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Long Term Production of Rose Flowers in the Greenhouse under different Cooling Methods: II. Responses of the Flower Bud

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Summary

The objective of the study was to determine the responses of rose flower buds to aerial environmental conditions. Since environmental conditions may affect various plant organs differently, it was important to determine the contribution of these organs to bud development. Rose plants were grown in a greenhouse in southern Israel for three years under different cooling systems throughout the summer. Evaporative cooling with a wet pad was the most effective system for preventing a decline in plant water potential, mainly during midsummer. Water potential of the flower bud was higher than that of the stem, regardless of season and treatment. The season of flower development had the most marked effect on flower bud fresh weight. Night cooling during spring and early summer was the only treatment that provided a slight increase in flower bud weight and in its relative weight out of the total flower weight. The increase in flower bud diameter was nearly linear with time, regardless of season, while stem elongation was logarithmic and then leveled off. The development of both organs extended much longer in the winter than in the summer, resulting in longer stems and larger buds. A mechanistic model was developed in order to determine the relative contribution of various organs to the bud. The flower stem and leaves contributed 50 to 67 % of the final bud dry weight, while the rest was comprised of the bud sepals, small bent branches and structural branches. The contribution by the bud sepals, was markedly enhanced, by night cooling. Fresh weight of the flower bud was highly correlated with flower leaf area and weight (including stem weight) but not with stem length.

Zusammenfassung

Langzeitkultur von Gewächshausrosen bei unterschiedlichen Kühlmethoden: II. Reaktionen der Blütenknospen. Gegenstand der Untersuchung war, die Reaktionen von Rosenblütenknospen auf atmosphärische Bedingungen im Gewächshaus zu ermitteln. Da diese Umweltbedingungen vermutlich unterschiedlich stark auf die einzelnen Pflanzenorgane einwirken, war es wichtig den Beitrag, den diese Organe zur Knospenbildung leisten, zu untersuchen. Hierfür wurden im Süden Israels drei Jahre lang Rosen in Gewächshäusern kultiviert, die während des Sommers mittels unterschiedlicher Methoden gekühlt wurden. Verdunstungskühlung mit Kühlmatten war die wirkungsvollste Methode, um vor allem im Hochsommer einen Rückgang des Pflanzenwasserpotentials zu verhindern. Das Wasserpotential der Blütenknospen war unabhängig von Jahreszeit und Behandlung höher als das der Stängel. Die Jahreszeit, in der sich die Blüten entwickelten, hatte den deutlichsten Effekt auf das Blütenknospenfrischgewicht. Nächtliche Kühlung im Frühjahr und Frühsommer war die einzige Behandlung, die zu einem geringfügigen Anstieg des Blütenknospengewichts und des relativen Gewichts im Verhältnis zum Blütengesamtgewicht führte. Der Anstieg des Blütenknospendurchmessers war unabhängig von der Jahreszeit annähernd linear zur Entwicklungsdauer, während das Längenwachstum des Stängels einen logarithmischen Verlauf nahm und dann abflachte. Die Entwicklung beider Organe dauerte im Winter sehr viel länger als im Sommer und führte zu längeren Stängeln und größeren Knospen. Es wurde ein Modell entwickelt, um den relativen Beitrag der einzelnen Organe zur Knospe zu bestimmen. Der Blütenstängel und die Blätter erbringen 50 bis 67 % des endgültigen Knospentrockengewichts, während der Rest aus den Kelchblättern, kleinen Nebentrieben und dem Pflanzengrundgerüst entsteht. Der Beitrag der Kelchblätter wird durch Nachtkühlung deutlich erhöht. Das Frischgewicht der Blütenknospen war stark mit der Blütenblattfläche und dem Gewicht (einschließlich Stängelgewicht) jedoch nicht mit der Stängellänge korreliert.

Key words. aerial environment – assimilate transport – CO_2 fixation by leaves and sepals – rose plant organs – plant water potential.

Introduction

Rose flowers grown in the greenhouse during the summer under warm climatic conditions are known to be of low quality, although the number of flowers may not be reduced (FERNANDEZ et al. 1994; VOGELEZANG et al. 2000; DAMKE and BHATTACHARJEE 2000). Flower stems become thin and short, but more critical is the marked decrease in flower buds, and in some cases, the more pale petals. It was shown earlier (PLAUT et al. 1979) that evaporative cooling by wet pad (WP) reduced the rate of flower formation of several rose cultivars, but improved their quality. URBAN et al. (1992) showed that at high temperatures high-pressure mist had a very minimal effect on flower stem elongation and on flower bud diameter, unless the greenhouse was enriched with CO_2. We showed in a previous study that WP had no significant beneficial effect on flower stem length and weight during the first half of the summer (DAYAN et al. 2005). Both stem length and weight were, however, improved during late summer; this was mainly attributed to the development of fewer flowers (DAYAN et al. 2005). MORTESEN (2001) found that adding humidity in the greenhouse increased the total number of rose flowers, but there was no significant rise in flower dry weight.

