Gartenbauwissenschaft, **67** (4). S. 143–147, 2002, ISSN 0016–478X. © Verlag Eugen Ulmer GmbH & Co., Stuttgart

Effect of Relative Air Humidity on Gas Exchange, Stomatal Conductance and Nutrient Uptake in Miniature Potted Roses

Einfluss von relativer Luftfeuchte auf den Gaswechsel, die Stomataleitfähigkeit und die Nährstoffaufnahme bei Miniatur-Topfrosen

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Summary

The study was conducted to evaluate the effect of relative air humidity (RH) and Ca/K ratio on the physiological reactions of potted miniature roses cv. 'Parade Fiesta'. The plants were grown at constant temperature and three RH levels (70 %, 80 % and 90 %) and fertilised with three nutrient solutions each containing a different Ca/K ratio. Decreasing the RH resulted in increasing stomatal conductance (g_S) despite RH during growth being highest when subjected to lower RH during measurements of photosynthesis. Transpiration increased linearly with decreasing RH and the slope was steepest for high RH-grown plants. The net photosynthesis of high RH-grown plants was unaffected by decreasing RH. Weight loss in detached leaves was highest in 90 % RH-grown plants, reaching 55 % loss after 6 h compared with 36 % loss in low RH-grown plants. This indicates that plants grown under constant and especially high RH have reduced ability to control stomatal closure. Low RH conditions resulted in increased uptake of Ca and K. The uptake pattern in leaves is identical to that in petals, and the increasing Mg content with decreasing Ca/K ratio reflects competition between the cations. The increased Ca content in the nutrient solution increased the Ca content in the plant and might improve post-harvest quality.

Zusammenfassung

Gegenstand der Untersuchung war, die Wirkung von relativer Luftfeuchtigkeit (RH) und Ca/K-Verhältnis auf die physiologischen Vorgänge von getopften Miniatur-Rosen der Sorte §Parade Fiesta§ einzuschätzen. Die Kultur der Pflanzen erfolgte bei konstanter Temperatur und drei RH-Niveaus (70 %, 80 % und 90 %), gedüngt wurde mit drei Düngerlösungen mit jeweils unterschiedlichem Ca/K-Verhältnis. Abnehmende RH bewirkte eine zunehmende Stomataleitfähigkeit (g_S) auch dann, wenn RH während des Wachstums am höchsten war und die Pflanzen bei der Photosynthemessung einer niedrigeren RH ausgesetzt wurden. Die Transpiration nahm linear zur abnehmenden RH zu, wobei diese Zunahme bei Pflanzen, die bei hoher RH kultiviert wurden, am stärksten ausgeprägt war. Die Nettophotosyntheserate von bei hoher RH kultivierten Pflanzen blieb von der abnehmenden RH unbeeinflusst. Der Gewichtsverlust von abgetrennten Blättern war bei mit 90 % RH kultivierten Pflanzen am höchsten und betrug 55 % Verlust nach 6 h im Vergleich zu 36 % bei niedrig RH-Pflanzen. Dies weist darauf hin, dass Pflanzen, die unter konstanten und besonders hohen RH kultiviert werden, nur begrenzte Kontrolle über das Schließen der Stomata haben. Geringere RH-Bedingungen bewirken eine zunehmende Aufnahme von Ca und K. Die Aufnahmemuster der Blätter ist mit denen der Blütenblätter identisch und der zunehmende Mg-Gehalt bei abnehmendem Ca/K-Verhältnis spiegelt die Konkurrenzbedingungen zwischen den Kationen wieder. Der zunehmende Ca-Gehalt der Nährlösung erhöht den Ca-Gehalt in der Pflanze und könnte zu einer Verbesserung der Nachermtequalität führen.

Introduction

The influence of relative air humidity (RH) on keeping quality has been largely overlooked in many published papers. High RH during the production of greenhouse plants is a major problem, especially during periods of low outside irradiance, when high levels of artificial light are being used or when energy-saving measures are in force (FJELD et al. 1994). It is well known that high RH increases the risk of fungal attacks such as *Botrytis*. Numerous research groups studying the effects of high RH on growth have found increased growth at high RH due to increased CO_2 uptake (GISLERØD and NELSON 1989; MORTENSEN and GISLERØD 1990). The role of the stomata in response to high RH has been reviewed by (BUNCE 1984), who also discussed the regulatory mechanisms (BUNCE 1996). It has been found that permanent (high) RH, irrespective of irradiance, light period or temperature, reduces the capacity of the stomata to regulate water loss (MORTENSEN and FJELD 1998). Leaves wilt instantly once removed from the plant and when the plants or cut flowers are transferred to conditions with lower RH. This has been seen in plantlets of *Gerbera* grown under high RH (OTTOSEN, unpublished results), with reduced regulatory ability causing the stomata to oscillate irregularly.

High RH is assumed to be associated with increased carbon uptake, especially under high CO_2 concentrations (GISLERØD and NELSON 1989). The complicated relations between RH and vapor pressure deficit (VPD) and gas exchange parameters have been studied for example by FRANKS et al. (1997) who examined the general responses of plants to changing air humidity in relation to changes in the light response curve.

