginning of cultivation is important for good flower production. A crown should be established to the plant by a high bending and/or harvesting height. The high plant density intensified production.

Various growing techniques had a minor effect on the vase life. The vase life of the sensitive cultivar ‘Mercedes’ could be improved with different cultivation conditions in winter. Petal carbohydrate contents could not explain differences in the vase life between different seasons, indicating that effects of supplemental light may be different from those of natural light. The calculated plant specific hazards for short vase life might open new approaches to understanding and improving the vase life.

Based on the results of the trials presented in this study, the following cultivation regime is suggested for more effective year-round greenhouse production of cut roses:

- Supplemental light >100, up to approximately 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, daily duration 18-20 hours, when the outdoor global radiation <250-300 W m^{-2} (approx. 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF)
- HPS lamps installed close to the vegetation, to warm the plants and dry the air simultaneously (diminished risk for diseases)
- Pure carbon dioxide enrichment at in average 800 ppm, gas pipes close to (under) the plant rows
- Shading screens and high pressure fogging system to assist in the temperature and humidity control; screens also to prevent night-time energy loss in winter
- Pipes for warming air temperature, installed also at plant row level to ensure good air circulation and warming of the substrate
- Plant rows well above the ground to ensure good air circulation
- High plant density, about 15-20 plants per square metre, dependent on light level
- Shoot bending growing system, bending of primary shoot before the stem is too wooden
- Few bent shoots (1-3) simultaneously, dependent on cultivar's growth vigour and harvesting height
- High harvesting height at the beginning of cultivation (≥ 3 harvests) to form a crown
- Integrated pest control
- Preservatives after harvest

This regime facilitates intensified cut rose production requiring a relatively small greenhouse area for optimal utilization of resources, including investments, energy and labour.

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REFERENCES

- Acock, B. and Nichols, R. 1979. Effects of sucrose on water relations of cut, senescing, carnation flowers. *Annals of Botany* 44: 221-230.
- Agbaria, H., Zamski, E. and Zieslin, N. 2001. Effects of gibberellin on senescence of rose flower petals. *Acta Horticulturae* 547: 269-279.
- Aikin, W. J. and Hanan, J. J. 1975. Photosynthesis in the rose; effect of light intensity, water potential and leaf age. *Journal of the American Society for Horticultural Science* 100: 551-553.
- Anon. 2004. Puutarhayritysrekisteri 2003. (Official statistics of Finland on horticulture in 2003). Helsinki: Information Centre of Ministry of Agriculture and Forestry. (in Finnish and Swedish).
- Apelbaum, A. and Yang, S. F. 1981. Biosynthesis of stress ethylene induced by water deficit. *Plant Physiology* 68: 594-596.
- Araki, T. 2001. Transition from vegetative to reproductive phase. *Current Opinion in Plant Biology* 4: 63-68.
- Armitage, A. M. and Tsujita, M. J. 1979. Supplemental lighting and nitrogen nutrition effects on yield and quality of 'Forever yours' roses. *Canadian Journal of Plant Science* 59: 343-350.
- Asaoka, M. and Heins, R. D. 1982. Influence of supplemental light and preforcing storage treatments on the forcing of 'Red Garnette' rose as a pot plant. *Journal of the American Society for Horticultural Science* 107: 548-552.
- Asen, S., Norris, K. H., Stewart, R. N. and Semeniuk, P. 1971. Effect of pH and concentration of the anthocyanin-flavanol co-pigment complex on the colour of 'Better Times' roses. *Journal of the American Society for Horticultural Science* 96: 770-773.
- Auge, R. M., Stodola, A. J. W. and Pennell, B. D. 1990. Osmotic and turgor adjustment in *Rosa* foliage drought-stressed under varying irradiance. *Journal of the American Society for Horticultural Science* 115: 661-667.
- Bathey, N. H. and Tooke, F. 2002. Molecular control and variation in the floral transition. *Current Opinion in Plant Biology* 5: 62-68.
- Bernier, G., Havelange, A., Houssa, C., Petitjean, A. and Lejeune, P. 1993. Physiological signals that induce flowering. *The Plant Cell* 5: 1147-1155.
- Bleeksma, H. C. and Van Doorn, W. G. 2003. Embolism in rose stems as a result of vascular occlusion by bacteria. *Postharvest Biology & Technology* 29: 335-341.
- Blom-Zandstra, M., Sander Pot, C., Maas, F. M. and Schapendonk, A. H. C. M. 1995. Effects of different light treatments on the nocturnal transpiration and dynamics of stomatal closure of two rose cultivars. *Scientia Horticulturae* 61: 251-262.
- Booker, J., Chatfield, S. and Leyser, O. 2003. Auxin acts in xylem-associated or medullary cells to mediate apical dominance. *The Plant Cell* 15: 495-507.
- Borochoy, A., Mayak, S. and Halevy, A. H. 1976. Combined effects of abscisic acid and sucrose on growth and senescence of rose flowers. *Physiologia Plantarum* 36: 221-224.
- Brandon, D. 1939. Seasonal variations of starch content in the genus *Rosa*, and their relation to propagation by stem cuttings. *The Journal of Pomology and Horticultural Science* 17: 233-253.
- Bredmose, N. 1993. Effects of year-round supplementary lighting on shoot development, flowering and quality of two glasshouse rose cultivars. *Scientia Horticulturae* 54: 69-85.
- Bredmose, N. 1998. Growth, flowering, and postharvest performance of single-stemmed rose (*Rosa hybrida* L.) plants in response to light quantum integral and plant population density. *Journal of the American Society for Horticultural Science* 123: 569-576.