While stem elongation requires the supply of assimilates, it is nevertheless a direct result of turgor pressure. Turgor pressure decreases if plant water potential drops as a result of high temperature and low humidity. The development of the flower bud is more complex, as it largely depends on assimilates imported from outside the bud. The level of assimilates transported to the bud was considered an important factor in its development (KHAYAT and ZIESLIN 1986, 1989; HALEVY 1987). Carbohydrate content of the petals was found to be lower when leaves were removed, suggesting their role in petal development (MARISSEN et al. 1995). Leaves of the flowering shoot turn into source leaves shortly after the flower bud becomes visible (MOR and HALEVY 1979). While the upper leaves export assimilates mainly to the flower bud, the lower leaves allocate more assimilates basipetally (MOR and HALEVY 1979; JIAO et al. 1989).

The development of the flower bud under different aerial environmental conditions will thus depend on their effects on the bud itself, on leaf photosynthesis and on transport of assimilates to the bud. While our previous paper reported on the response of flower production to environmental control systems (DAYAN et al. 2005), the present study is concentrated in the response of the flower bud and its resources. The relationships between the whole flower size and flower bud development had thus to be studied. The effects of the environmental conditions in the greenhouse on leaf photosynthesis, transport of assimilate to the bud and direct supply of dry matter by the bud itself may be variable. A main objective of the study was thus to detect the contribution of the different sources to the development of the flowering bud, and a mechanistic model was used for this purpose.

Materials and Methods

The greenhouse and its control systems are described in our previous paper (DAYAN et al. 2005). Four chambers were used for the present study: natural ventilation (NV), to be considered as the control; NV and shading; forced ventilation and wet pad (WP) and NV and night cooling by an air conditioner. No alterations were conducted in the environmental control systems during the 3 years of the experiment (1996 to 1999), and conditions were nearly identical throughout the years, as outlined (DAYAN et al. 2005). Details on planting and growing methods, irrigation and fertilization, horticultural techniques, picking and sorting of flowers are outlined in our previous paper (DAYAN et al. 2005).

Flowers were sorted and grouped according to stem length (40–50, 50–60, 60–70 and >70 cm) for determination of flower quality. Bud final weight, height and diameter were determined on samples of 20 flowers taken weekly from each group and treatment. The rate of bud development was determined on 40 buds per treatment. This was conducted several times throughout the year by measuring the changes in bud diameter twice a week starting at an early developmental stage, when bud could be measured, up to harvest stage.

The relative contribution of dry mass (DM) by different plant organs was determined according to a mechanistic model. This was based on the assumption that the following four sources contributed to the bud DM: S+L = the flower stem and leaves on this stem; B = the flower bud itself; C = the plant canopy, which refers to bent branches that did not bear any flowers to be picked; and T = structural branches at the plant base. One or more of these organs were removed or wrapped with aluminum foil (to avoid light interception) shortly after being visible (Table 1). The structural branches (T) were neither removed nor wrapped. Seven replicates were conducted for each removal treatment and environmental control. Bud dry weight of all treatments was determined at the regular harvest

Table 1. List of manipulations performed on rose plants and symbols for flower bud and stem+leaves[1] dry mass as a result of these manipulations. MB = dry mass of bud; M(S+L) = dry mass of stem+leaves. Dry mass contribute by the following organs: ($_{s+l}$ = stem+leaves; $_b$ = bud; $_c$ = canopy[2]; $_t$ = structural branches at plant base).

Treatment No.	Description of treatments	Mass of bud or stem + leaves[1]
1	Control, no treatment performed	$MB_{s+l, b, c, t}$
2	Leaves removed and stem wrapped[3]	$MB_{b, c, t}$
3	Bud wrapped[3]	$MB_{s+l, c, t}$
4	As control, but canopy[2] removed	$MB_{s+l, b, t}$
5	As 4, but stem + leaves mass determined	$M(S+L)_{s+l, b, t}$
6	Leaves removed, stem and bud wrapped and canopy removed	MB_t
7	As 1, but stem + leaves mass determined	$M(S+L)_{s+l, b, c, t}$

[1]Stem+leaves refer to the flower stem and the leaves on this stem.
[2]Canopy refers to all bent branches, which did not bear flowers to be harvested.
[3]Stem or/and buds were wrapped and fully covered with aluminium foil, so that photosynthetic activity was negligible.

stage. The relative contribution of these four sources to bud development was calculated according to the following equations. (Symbols are presented in Table 1).

1. $S+L = (MB_{s+l, b, c, t} - MB_{b, c, t}) / MB_{s+l, b, c, t}$

2. $B = (MB_{s+l, b, c, t} - MB_{s+l, c, t}) / MB_{s+l, b, c, t}$

3. $C = [(MB_{s+l, b, c, t} - MB_{s+l, b, t}) / MB_{s+l, b, c, t}] - [(M(S+L)_{s+l, b, c, t} - M(S+L)_{s+l, b, t}) / M(S+L)_{s+l, b, c, t}]$

4. $T = MB_{s+l, b, c, t} - \{(MB_{s+l, b, c, t} - MB_{b, c, t}) / MB_{s+l, b, c, t}\} - \{(MB_{s+l, b, c, t} - MB_{s+l, c, t}) / MB_{s+l, b, c, t}\} - \{[(MB_{s+l, b, c, t} - MB_{s+l, b, t}) / MB_{s+l, b, c, t}] - [(M(S+L)_{s+l, b, c, t} - M(S+L)_{s+l, b, t}) / M(S+L)_{s+l, b, c, t}]\}$

The calculations are based on the following assumptions:

1. The source of dry matter transported to the bud was photosynthetic activity of the specific organ.
2. The relative contribution of the various organs to the flower bud was not affected by removal of other organs.
3. Transport of stored materials out of the wrapped flower stem was relatively negligible.
4. There was no transport of dry mass out of the flower bud.
5. The canopy was only a source contributing to the bud and to the stem and leaves.

When removed, the contribution by the stem and leaves was accordingly reduced.

Water potentials (Ψ) of rose flowers and buds were determined with a pressure chamber during midday. Flowers contained stems 15-cm long with the youngest leaves and the buds. The buds were cut at the bases of their peduncles, and no leaves were included.

Rates of CO_2 fixation of leaves and of bud sepals were determined several times during the seasons using a LiCor 6200 apparatus. CO_2 fixation rate of sepals was

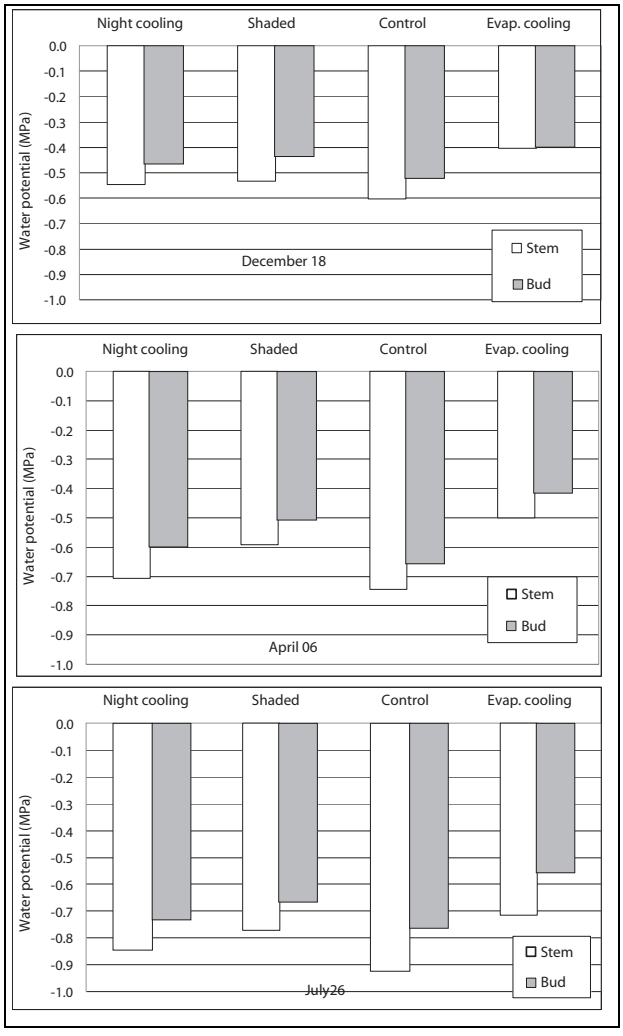


Fig. 1. Water potential of rose flowers (including stems, leaves and buds) and flower buds (determined separately) at different seasons.

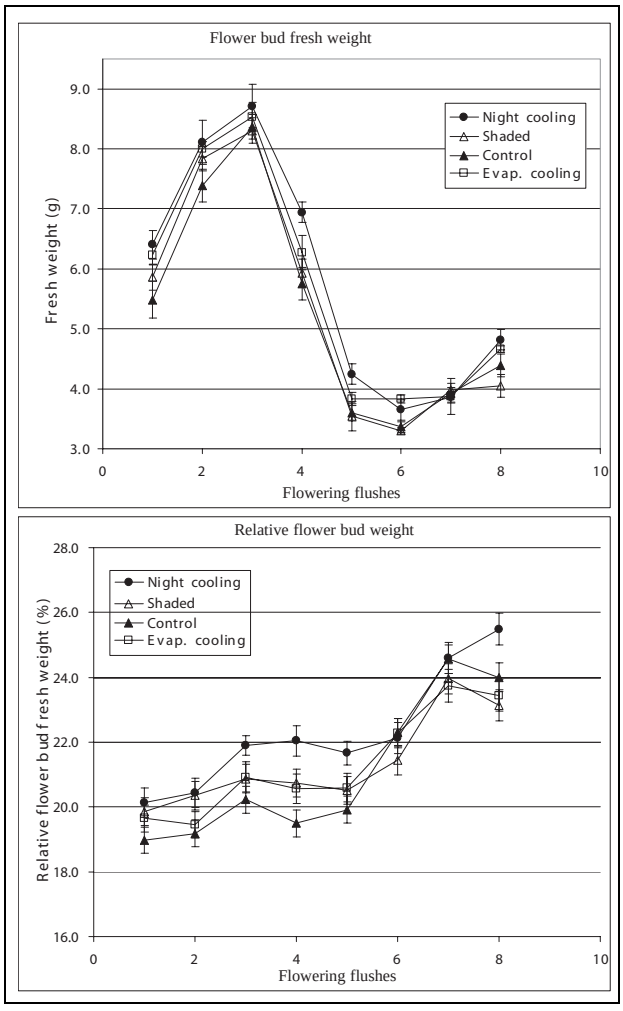


Fig. 2. (A) Effect of environmental control systems on average fresh weight of flower buds as determined in eight flowering flushes throughout most of the year. The flushes were conducted as following: **1**: 12/12–23/01; **2**: 31/01–15/03; **3**: 23/03–01/05; **4**: 09/05–10/06; **5**: 18/06–15/07; **6**: 21/07–20/08; **7**: 25/08–29/09; **8**: 02/10–06/11. (B) Relative weight of the flower bud out of the whole flower throughout the eight flowering flushes.

measured after being detached and spread in the chamber of the LiCor apparatus.