- Bredmose, N. 2000. Light quantum integral and plant density affects bud and shoot growth, fresh biomass production and bloom quality in single-stemmed roses. *Acta Horticulturae* 515: 105-109.
- Bredmose, N., Hansen, J. and Nielsen, J. 2001. Topographic influences on rose bud and shoot growth and flower development are determined by endogenous axillary bud factors. *Acta Horticulturae* 547: 177-183.
- Brown, W. W. and Ormrod, D. P. 1980. Soil temperature effects on greenhouse roses in relation to air temperature and nutrition. *Journal of the American Society for Horticultural Science* 105: 57-59.
- Byrne, T. G. and Doss, R. P. 1981. Development time of 'Cara Mia' rose shoots as influenced by pruning position and parent shoot diameter. *Journal of the American Society for Horticultural Science* 106: 98-100.
- Carpenter, W. J. and Anderson, G. A. 1972. High intensity supplementary lighting increases yields of greenhouse roses. *Journal of the American Society for Horticultural Science* 97: 135-138.
- Carpenter, W. J. and Rasmussen, H. P. 1974. The role of flower and leaves in cut flower water uptake. *Scientia Horticulturae* 2: 293-298.
- Chimonidou-Pavlidou, D. 1996. Effect of water stress at different stages of rose development. *Acta Horticulturae* 424: 45-51.
- Chimonidou-Pavlidou, D. 1999. Irrigation and sensitive stages of rose development. *Acta Horticulturae* 481: 393-401.
- Cline, M. G. 1991. Apical dominance. *The Botanical Review* 57: 318-358.
- Cockshull, K. E. 1975. Roses II: The effects of supplementary light on winter bloom production. *Journal of Horticultural Science* 50: 193-206.
- Cockshull, K. E. and Horridge, J. S. 1977. Apical dominance and flower initiation in the rose. *Journal of Horticultural Science* 52: 421-427.
- Crabbe, J. and Barnola, P. 1996. A new conceptual approach to bud dormancy in woody plants. In: Lang, G. A. (ed.). *Plant dormancy: physiology, biochemistry and molecular biology*. Wallingford, CAB International. p. 83-113. ISBN 0-85198-978-0.
- Dambre, P., Blindeman, L. and Van Labeke, M. C. 2000. Effect of planting density and harvesting method on rose flower production. *Acta Horticulturae* 513: 129-135.
- Darlington, A. B. and Dixon, M. A. 1991. The hydraulic architecture of roses (*Rosa hybrida*). *Canadian Journal of Botany* 69: 702-710.
- De Vries D. P., De Kuiper, E. P. M and Dubois, L. A. M. 1981. Anatomy of flower differentiation and abortion, in relation to the growth and development of hybrid tea-rose seedlings. *Scientia Horticulturae* 14: 377-385.
- De Vries, D. P. and Dubois, L. A. M. 1978. On the transmission of the yellow flower colour from *Rosa foetida* to recurrent flowering hybrid tea-roses. *Euphytica* 27: 205-210.
- De Vries D. P. and Dubois, L. A. M. 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 Horticulturae* 21: 375-379.
- De Vries D. P. and Dubois, L. A. M. 1984. Scion-rootstock relationship in hybrid tea cut roses on *Rosa canina* 'Inermis'. *Netherlands Journal of Agricultural Science* 32: 3-7.
- De Vries D. P. and Dubois, L. A. M. 1992. Variation in the shoot production of 'Sonia' cut rose plants, originating from grafting scions of different nodal positions. *Gartenbauwissenschaft* 57: 64-68.
- De Vries, D. P., Smeets, L. and Dubois, L. A. M. 1982. Interaction of temperature and light on growth and development of hybrid tea-rose seedlings, with reference to breeding for low-energy requirements. *Scientia Horticulturae* 17: 377-382.

- Dieleman, J. A., Verstappen, F. W. A. and Kuiper, D. 1998a. Bud break and cytokinin concentration in bleeding sap of *Rosa hybrida* as affected by the genotype of the rootstock. *Journal of Plant Physiology* 152: 468-472.
- Dieleman, J. A., Verstappen, F. W. A. and Kuiper, D. 1998b. Root temperature effects on growth and bud break of *Rosa hybrida* in relation to cytokinin concentrations in xylem sap. *Scientia Horticulturae* 76: 183-192.
- Dieleman, J. A., Verstappen, F. W. A., Nicander, B., Kuiper, D., Tillberg, E. and Tromp, J. 1997. Cytokinin in *Rosa hybrida* in relation to bud break. *Physiologia Plantarum* 99: 456-464.
- Drüge, U. 2000. Influence of pre-harvest nitrogen supply on post-harvest behaviour of ornamentals: importance of carbohydrate status, photosynthesis and plant hormones. *Gartenbauwissenschaft* 65: 53-64.
- Durkin, D. 1979. Some characteristics of water flow through isolated rose segments. *Journal of American Society of Horticultural Science* 104: 777-783.
- Evans, R. Y. and Reid, M. S. 1988. Changes in carbohydrates and osmotic potential during rhythmic expansion of rose petals. *Journal of the American Society for Horticultural Science* 113: 884-888.
- Faust, M. 1989. *Physiology of temperate zone fruit trees*. USA, John Wiley & Sons. 338 p.
- Fjeld, T., Gislerød, H. R., Revhaug, V. and Mortensen, L. M. 1994. Keeping quality of cut roses as affected by high supplementary irradiation. *Scientia Horticulturae* 57: 157-164.
- Fjeld, T., Mortensen, L. M., Gislerød, H. R. and Revhaug, V. 1992. Winter production of cut roses: effects on keeping quality. *Norwegian Journal of Agricultural Sciences* 6: 275-278.
- Fuchs, H. W. M. 1986. Harvesting, pruning, and root reactions of roses. *Acta Horticulturae* 189: 109-115.
- Garello, G., Menard, C., Dansereau, B. and Le Page-Degivry, M. T. 1995. The influence of light quality on rose flower senescence: involvement of abscisic acid. *Plant Growth Regulation* 16: 135-139.
- Gocal, G. F. W., Pharis, R. P., Yeung, E. C. and Pearce, D. 1991. Changes after decapitation in concentrations of indole-3-acetic acid and abscisic acid in the larger axillary bud of *Phaseolus vulgaris* L. cv Tender Green. *Plant Physiology* 95: 344-350.
- Gonzalez-Real, M. M. and Baille, A. 2000. Changes in leaf photosynthetic parameters with leaf position and nitrogen content within a rose plant canopy. *Plant, Cell & Environment* 23: 351-363.
- Goszczyńska, D., Ttzhaki, H., Boročov, A. and Halevy, A. H. 1990a. Effects of sugar on physical and compositional properties of rose petal membranes. *Scientia Horticulturae* 43: 313-320.
- Goszczyńska, D. M., Zieslin, N., Mor, Y. and Halevy, A. H. 1990b. Improvement of postharvest keeping quality of 'Mercedes' roses by gibberellin. *Plant Growth Regulation* 9: 293-303.
- Grange, R. I. and Hand, D. W. 1987. A review of the effects of atmospheric humidity on the growth of horticultural crops. *Journal of Horticultural Science* 62: 125-134.
- Halevy, A. H. 1972a. Phytohormones in flowering regulation of self-inductive plants. *Proc. 18th International Horticultural Congress in Tel-Aviv* 5: 187-198.
- Halevy, A. H. 1972b. Water stress and timing of irrigation. *HortScience* 7: 113-114.
- Halevy, A. H. 1987. Assimilate allocation and flower development. In: Atherton, J. G. (ed.). *Manipulation of flowering*. London, Butterworths. p. 363-378.
- Halevy, A. H. and Mayak, S. 1974. Improvement of cut flower quality opening and longevity by pre-shipment treatments. *Acta Horticulturae* 43: 335-347.
- Halevy, A. H. and Mayak, S. 1979. Senescence and postharvest physiology of cut flowers, part 1. *Horticultural Reviews* 1: 204-236.