Results

There were slight effects of the various systems on greenhouse climate (DAYAN et al. 2000). Wet pad reduced air temperature at the height of the flower buds by 2.0 to 3.0 °C during June through September and increased RH by 10 to 15 %. The effect was smaller during the rest of the year. Shading reduced air temperature by 1.0 °C and had hardly any effect on RH. Leaf and flower bud temperatures were also reduced with WP by approximately 2.0 °C in midsummer, 1.0 to 1.5 °C during early and late summer, and 0.5 °C in October. Shading reduced these temperatures only during midsummer, by 0.6 to 1.0 °C. Night cooling reduced air, leaf and flower bud temperatures during the night by 3.0 °C.

Fig. 1 shows, that the lowest Ψ values were found in midsummer in the control chamber. Water potentials of stems with leaves were always lower than those of buds, probably because water capacity of the bud was higher than that of leaves and rates of water losses were lower.

Whereas all cooling treatments raised Ψ of stems and buds, Cooling with WP was the most effective system. It raised the stem Ψ during mid-summer by 0.20 to 0.25 MPa as compared to the control. Shading raised it only by 0.1 to 0.15 MPa and night cooling had nearly no significant effect (Fig. 1).

The factor, which had the most striking effect on flower bud fresh weight, was the season of their development (Fig. 2A) and their maximal weight was during March to May, reaching nearly 9.0 g per bud. The different environmental control systems had a limited effect on bud fresh weight throughout the year (Fig. 2A). A significant increase in bud weight was found only under night cooling during spring and early summer (April–May). The effect of night cooling on bud size as compared with that of the whole flower can be seen

Table 2. Relative contribution (in %) of four rose organs (or group of organs) to the final dry weight of the flower bud, during three different seasons and under different environmental control systems. The relative contributions of these sources were calculated according to the mechanistic model (see Materials and Methods).

Month	Plant organ(s)	Environmental control system			
		Control	Evap. cooling	Shaded	Night cooling
Jan.	S+L	56.15	57.17	52.05	n.o.
	B	18.20	17.22	15.95	
	C	14.06	13.97	17.00	
	T	11.59	11.64	15.00	
	Total	100.00	100.00	100.00	
June	S+L	50.44	60.86	49.66	50.71
	C	17.23	10.05	15.16	22.61
	B	16.85	18.33	16.23	15.08
	T	15.48	10.76	18.95	11.60
	Total	100.00	100.00	100.00	100.00
Sep–Oct	S+L	56.85	65.09	50.18	51.28
	B	19.85	17.79	15.20	27.89
	C	12.55	8.44	16.67	10.72
	T	10.75	8.68	17.95	10.10
	Total	100.00	100.00	100.00	100.00

S+L: Stem and Leaves; B: Bud; C: Canopy; T: Structural branches; n.o.: not operating

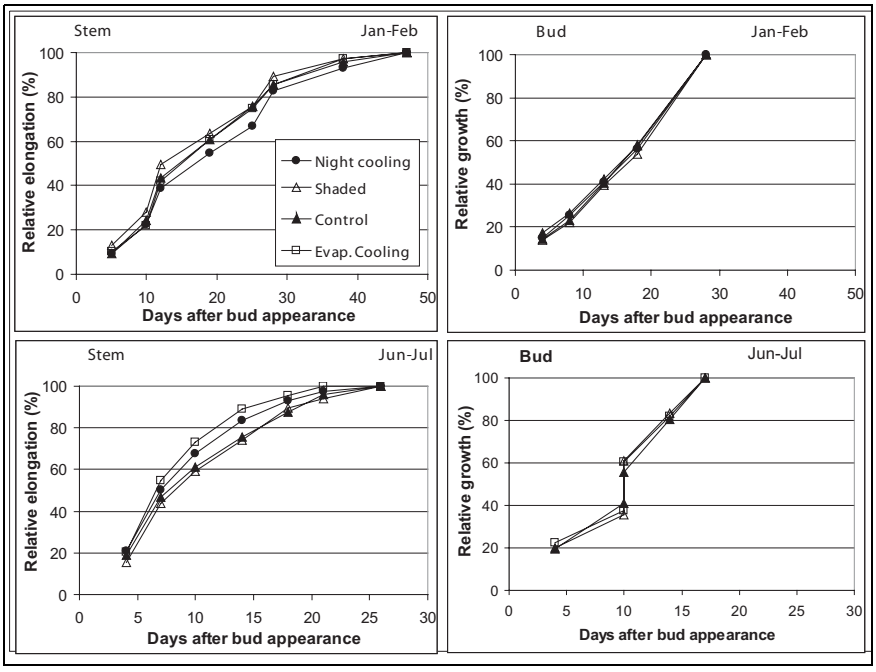


Fig. 3. Relative rate of stem elongation and bud growth in diameter during midwinter and midsummer.

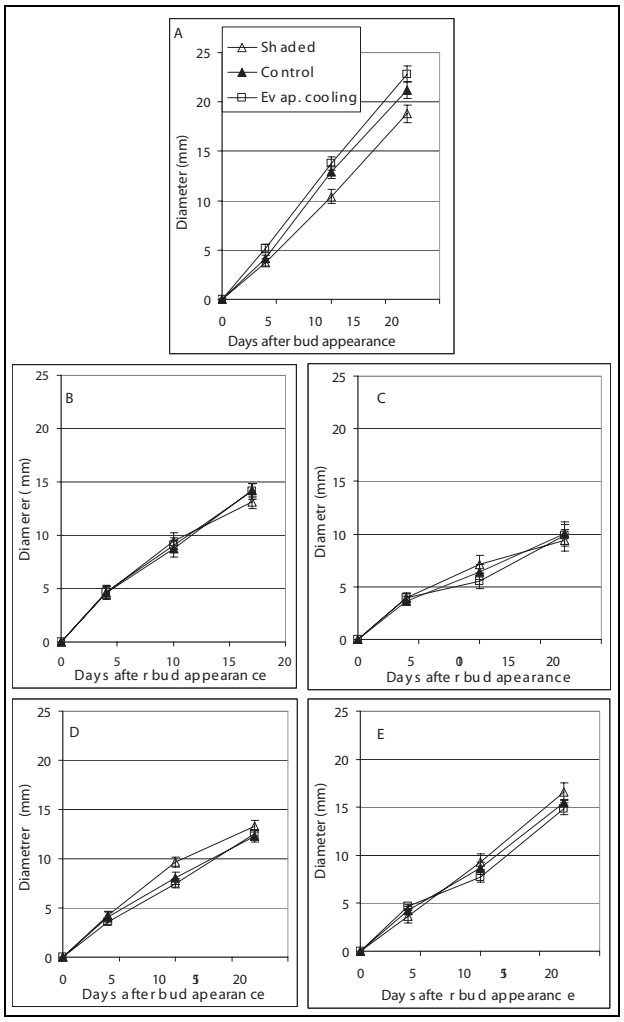


Fig. 4. The effect of various manipulative treatments of the rose plant (removal or wrapping of specific organs with aluminium foil) on growth of the flower bud in diameter under different environmental conditions. The following manipulations were conducted at the 5th flowering flush during the second half of June and early July. (**A**): Control, flower remained intact and no part of the plant was covered. (**B**): Leaves of the flower removed and stem was wrapped. (**C**): As in (**B**), but bud was also covered and canopy removed. (**D**): Only bud wrapped. (**E**): Canopy removed.

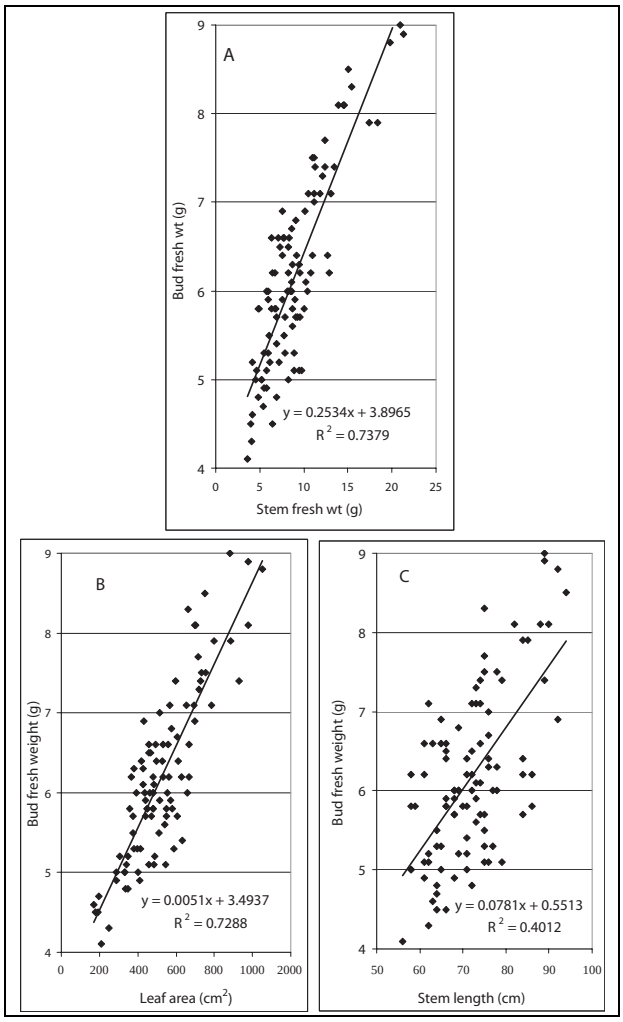


Fig. 5. Relationships between vegetative parameters of the flower and bud fresh weight: (**A**) fresh weight of flower stem including leaves; (**B**) leaf area of the flower stem; (**C**) stem length. The linear correlations were calculated on 100 flowers, which were picked at the 3rd flowering flush (for exact timing see Fig. 2).

when the fresh weight of buds is calculated as percentage of the whole flower (Fig. 2B). The percentage of bud weight was significantly higher in this treatment during flushes 3 to 5 and 8, namely during spring, early summer and autumn, suggesting that night cooling had a direct effect on the flower bud. The differences between treatments in relative flower bud weight were relatively small and mostly insignificant, but the lowest relative flower bud weight was found in the control treatment. The longer the flower stem the larger was the flower bud (not presented).