- Halevy, A. H. and Mayak, S. 1981. Senescence and postharvest physiology of cut flowers, part 2. Horticultural Reviews 3: 59-143.
- Halevy, A., Torre, S., Borochoy, A., Porat, R., Philosoph-Hadas, S., Meir, S. and Friedman, H. 2001. Calcium in regulation of postharvest life of flowers. Acta Horticulturae 543: 345-351.
- Halevy, A. H. and Zieslin, N. 1969. The development and causes of petal blackening and malformation of Baccara rose flowers. Acta Horticulturae 15: 149-156.
- Hazendonk, A. and Van der Wurff, T. 1995. Houdbaarheid van rozen op stek en op onderstam. Rapport 211. Proefstation voor de Bloemisterij in Nederland, Aalsmeer. 24 p.
- Hendriks, L. and Ludolph, D. 1987. Assimilationsbelichtung von Rosen. Deutcher Gartenbau 49: 2893-2895.
- Ho, L. C. and Nichols, R. 1977. Translocation of ¹⁴C-sucrose in relation to changes in carbohydrate content in rose corollas cut at different stages of development. Annals of Botany 41: 227-242.
- Hutchings, M. J. and De Kroon, H. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. Advances in Ecological Research 25: 159-238.
- Hyttinen, T. 1998. Tekovalon laadun, taimityypin ja kuivuusstressin vaikutukset leikkoruusun maljakkokestävyYTEEN ja sadon laatuun. M.Sc. Thesis, University of Helsinki. Finland. 75 p. + 9 app.
- Ichimura, K., Musaka, Y., Fujiwara, T., Kohata, K., Goto, R. and Suto, K. 1999. Possible roles of methyl glucoside and *myo*-inositol in the opening of cut roses flowers. Annals of Botany 83: 551-557.
- Jarvis, P. G. and Morison, J. I. L. 1981. The control of transpiration and photosynthesis by stomata. In: Jarvis, P. G. and Mansfield, T. A. (eds.). Stomatal Physiology. Society for Experimental Biology. Seminar Series 8. Cambridge University Press. p. 247-279.
- Jensen, H. E. K. 1979. Hvilettemperatures virkning på udbytte og ekonomi i væksthusroser, *Rosa* L. Tidsskrift for planteavl 83: 432-440.
- Jiao, J., Gilmour, M. J., Tsujita, M. J. and Grodzinski, B. 1989. Photosynthesis and carbon partitioning in Samantha roses. Canadian Journal of Plant Science 69: 577-584.
- Jiao, J. and Grodzinski, B. 1998. Environmental influences on photosynthesis and carbon export in greenhouse roses during development of the flowering shoot. Journal of the American Society for Horticultural Science 123: 1081-1088.
- Jiao, J., Tsujita, M. J. and Grodzinski, B. 1991. Optimizing aerial environments for greenhouse rose production utilizing whole-plant net CO₂ exchange rate. Canadian Journal of Plant Science 71: 253-261.
- Kaltaler, R. E. L. and Steponkus, P. L. 1974. Uptake and metabolism of sucrose in cut roses. Journal of the American Society for Horticultural Science 99: 490-493.
- Kapchina-Toteva, V., Somleva, M. and Van Telgen, H. J. 2002. Anticytokinin effect on apical dominance release in *in vitro* cultured *Rosa hybrida* L. Biologia Plantarum 45: 183-188.
- Kapchina-Toteva, V., Van Telgen, H. J. and Yakimova E. 2000. Role of phenylurea cytokinin CPPU in apical dominance release in *in vitro* cultured *Rosa hybrida* L. Journal of Plant Growth Regulation 19: 232-237.
- Khayat, E. and Zieslin, N. 1982. Environmental factors involved in the regulation of sprouting of basal buds in rose plants. Journal of Experimental Botany 33: 1286-1292.
- Khayat, E. and Zieslin, N. 1986. Effect of different night temperature regimes on the assimilation, transport and metabolism of carbon in rose plants. Physiologia Plantarum 67: 608-613.
- Khayat, E. and Zieslin, N. 1987. Effect of night temperature on the activity of sucrose phosphate synthase, acid invertase, and sucrose synthase in source and sink tissues of *Rosa hybrida* cv Golden Times. Plant Physiology 84: 447-449.