The large differences in flower bud size throughout the season (Fig. 2A) were further studied by comparing their relative growth rate compared to that of the stem (Fig. 3). Stem length and bud diameter were measured once every 3 to 5 days from the day of bud appearance up to harvest. In order to compare between stem and bud growth, their relative growth was calculated as percentage of the final length or diameter. Elongation of the stem was nearly logarithmic at early stages and with time it turned to be asymptotic, while bud growth was nearly linear throughout the entire period. The stem reached its final length after 21 days in the summer, when it was 50 to 60 cm long (slightly but insignificantly affected by treatments). In the winter, it also reached this size after 21 days but continued to elongate up to 38 days. The final bud diameter was 18 to 22 mm after 17 days in the summer (also not affected significantly by treatments), and only 13 to17 mm after the same time in the winter, but continued to grow up to 28 days, when its diameter was 23 to 28 mm (Fig. 3).

The contribution of different organs of the rose plant to the flower bud was evaluated using the mechanistic model. The initial rates of bud diameter increase (0 to 5 days), were not yet affected by the manipula-

Table 3. Rates of photosynthetic CO_2 fixation and water vapour conductance of rose leaves and sepals at different months throughout the last year.

Date	Organ		Environmental control system			
			Control	Evap. cooling	Shading	Night cooling
Rates of photosynthetic CO_2 fixation (μMol m^{-2} s^{-1})						
14/03	Leaves	Aver.	12.26	14.95	10.92	12.42
		SE	1.24	1.27	0.78	1.41
23/06	Leaves	Aver.	13.49	15.51	11.51	13.81
		SE	1.18	1.39	1.27	1.41
24/11	Leaves	Aver.	10.34	10.48	8.52	n.o.
		SE	0.41	0.32	0.28	
24/11	Sepals	Aver.	2.71	2.53	n.d.	n.o.
		SE	0.35	0.56		
Rates of water vapour conductance (mMol m^{-2} s^{-1})						
14/03	Leaves	Aver.	0.298	0.383	0.241	0.323
		SE	0.086	0.024	0.044	0.068
23/06	Leaves	Aver.	0.415	0.744	0.332	0.486
		SE	0.093	.125	0.113	0.029
24/11	Leaves	Aver.	0.217	0.249	0.180	n.o.
		SE	0.020	0.015	0.011	
24/11	Sepals	Aver.	0.235	0.214	n.d.	n.o.
		SE	0.029	0.042		

n.o.: not operating; n.d.: not determined

tions of the rose plant or removals of organs, as it was probably the product of early stored materials. Environmental effects were also small during the initial 5 days (Fig. 4). The increases in bud diameter in the control unmanipulated plants (Fig. 4A) were thereafter larger than at any other treatment. The lowest rates of bud growth were found when the leaves were removed, stem and bud wrapped (Fig. 4C). Whereas the effect of shading was small as compared with the control, wet pad enhanced bud growth rate significantly under leaf removal and stem wrapping, leaf removal and stem and bud wrapping and canopy removal (Fig. 4B, C and E). Bud growth was decreased by wet pad when only the bud was wrapped (Fig. 4D).

The major contributor to the flower bud was the flower stem with leaves, which contributed over 50 % and in some cases up to 65 % of its dry weight (Table 2). The relative contribution of the stem with leaves decreased during midsummer in the control treatment. This decrease was compensated by a relative increase in the contribution of the canopy (C) and structural branches (T). The wet pad system significantly increased the contribution of the flower stem with leaves as compared to the control both in June and in October, while no real effect of the wet pad could be seen in January. Shading reduced the relative contribution of the stem with leaves as well as the contribution of the bud itself as compared to the control. The reduction was found in this treatment even in January, although shading was only partly operative during January. Most interesting is the increase in contribution of the bud sepals by night cooling over that of the control, reaching nearly 28 % of its total dry weight in October and even 22 % in June.

The highest rate of photosynthetic CO_2 fixation and water vapour conductance of leaves was found under WP, which was most prominent in June (Table 3). The lowest fixation rates and vapour conductances were found under shading even in June, when radiation flux density was maximal. The rates of photosynthesis in all chambers were slightly reduced in March as compared to June, but sharply reduced in November. The rate of photosynthesis of sepal leaves, which was calculated on unit leaf area, was about one fourth of that of regular leaves, while water vapour conductance was similar (Table 3), indicating that the activity of the photosynthetic apparatus of sepal leaves must have been much lower.