- Khayat, E. and Zieslin, N. 1989. Translocation of ^{14}C , carbohydrate content and activity of the enzymes of sucrose metabolism in rose petals at different night temperatures *Physiologia Plantarum* 76: 581-585.
- Khosh-Khui, M. and George, R. A. T. 1977. Responses of glasshouse roses to light conditions. *Scientia Horticulturae* 6: 223-235.
- Kool, M. T. N. 1996. System development of glasshouse roses. Dissertation. Wageningen Agricultural University. The Netherlands. 143 p.
- Kool, M. T. N. 1997. Importance of plant architecture and plant density for rose crop performance. *Journal of Horticultural Science* 72: 195-203.
- Kool, M. T. N., De Graaf, R. and Rou-Haest, C. H. M. 1997. Rose flower production as related to plant architecture and carbohydrate content: effect of harvesting method and plant type. *Journal of Horticultural Science* 72: 623-633.
- Kool, M. T. N. and Lenssen, E. F. A. 1997. Basal-shoot formation in young rose plants: Effects of bending practices and plant density. *Journal of Horticultural Science* 72: 635-644.
- Kool, M. T. N. and Van de Pol., P. A. 1993. Controlling the plant development of *Rosa hybrida* 'Motrea'. *Scientia Horticulturae* 53: 239-248.
- Kool, M. T. N. and Van de Pol., P. A. 1996. Long-term flower production of a rose crop. I. The influence of planting system and rootstock clone. *Journal of Horticultural Science* 71: 435-443.
- Kuiper, D., Ribot, S., Van Reenen, H. S. and Marissen, N. 1995. The effect of sucrose on the flower bud opening of 'Madelon' cut roses. *Scientia Horticulturae* 60: 325-336.
- Lieth, J. H. and Kim, S. H. 2001. Effects of shoot-bending in relation to root media on cut-flower production. *Acta Horticulturae* 547: 303-310.
- Lieth, J. H. and Pasian, C. C. 1990. A model for net photosynthesis of rose leaves as a function of photosynthetically active radiation, leaf temperature, and leaf age. *Journal of the American Society for Horticultural Science* 115: 486-491.
- Lieth, J. H. and Pasian, C. C. 1991. A simulation model for the growth and development of flowering rose shoots. *Scientia Horticulturae* 46: 109-128.
- Lineberger, R. D. and Steponkus, P. L. 1976. Identification and localization of vascular occlusions in cut roses. *Journal of the American Society for Horticultural Science* 101: 246-250.
- Maas, F. M. and Bakx, E. J. 1995. Effects of light on growth and flowering of *Rosa hybrida* 'Mercedes'. *Journal of the American Society for Horticultural Science* 120: 571-576.
- Maas, F. M., Hofman-Eijer, L. B. and Hulsteijn, K. 1995. Flower morphogenesis in *Rosa hybrida* 'Mercedes' as studied by cryo-scanning electron and light microscopy. Effects of light and shoot position on a branch. *Annals of Botany* 75:199-205.
- Marcelis-van Acker. C. A. M. 1993. Morphological study of the formation and development of basal shoots in roses. *Scientia Horticulturae* 54:143-152.
- Marcelis-van Acker. C. A. M. 1994. Effect of assimilate supply on development and growth potential of axillary buds in roses. *Annals of Botany* 73: 415-420.
- Marcelis-van Acker. C. A. M. 1995. Effect of temperature on development and growth potential of axillary buds in roses. *Scientia Horticulturae* 63: 241-250.
- Marissen, N. 1991. Osmotic potential and carbohydrate contents in the corolla of the rose cv. Madelon. *Acta Horticulturae* 298: 145-152.
- Marissen, N. 2001. Effects of pre-harvest light intensity and temperature on carbohydrate levels and vase life of cut roses. *Acta Horticulturae* 543: 331-336.
- Marissen, N. and La Brijn, L. 1995. Source-sink relations in cut roses during vase life. *Acta Horticulturae* 405: 81-88.
- Martin, G. C. Apical dominance. *HortScience* 22: 824-833.

- Mayak, S. 1987. Senescence of cut flowers. *HortScience* 22: 863-865.
- Mayak, S. and Halevy, A. H. 1970. Cytokinin activity in rose petals and its relation to senescence. *Plant Physiology* 46: 497-499.
- Mayak, S. and Halevy, A. H. 1972. Interrelationships of ethylene and abscisic acid in the control of rose petal senescence. *Plant Physiology* 50: 341-346.
- Mayak, S. and Halevy, A. H. 1974. The action of kinetin in improving the water balance and delaying senescence processes of cut rose flowers. *Physiologia Plantarum* 32: 330-336.
- Mayak, S., Halevy, A. H., Sagie, S., Bar-Yoseph, A. and Bravdo, B. 1974. The water balance of cut rose flowers. *Physiologia Plantarum* 31: 15-22.
- Mayak, S., Meir, S. and Ben-Sade, H. 2001. The effect of transient water stress on sugar metabolism and development of cut flowers. *Acta Horticulturae* 543: 191-197.
- Menard, C. and Dansereau, B. 1996. Impact of growth conditions on yield and quality of cut roses. *Acta Horticulturae* 424: 103-105.
- Menard, C., Dansereau, B., Garello, G. and Le Page-Degivry, M Th. 1996. Influence of nitrogen supply on ABA levels and flower senescence in *Rosa hybrida* cv Royalty. *Acta Horticulturae* 424: 151-155.
- Moe, R. 1971. Factors affecting flower abortion and malformation in roses. *Physiologia Plantarum* 24: 291-300.
- Moe, R. 1972. Effect of daylength, light intensity, and temperature on growth and flowering in roses. *Journal of the American Society for Horticultural Science* 97: 796-800.
- Moe, R. 1974. Ny metode for oppval av roser på egen rot. *Gartner Yrket* 64: 828-832.
- Moe, R. 1975. The effect of growing temperature on keeping quality of cut roses. *Acta Horticulturae* 41: 77-92.
- Moe, R. and Kristoffersen, T. 1969. The effect of temperature and light on growth and flowering of rosa 'Baccara' in greenhouses. *Acta Horticulturae* 14: 157-166.
- Mor, Y. and Halevy, A. H. 1979. Translocation of ¹⁴C assimilates in roses. I. The effect of the age of the shoot and the location of the source leaf. *Physiologia Plantarum* 45: 177-182.
- Mor, Y. and Halevy, A. H. 1980. Promotion of sink activity of developing rose shoots by light. *Plant Physiology* 66: 990-995.
- Mor, Y. and Halevy, A. H. 1984. Dual effect of light on flowering and sprouting of rose shoots. *Physiologia Plantarum* 61: 119-124.
- Mor, Y., Halevy, A. H. and Porath, D. 1980. Characterization of the light reaction in promoting the mobilizing ability of rose shoot tips. *Plant Physiology* 66: 996-1000.
- Mortensen, L. M. 1987. Review: CO₂ enrichment in greenhouses. Crop responses. *Scientia Horticulturae* 33: 1-25.
- Mortensen, L. M. 1995. Diurnal carbon dioxide exchange rates of greenhouse roses under artificial light as compared with daylight conditions in summer. *Acta Agriculturae Scandinavica, Section B, Soil and Plant Science* 45: 148-152.
- Mortensen, L. M. 2001. Greenhouse climate and keeping quality of roses. *Acta Horticulturae* 543: 199-205.
- Mortensen, L. M. and Fjeld, T. 1998. Effects of air humidity, lighting period and lamp type on growth and vase life of roses. *Scientia Horticulturae* 73: 229-237.
- Mortensen, L. M. and Gislerød, H. R. 1994. Effects of summer lighting, plant density, and pruning method on yield and quality of greenhouse roses. *Gartenbauwissenschaft* 59: 275-279.
- Mortensen, L. M. and Gislerød, H. R. 1996. The effect of root temperature on growth, flowering, and vase life of greenhouse roses grown at different air temperatures and CO₂ concentrations. *Gartenbauwissenschaft* 61: 211-214.
- Mortensen, L. M. and Gislerød, H. R. 1997. Effect of air humidity and air movement on the growth and keeping quality of roses. *Gartenbauwissenschaft* 62: 273-277.