A regression analysis of the fresh weight of buds and flower stem (including leaves) and leaf area is shown in Fig. 5. The analysis was based on measurements of 100 flowers of different sizes harvested during the winter. The R^2 values for the linear regression lines between bud fresh weight and both stem weight and leaf area were much higher than between bud fresh weight and stem length.

Bud shape, as determined by the height/diameter ratio, was between 1.45 and 1.57, and was not affected, significantly by environmental conditions. This does not agree with CHIMONIDOU-PAVLIDOU et al. (1996), who found that height of the flower bud was reduced under stress conditions, but probably only at more extreme conditions than those in the present study.

Discussion

One of the main findings of the present study is the potential high weight of the flower buds, which was obtained in the winter and was not affected by environmental control (Fig. 2). This cannot be attributed to a higher photosynthesis rate, which is ultimately responsible for the formation of needed assimilates, as the rate of photosynthesis of flower leaves was the highest during midsummer at all environmental conditions (Table 3). It is thus likely that the limiting factor was translocation of freshly produced assimilates by the leaves provided that those assimilates are the major source for bud growth. MOR and HALEVY (1979) showed that photosynthesis of the upper leaves was sufficient for the assimilate supply to the bud. Export rates were sensitive to high temperatures, even more sensitive than carbon fixation (JIAO and GRODZINSKI 1998), and the average rate of CO_2 fixation may thus not represent actual contributions to the bud. OTTOSEN et al. (2002) even showed that net photosynthesis was not affected by changes in relative humidity of the greenhouse, although transpiration was markedly changed.

The high correlation between flower bud weight and flower leaf area (Fig. 5) indicates that bud development was dependent on concurrent produced assimilates. This derives also from our model (Table 3), which suggests, that about 50 to 65 % of the final bud dry weight is derived from flower leaves and stem. The rest is de-

rived from bud sepals and stored assimilates in structural branches (Table 2). The stored assimilates must have served as the major source for bud development at early stages, when leaf area was still small. Thus environmental conditions and organ removal had no effect on bud growth during its early growth stage (Fig. 3 and Fig. 4). We found that the bud developed simultaneously with the stem and leaves, which is in contrast to the model of LIETH and PASIAN (1991), who showed that buds started to develop when stems reached nearly their final length.

According to our model assimilates of the flower bud sepal leaves contributed 10–28 % of the bud dry weight (Table 2). This relatively high percentage is quite striking in light of the low sepal photosynthetic rates (Table 3). The rate of CO_2 fixation by all the sepals of one bud was proximately 6.5–7.5 x 10^{-4} μmol s^{-1}, based on average sepal leaf area and assuming that all the sepals were exposed to solar radiation. Total area of the leaves on one flower stem was 400 (±100) cm^2, and the rate of photosynthesis would be 600 times of that of the sepals (based on data of Table 3), also assuming that all the leaves were exposed to radiation. Assimilates produced by leaves would still exceed that of sepals by many folds, even if all the leaves were not exposed to radiation, and a fraction of them did not contribute to the bud (MOR and HALEVY 1979; JIAO et al. 1989). It is thus striking that the contribution of leaves and stem to the final bud dry weight was only about 2 to 4 times that of the sepals. This implies that photosynthates produced at a distance away from the site of consumption is not as an efficient source as those supplied by the sepals of the bud. GANELEVIN and ZIESLIN (2002) also showed that photosynthesis of sepals plays an important role in petal development and that sucrose content of petals was much lower in desepalled buds. The contribution of the stem and leaves decreased even more during midsummer in the control, probably due to decreased assimilate production under high temperature stress, as shown by JIAO and GRODZINSKI (1998).

Similar results to our findings, that pad and fan hardly improved flower bud size, were also shown by URBAN et al. (1992). Similarly, no improvement of flower bud size was found by shading. In contrast to a potential improvement, due to reduced temperature there was a decrease in photosynthesis (Table 3), which probably resulted in reduced transportable dry matter. In contrast, night cooling increased bud size significantly during spring and early summer (Fig. 2). This cannot be attributed to enhanced bud development during the day, as environmental conditions during the day and water status of stem and bud of this chamber were similar to the control (Fig. 1). The improved flower bud by night cooling could be attributed to one or more of the following phenomena: (a) A direct effect on bud extension, (b) higher export rates of assimilates out of the leaves and stem, (c) reduced respiration losses during the cooler nights.

Earlier findings show, that night-cooling significantly increased the modulus of elasticity of the flower bud tissues (PLAUT et al. 2001). This would imply that the bud tissue was more rigid and, therefore, less susceptible and its turgor was less reduced at decreased plant water potentials and slight dehydration during the day, and result in improved cell expansion and better growth.

The second possibility, that transport to the bud was increased by night cooling, can be supported by the findings of JIAO and GRODZNSKI (1998), who claimed that transport of assimilates was more sensitive to high temperature than photosynthesis. KHAYAT and ZIESLIN (1986) found less active transport of photosynthates from stem leaves to the flower bud of roses at low night temperatures. The present study, as well, implies that lowered night temperatures did not enhance transport of assimilates to the flower bud, since the relative contribution of the bud sepals was markedly enhanced at night cooling in October but not in January (Table 2). It cannot be concluded from the present study to what extend night cooling reduced the rate of respiration as was shown by KHAYAT and ZIESLIN (1986).