- Mortensen, L. M. and Gislerød, H. R. 1999. Influence of air humidity and lighting period on growth, vase life and water relations of 14 rose cultivars. *Scientia Horticulturae* 82: 289-298.
- Mortensen, L. M. and Gislerød, H. R. 2000. Effect of air humidity on growth, keeping quality, water relations, and nutrient content of cut roses. *Gartenbauwissenschaft* 65: 40-44.
- Mortensen, L. M., Gislerød, H. R. and Mikkelsen, H. 1992a. Effects of different levels of supplementary lighting on the year-round yield of cut roses. *Gartenbauwissenschaft* 57: 198-202.
- Mortensen, L. M., Gislerød, H. R. and Mikkelsen, H. 1992b. Maximizing the yield of greenhouse roses with respect to artificial lighting. *Norwegian Journal of Agricultural Sciences* 6: 27-34.
- Mullins, M. G. 1965. Lateral shoot growth in horizontal apple stem. *Annals of Botany* 29: 73-78.
- Nell, T. A. and Rasmussen, H. P. 1979. Flower development and blindness in roses: An SEM study. *Journal of the American Society for Horticultural Science* 104: 18-20.
- Ohkawa, K. and Suematsu, M. 1999. Arching cultivation techniques for growing cut-roses. *Acta Horticulturae* 482: 47-52.
- Outa, P. and Särkkä, L. 2004. Hiilidioksidilannoituksen vaikutus leikkoruusun viljelyn kannattavuuteen – tilamallitarkastelu. *Suomen Maataloustieteellisen Seuran tiedote* 20: 142.
- Parups, E. V. and Molnar, J. M. 1972. Histochemical study of xylem blockage in cut roses. *Journal of the American Society for Horticultural Science* 97: 532-534.
- Parups, E. V. and Voisey, P. W. 1976. Lignin content and resistance to bending of pedicel in greenhouse-grown roses. *Journal of Horticultural Science* 51: 253-259.
- Pien, H., Bobelyn, E., Lemeur, R. and Van Labeke, M. C. 2001. Optimising LAI in bent rose shoots. *Acta Horticulturae* 547: 319-327.
- Pien, H., Lemeur, R. and Van Labeke, M. C. 2000. Influence of PAR flux and temperature on the flower bud abortion of rose (*Rosa hybrida* cv. Frisco) and the carbon balance of the shoot. *Acta Horticulturae* 515: 119-127.
- Put, H. M. C. and Clerckx, A. C. M. 1988. The infiltration ability of micro-organisms *Bacillus*, *Fusarium*, *Cluyveromyces* and *Pseudomonas* spp. into xylem vessels of *Gerbera* cv. 'Fleur' and *Rosa* cv. 'Sonia' cut flowers: a scanning electron microscope study. *Journal of Applied Bacteriology* 64: 515-530.
- Put, H. M. C. and Van der Meyden, T. 1988. Infiltration of *Pseudomonas putida* cells, strain 48, into xylem vessels of cut *Rosa* cv. Sonia. *Journal of Applied Bacteriology* 64: 197-208.
- Rasmussen, H. P. and Carpenter, W. J. 1974. Changes in the vascular morphology of cut rose stems: a scanning microscope study. *Journal of the American Society for Horticultural Science* 99: 454-459.
- Rathmell, J. K. 1969. Cutting and handling flowers. In: Mastalerz, J. W. and Langhans, R. W. (eds.). *Roses*. Pennsylvania Flower Growers, NY Flower Growers Ass. Inc. p. 136-143.
- Ripatti, S. and Palmgren, J. 2000. Estimation of multivariate frailty models using penalized partial likelihood. *Biometrics* 56: 1016-1022.
- Ristimäki, P. 1988. Leikkoruusun viljely. Helsinki, Kauppapuutarhaliitto r.y. 64 p.
- Sallanon, H., Tort, M. and Coudret, A. 1993. The ultrastructure of micropropagated and greenhouse rose plant stomata. *Plant, Cell, Tissue and Organ Culture* 32: 227-233.
- Shimizu-Sato, S. and Mori, H. 2001. Control of outgrowth and dormancy in axillary buds. *Plant Physiology* 127: 1405-1423.
- Shin, H. K., Lieth, J. H. and Kim, S. H. 2001. Effects of temperature on leaf area and flower size in rose. *Acta Horticulturae* 547: 185-191.

- Slootweg, G. 1997. Post-harvest water uptake and stem conductance of cut roses cv. Sonia grown with supplemental lighting. *Acta Horticulturae* 418: 107-110.
- Slootweg, G. and Van Meeteren, U. 1991. Transpiration and stomatal conductance of roses cv. Sonia grown with supplemental lighting. *Acta Horticulturae* 298: 119-125.
- Stafstrom, J. P. 1988. Dormancy in pea axillary buds. *Planta* 205: 547-552.
- Särkkä, L. 2004. Taittaminen eduksi Amadeus-ruusulle. *Puutarha & kauppa* 8 (27/28): 17-19.
- Särkkä, L., Kaunisto, T. and Rauniomaa, E. 2001. Leikkoruusun viljelyn tehostaminen – tiheäviljelytuotanto ja sen talous (Intensified cut rose production – dense production and its costs). Jokioinen, MTT:n julkaisuja. Sarja A 103. ISBN 951-729-641-X. 50 p. + 6 app.
- Tamas, I. A. 1995. Hormonal regulation of apical dominance. In: Davies, P. J. (ed.). *Plant hormones*. 2nd edition. The Netherlands, Kluwer Academic Publishers. ISBN 0-7923-2984-8. p. 572-597.
- Tillge, L., Jensen, H. E. and Bredmose, N. 1974. Plantetaethedens og grundstammens indflydelse på udbytte og kvalitet hos tre sorter af væksthuseroser. *Statens Forsøgsvirksomhed i Plantekultur, Danmark. Beretning 1134*: 53-66.
- Torre, S., Borochoy, A. and Halevy, A. H. 1999. Calcium regulation of senescence in rose petals. *Physiologia Plantarum* 107: 214-219.
- Torre, S. and Fjeld, T. 2001. Water loss and postharvest characteristics of cut roses grown at high or moderate relative humidity. *Scientia Horticulturae* 89: 217-226.
- Torre, S., Fjeld, T., Gislørød, H. R. and Moe, R. 2003. Leaf anatomy and stomatal morphology of greenhouse roses grown at moderate or high air humidity. *Journal of the American Society for Horticultural Science* 128: 598-602.
- Tsujita, M. J. and Dutton, R. G. 1983. Root zone temperature effects on greenhouse roses in relation to supplementary lighting at reduced air temperature. *HortScience* 18: 874-876.
- Turner, L. B. 1993. The effect of water stress on floral characters, pollination and seed set in white clover (*Trifolium repens* L.). *Journal of Experimental Botany* 44:1155-1160.
- Urban, L., Bearez, P., Barthelemy, L. and Six, S. 2002. Effect of elevated CO₂ on leaf water relations, water balance and senescence of cut roses. *Journal of Plant Physiology* 159: 717-723.
- Van den Berg, G. A. 1987. Influence of temperature on bud break, shoot growth, flower bud atrophy and winter production of glasshouse roses. Dissertation. Wageningen Agricultural University. The Netherlands. 170 p.
- Van Doorn, W. G. 1989. Role of physiological processes, microorganisms, and air embolism in vascular blockage of cut rose flowers. *Acta Horticulturae* 261: 27-34.
- Van Doorn, W. G. 1990. Aspiration of air at the cut surface of rose stems and its effect on the uptake of water. *Journal of Plant Physiology* 137: 160-164.
- Van Doorn, W. G. 1997. Water relations of cut flowers. *Horticultural Reviews* 18:1-85.
- Van Doorn, W. G. 2001. Role of soluble carbohydrates in flower senescence: a survey. *Acta Horticulturae* 543: 179-183.
- Van Doorn, W. G., Buidis, H. C. E. M. and De Witte, Y. 1986. Effect of exogenous bacterial concentrations on water relations of cut rose flowers. II. Bacteria in the vase solution. *Acta Horticulturae* 181: 463-465.
- Van Doorn, W. G., De Stigter, H. C. M., De Witte, Y. and Boekestein, A. 1991a. Microorganisms at the cut surface and xylem vessels of rose stems: a scanning electron microscope study. *Journal of Applied Bacteriology* 70: 34-39.
- Van Doorn, W. G., Groenewegen, G., Van de Pol, P. A. and Berkholst, C. E. M. 1991b. Effects of carbohydrate and water status on flower opening of cut Madelon roses. *Postharvest Biology and Technology* 1: 47-57.
- Van Doorn, W. G., Schurer, K. and De Witte Y. 1989. Role of endogenous bacteria in vascular blockage of cut rose. *Journal of Plant Physiology* 134: 375-381.