In conclusion, since the size of the flower stem and leaves are important factors in determining the size of the bud (Fig. 5), maximal stem and leaf size is required in order to obtain large buds. Evaporative cooling was found to be the best method for maximal photosynthetic rates (Table 3), highest plant water potentials (Fig. 1), highest rate of stem elongation (Fig. 3) and total flower weight (DAYAN et al. 2005). Canopy transpiration was not sufficient to cool plant canopy, and an adequate cooling system, like a WP system is needed mainly during the summer, as was also recommended by others (BAILLE et al. 1994). Night cooling, however, had the most favourable effect on the buds.

References

BAILLE, M., A. BAILLE and D. DELMOND 1994: Microclimate and transpiration of greenhouse rose crops. Agric and Forest Meteor. **71**, 83–97.

CHIMONIDOU-PAVLIDOU, D., A. MORISOT and P. RICCI 1996: Effect of water stress at different stages of rose development. Acta Hort. **424**, 45–51.

DAMKE, M.M. and S.K. BHATTACHARJEE 2000: Relationship between flower yields, flower character and weather parameters as influenced by NPK fertilization in 'Super Star' roses. Jour. Ornam. Hort. New-Series **3**, 83–86.

DAYAN, E. M. FUCHS, Z. PLAUT, E. PRESNOV, A. GRAVA, E. MATAN and A. SOLPHOY 2000: Cooling of roses in greenhouses. Acta Hort. **534**, 351–360.

DAYAN, E. M. FUCHS, Z. PLAUT, E. PRESNOV, E. MATAN and A. SOLPHOY 2005: The effect of cooling method, age and season on amount and quality of greenhouse roses. Eur. J Hort. Sci. **70**, 257–264.

FERNANDEZ, H., H. CONTI, A. DI BENEDETTO and O.R. LARROQUE 1994: Heat stress and cut roses in Argentina. Acta Hort. **357**, 123–133.

GANELEVIN, R. and N. ZIESLIN 2002: Contribution of sepals and gibberellin treatments to growth and development of rose (*Rosa hybrida*) flowers. Plant Growth Regulation **37**, 255–261.

HALEVY, A.H. 1987: Assimilation allocation and flower development. In: ATTERTON, J.G. (ed): Manipulation of flowering. Butterworths, London, 363–378.

JIAO, J., M. GILMOUR, M.J. TSUJITA and B. GRODZINSKI 1989: Photosynthesis and carbon partitioning in Samantha roses. Can. J. Plant Sci. **69**, 577–584.

JIAO, J. and B. GRODZINSKI 1998: Environmental influences on photosynthesis and carbon export in greenhouse roses during development of the flowering shoot. J. Am. Soc. Hort. Sci. **123**, 1081–1088.

KHAYAT, E. and N. ZIESLIN 1986: Effect of different night temperature regimes on assimilation, transport and metabolism of carbon in rose plants. Physiol.Plant. **84**, 447–449.

KHAYAT, E. and N. ZIESLIN 1989: Translocation of ^{14}C, carbohydrate content and activity of the enzymes of sucrose metabolism in rose petals at different night temperature. Physiol.Plant. **76**, 581–585.

LIETH, J.H. and C.C. PASIAN 1991: A simulation model for the growth and development of flowering rose shoots. Scientia Hort. **46**, 129–135.

MARISSEN, N., L. LA BRIJN, T. JELD and E. STROMME 1995: Source-sink relations in cut roses during vase life. Acta Hort. **405**, 81–88.

MOR, Y. and A.H. HALEVY 1979: Translocation of ^{14}C-assimilates in roses. I. The effect of age of the shoot and the location of the source leaf. Physiol. Plant. **45**, 177–182.

MORTENSEN, L.M., C.O. OTTOSEN and H.R. GISLEROD 2001: Effects of air humidity and K:Ca ratio on growth, morphology, flowering and keeping quality of pot roses. Scientia Hort. **90**, 131–141.

OTTOSEN, C.O., L.M. MORTTENSEN and H.R., GISLEROD 2002: Effect of relative humidity on gas exchange, stomatal conductance and nutrient uptake in miniature potted roses. Gartenbauwissenschaft **67**, 143–147.

PLAUT, Z., N. ZIESLIN, A. GRAVA and M. GAZIT 1979: The response of rose plants to evaporative cooling: Flower production and quality. Scientia Hort. **11**, 183–190.

PLAUT, Z., E. DAYAN, A. GRAVA, E. MATAN, I. DORI, Y. PRESNOV and L. BEN-YUNES 2001: Water relations of rose flowering buds and their relation to flower development and quality. Acta Hort. **547**, 235–243.

URBAN, L., I. LANGELEZ, A. MORISOT and P. PYRRHA 1992: Effect of high-pressure mist and daytime continuous CO_2 supplement on plant water status and quality of 'Sonia' rose plants grown on rockwool. Adv. Ort. Sci. **6**, 77–81.

VOGELEZANG, J.V.M., HOOG, N. MARISSEN, J. Jr. DE HOOG and M. BODSON 2000: Effects of diurnal temperature strategies on carbohydrate content and flower quality of greenhouse roses. Acta Hort. **515**, 111–118.

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