- Van Labeke, M. C., Dambre, P. and Bodson, M. 2000. Effects of supplementary lighting and bending technique on growth, flowering and carbohydrate status of *Rosa hybrida* 'Frisco'. *Acta Horticulturae* 515: 245-255.
- Van Labeke, M. C., Dambre, P., Bodson, M. and Pien, H. 2001. Developmental changes in carbohydrate content in young rose shoots (*Rosa hybrida* 'Frisco'). *Acta Horticultiurae* 547: 193-201.
- Van Meeteren, U., Van Gelder, H. and Van De Peppel A. C. 1995. Aspects of carbohydrate balance during floret opening in Freesia. *Acta Horticulturae* 405: 117-122.
- Van Nocker, S. 2001. The molecular biology of flowering. *Horticultural Reviews* 27: 1-39.
- Veen, H. 1983. Silver thiosulphate: an experimental tool in plant science. *Scientia Horticulturae* 20: 211-224.
- Vergauwen, R., Van Den Ende, W. and Van Laere, A. 2000. The role of fructan in flowering of *Campanula rapunculoides*. *Journal of experimental Botany* 51: 1261-1266.
- Vogelezang, J. V. M., De Hoog Jr., J. and Marissen, N. 2000. Effects of diurnal temperature strategies on carbohydrate content and flower quality of greenhouse roses. *Acta Horticulturae* 515: 111-118.
- Warner, R. M. and Erwin, J. E. 2002. Estimation of total canopy photosynthetic capacity of roses grown under two canopy management systems. *Acta Horticulturae* 580: 89-93.
- Woltering, E. J. 1987. The effects of leakage of substances from mechanically wounded rose stems on bacterial growth and flower quality. *Scientia Horticulturae* 33: 129-136.
- Zieslin, N. 1981. Plant management of greenhouse roses. Flower cutting procedure. *Scientia Horticulturae* 15: 179-186.
- Zieslin, N. 1989. Postharvest control of vase life and senescence of rose flowers. *Acta Horticulturae* 261: 257-264.
- Zieslin, N., Haaze, H. and Halevy, A. H. 1976. Components of axillary bud inhibition in rose plants. II. The effect of bud position on degree of inhibition. *Botanical Gazette* 137: 297-300.
- Zieslin, N. and Halevy, A. H. 1975. Flower bud atrophy in 'Baccara' roses. II. The effect of environmental factors. *Scientia Horticulturae* 3: 383-391.
- Zieslin, N. and Halevy, A. H. 1976. Flower bud atrophy in 'Baccara' roses. VI. The effect of environmental factors in gibberellin activity and ethylene production in flowering and non-flowering shoots. *Physiologia Plantarum* 37: 331-335.
- Zieslin, N. and Halevy, A. H. 1978. Components of axillary bud inhibition in rose plants. III. Effect of stem orientation and changes of bud position on the stem by budding. *Botanical Gazette* 139: 60-63.
- Zieslin, N., Hurwitz, A. and Halevy, A. H. 1975. Flower production and the accumulation and distribution of carbohydrates in different parts of Baccara rose plants as influenced by various pruning and pinching treatments. *Journal of Horticultural Science* 50: 339-348.
- Zieslin, N. and Khayat, E. 1982. Environmental factors involved in the regulation of sprouting of basal buds in rose plants. *Journal of Experimental Botany* 33: 1286-1292.
- Zieslin, N. and Khayat, E. 1983. Involvement of cytokinin, ABA and endogenous inhibitors in sprouting of basal buds in rose plants. *Plant Growth Regulation* 1: 279-288.
- Zieslin, N., Kohl Jr., H. C., Kofranek, A. M. and Halevy, A. H. 1978a. Changes in the water status of cut roses and its relationship to bent-neck phenomenon. *Journal of the American Society for Horticultural Science* 103: 176-179.
- Zieslin, N. and Moe, R. 1985. *Rosa*. In: Halevy, A. H. (ed.). *Handbook of flowering*, vol. 4. Boca Raton, CRC Press. p. 214-225.
- Zieslin, N. and Mor. Y. 1981. Plant management of greenhouse roses. Formation of renewal canes. *Scientia Horticulturae* 15:67-75.
- Zieslin, N. and Mor, Y. 1990. Light on roses. A review. *Scientia Horticulturae* 43: 1-14.

- Zieslin, N., Spiegelstein, H. and Halevy, A. H. 1978b. Components of axillary bud inhibition in rose plants. IV. Inhibitory activity of plant extracts. *Botanical Gazette* 139: 64-68.
- Zieslin, N., Starkman, F. and Zamski, E. 1989. Growth of rose flower peduncles and effects of applied plant growth regulators. *Plant Growth Regulation* 8: 65-76.
- Zieslin, N. and Tsujita, M. J. 1990. Response of miniature roses to supplementary illumination. 2. Plant Development and cold storage. *Scientia Horticulturae* 42: 123-131.

SELOSTUS

Leikkoruusun sadon määrä, laatu ja maljakkokestävyys ympärivuotisessa kasvihuoneviljelyssä

Leikkoruusu on Suomen kaupallisesti tärkein leikkokukka. Vuonna 2003 sen kokonaisviljelypinta-ala oli 32 hehtaaria, mikä on noin 75% leikkokukka-alasta, kun sipulikukkien osuus puuttuu laskelmasta. Puolta ruusun pinta-alasta viljeltiin keskeytymättä ympäri vuoden käyttämällä tekovaloja joko vain talvikaudella tai koko vuoden aina kun luonnonvalon määrä alitti minimitason. Öisin pidettiin useimmiten muutaman tunnin valotustauko. Laadullisesti ja määrällisesti hyvän sadon tuottaminen ei ole loka-helmikuun välisenä aikana mahdollista ilman tekovaloja.

Tutkimuksen alkaessa vuonna 1992 tekovalojen käyttömäärät olivat nykyistä alhaisemmat ja lyhytkestoinen lepojakso oli keskitalvella yleinen. Korkean energian hinnan myötä kiinnostus lepotaukoon on jälleen kasvanut. Tutkimuksen tarkoituksena oli saada käytäntöä palvelevaa tietoa. Tavoitteena oli parantaa leikkoruusun sadon määrää, laatua ja maljakkokestävyyttä ympärivuotisessa viljelyssä tutkimalla eri viljelyolosuhteiden, viljelymenetelmien, lajikkeiden ja kasvien ominaisuuksien vaikutuksia näihin tekijöihin. Tutkimuksen pääpaino oli talvikauden viljelyssä.

Tutkimuksen ruusulajikkeet olivat Mercedes, Frisco, Sacha, Dream, Indian Femma ja Lorena. Tutkimuksen alussa valtalajikkeena oli Mercedes, jonka talviviljelyssä oli mm. heikkoon maljakkokestävyyteen liittyviä ongelmia. Frisco-lajikkeella oli talviviljelyssä saatu hyviä käytännön kokemuksia.

Säteilymääränä $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (yhteyttämislle aktiivisen aallonpituusalueen säteilyä) osoittautui liian alhaiseksi takaamaan hyvän sadon määrän ja laadun keskitalven neljän viikon lepojakson jälkeisessä satojaksossa. Kun kasveja kasvatettiin koko talven, $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF osoittautui vastaavasti liian alhaiseksi säteilymääräksi. Sadon määrä ja laatu olivat korkeat koko vuoden, kun säteilymäärä oli $220 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF 20 h d^{-1} ja lamput paloivat päivällä aina kun luonnonvalon määrä alitti minimitason.

Nuorilla Mercedes-ruusuilla tutkittiin lepotilan pituuden ja hyötölämpötilan nostonopeuden vaikutusta satoon. Kuuden viikon lepotilan jälkeen hidaskasvun nosto alhaisessa valotasossa ($65 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF 20 h d^{-1}) tuotti laadullisesti heikoimman sadon. Samanpituisten lepotilan jälkeen nopea lämpötilan nosto ja vastaavasti lyhyen (2 viikkoa) lepotilan jälkeen hidaskasvun nosto antoivat hyvän satomäärän, kun valoa annettiin 100

$\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF 20 h d^{-1} . Tämä viittaa siihen, että kasvin fysiologisessa tilassa tapahtuu muutoksia lepojakson pidentyessä.

Lepotilan jälkeen kasvit perinteisesti leikataan, jolloin ne jäävät yleensä lähes lehdettömiksi. Leikkaamista verrattiin versojen taittamiseen hyödyn alussa. Taitettaessa kasveihin jäi yhteyttävää lehtipinta-alaa, jonka oletettiin parantavan kasvuun lähtöä ja sadon muodostusta. Sekä Mercedes- että Frisco-lajikkeen ensimmäinen hyödyn jälkeinen sato oli määrältään parempi kuin leikatuista kasveista. Versojen taittaminen pidentäi myös kukkaversoja.

Perinteisessä viljelymenetelmässä sokeat (kukattomat) versot leikataan satojakson lopussa. Sadonkorjuun ja sokeiden versojen leikkaamisen seurauksena kasveista poistuu satojakson aikana suurin osa lehtimassasta. Sokeiden versojen leikkaamista verrattiin versojen taittamiseen, jolloin lehtipinta-alaa jäi kasviin enemmän. Sokeiden versojen taittaminen paransi Mercedes-lajikkeen sadon määrää ja laatua, mutta ei Frisco-lajikkeen satomäärää. Mercedes ei ole yhtä voimakaskasvuinen lajike kuin Frisco. Sadonkorjuukorkeus on perinteisessä viljelymenetelmässä tärkeä, koska kasviin jäävien lehtien lukumäärä sadonkorjuun jälkeen riitti takaamaan hyvän seuraavan sadon määrän Frisco-lajikkeella.

Versojen taittamistekniikka viljelymenetelmänä yleistyi 1990-luvulla. Siinä versoja taitetaan viljelyn alusta asti ja kasviritvit on nostettu maanpinnan yläpuolelle, jotta ilma kiertää kasvustossa paremmin ja työergonomia paranee. Tässä tutkimuksessa kyseistä viljelytekniikkaa kehitettiin tutkimalla versojen taittamiskorkeuden ja sadonkorjuukorkeuden merkitystä sadon määrään ja laatuun taajassa taimitiheydessä. Tulosten perusteella kasvien tarvitsema taitettujen versojen lukumäärä ei ole suuri, vain yhdestä kolmeen lajikkeen rehevyydestä riippuen. Viljelyn alussa taimeen pitää rakentaa kruunu eli leikata kukat muutaman satokerran ajan riittävän korkealta. Versojen taittaminen viljelyn alussa sekä sadonkorjuu korkealta edistivät uusien, hyvien pohjaversojen muodostumista, jotka taas ovat hyvän satomäärän edellytys. Korjuukorkeuden valinnalla, suurella taimitiheydellä ja runsaalla tekovalon määrällä satomäärät olivat hyvin suuria vuoden kestävässä viljelyssä. Tämä oli myös taloudellisesti kannattavaa.

Viljelytekniikalla oli vähäinen vaikutus kun taas viljelyolosuhteilla oli selvä vaikutus kukkien maljakkokestävyys. Mercedes-lajikkeen kukkien niskat olivat alttiita nuokahtamaan, kun taas Frisco-lajikkeen kukat vanhenivat maljakossa. Niska-alue voi kärsiä veden puutteesta ja nuokahtaa, kun lehdet haihduttavat enemmän kuin kukkavarsi pystyy kuljettamaan vettä maljakosta. Mercedes-ruusujen maljakkokestävyys oli parempi ympärivuotisessa keskeytymättömässä viljelyssä kuin keskitalvella pidetyn muutaman viikon

pituisen lepojaksen jälkeen. Tekovalon määrällä oli vähäisempi merkitys kestävyteen kuin luonnonvalon määrällä, mikä saattaa myös liittyä valon laatuun. Valotusaika ja valotuksen yökatkosten määrä vaikuttivat kukkien maljakkokestävyysiin mm. kasvien välisen vaihtelun kautta. Kasvikohtaisten riskien estimointi voi lisätä uusien tulkintojen mahdollisuuksia maljakkokestävyuden vaihteluiden syistä. Kasvien iällä ja lisäysmateriaalilla oli vaikutusta maljakkokestoon. Nuorien ja perusrunkoisten kasvien kukkien riski heikommalle maljakkokestolle oli suurempi kuin vanhemmilla ja omajuurisilla kasveilla. Tähän oli osittain syynä pidemmät kukkaversot ja suurempi lehtipinta-ala, jotka lisäsivät Mercedes-lajikkeen riskiä lyhyeen maljakkokestoon; Frisco-lajikkeella vastaavaa ei ilmennyt.

Liukoisten hiilihydraattien ja tärkkelyksen pitoisuudet olivat talvella tekovalossa kasvaneiden ruusujen terälehdissä korkeammat kuin kesällä luonnonvalossa kasvaneiden kukkien terälehdissä. Korkeata sokeripitoisuutta on pidetty edellytyksenä hyvälle maljakkokestolle. Koska maljakkokestävyys on yleensä parempi kesällä kuin talvella, terälehtien sokeripitoisuuksia ei voida pitää hyvänä kestävyiden mittana verrattaessa eri valo-olosuhteissa kasvaneita kasveja toisiinsa. Valon laadulla saattaa olla vaikutusta terälehtien sokeripitoisuuksiin. Korkeata sokeripitoisuutta on pidetty myös edellytyksenä hyvälle kukkien avautumiselle maljakossa. Frisco-lajikkeen terälehtien sokeripitoisuudet olivat talvella korkeammat kuin Mercedes-lajikkeen, mikä selittäisi käytännön kokemuksen, jossa Friscon kukat voidaan kerätä nuppisempina kuin Mercedeksen.

Tämän tutkimuksen perusteella luotiin suositukset tehostettuun leikkoruusun tuotantoon, jossa käytetään mm. taittamistekniikkaa, runsaasti tekovaloa ja taajaa taimitiheyttä. Näin tehostetulla viljelymenetelmällä ei tarvita suuria kasvihuonepinta-aloja. Siten mm. tarvittavat investoinnit, energian käyttö ja työvoiman tarve kohdistuvat suhteellisen pienelle pinta-alalle.