Ca is conducted passively via the xylem (BANGERTH 1979) and the Ca content in low-transpiring organs such as flowers, predominantly supplied by through the phloem, is therefore low. High growth rates of low-transpiring organs increase the risk that tissue content of Ca will fall below the critical level for cell wall stabilisation and membrane integrity (MARSCHNER 1995). Since Ca has a stabilising effect on cell membranes, it is suggested that it affects the production of ethylene; high Ca concentrations cause a lower ethylene production in rose petals (ELAD and VOLPIN 1988). An increased K/Ca ratio in cut roses is indicated by symptoms such as dry spot and bent necks (TORRE et al. 2001).

The aim of this experiment was to study the effects of cultivation at different air RH and Ca/K ratios. We evaluated the effects on the nutrient composition of leaves and flowers and the degree to which stomatal control is disrupted due to high air humidity conditions. Growth and post-harvest performance have been covered in a separate paper (MORTENSEN et al. 2001).

Materials and Methods

Potted miniature rose plants of cv. 'Parade Fiesta' were studied at Særheim Research station. They were grown under controlled conditions in six greenhouse chambers in the recommended cultivation conditions of 23 °C/20 °C day/night and 800 ppm CO_2 at relative air humidities of 70 %, 80 % and 90 % (or 17, 12 and 7 kPa respectively)(two chambers for each humidity level) containing in total 42 pots (MORTENSEN et al. 2001). The plants were watered daily with three different nutrient solutions (in all chambers): (1) low Ca/K ratio (28 ppm Ca and 414 ppm K), (2) medium Ca/K ratio (160 ppm Ca and 156 ppm K), and (3) high Ca/K ratio (220 ppm Ca and 39.1 ppm K). Plant nutrient analysis was performed on three plants per treatment and chamber in total 36 analysis of flowers and leaves (HS-Miljö lab, Kalmar-Kronoberg, Sweden).

Leaf gas exchange

The net rate of photosynthesis (P_n) was measured with a differential CO_2/H_2O Infrared Gas Analyser CIRAS-1 (PP-systems, Hitchin, UK). The second most recent fully expanded leaf at a PPFD level of 550 µmol m^{-2} s^{-1} was used. The analyser was connected to an automatically light and temperature controlled leaf chamber (PLC, PP-systems, Hitchin, UK) shortly before the plants started to flower. The measurements were taken at a leaf temperature of 23 °C and stepwise levels of 70 %, 50 % and 30 % RH at 800 ppm CO_2. Gas exchange parameters (Net photosynthesis: P_n, stomatal conductance: g_s, transpiration: T and internal CO_2 concentration: C_i) were recorded for each leaf when steady state had been reached. Each treatment was measured twice, yielding a total of 36 leaves per treatment.

Stomatal resistance (g_r) was measured with a porometer (AP4, DeltaT, Cambridge, UK) at similar leaf positions, but under ambient light, temperature and air humidity conditions in the chamber. To ensure uniform light conditions, all measurements were taken between 10.00 and 15.00 h on days with uniform cloud cover. Gas exchange measurements were performed in parallel and on leaves in similar position and stage of development. The leaves selected were fully developed and in well-exposed positions. Six leaves per treatment and chamber were used, i.e. a total of 144 measurements per leaf per day.

Results

Gas exchange

Since the results do not show any significant difference with respect to the gas exchange capacity of rose plants grown at different Ca/K ratios, the data are pooled in the following analysis. The responses of the photosynthetic parameters show a higher net photosynthesis (P_n) in leaves grown at the highest RH (90 %) (Fig. 1c), and transpiration (T) is lower with lower relative air humidity (RH) conditions during growth (fig. 1b) reflecting the lower g_s. Decreasing the RH of the air to simulate the effect of plants being moved to post-harvest conditions resulted in increased g_s irrespective of treatment during cultivation (Fig. 1a). The reduction in T, when RH was lowered from 70 % to 50 % during the measurement sessions was greater than from 50 % to 30 %. In addition, the period of time to steady state was generally shorter (data not shown), indicating swifter stomatal regulation. The stomatal conductance was highest in plants grown under high RH conditions and the increase in g_s relatively higher in low air humidity.

T increased linearly when the leaves were subjected to decreasing RH and the slope was steepest for plants that had been grown in high RH (Fig. 1b). The P_n of plants grown in high RH was greater than in plants grown at the other levels, but was unaffected by decreased RH (Fig. 1c).

Table 1. Stomatal resistance (g_r) at three different Ca/K ratios of leaves grown at three different RH levels. (N=60, ±SE).
Stomatawiderstand (g_r) bei drei unterschiedlichen Ca/K-Verhältnissen gemessen an Blättern von Pflanzen, die bei drei unterschiedlichen RH-Niveaus kultiviert wurden. (N=60, ±SE).

% RH	Stomatal resistance
70	2.74 ± 0.12
80	1.70 ± 0.08
90	1.34 ± 0.06
Ca/K	
Low	1.86 ± 0.02
Medium	2.08 ± 0.03
High	1.85 ± 0.03
RH%	***
Ca/K	**
RH x Ca/K	ns

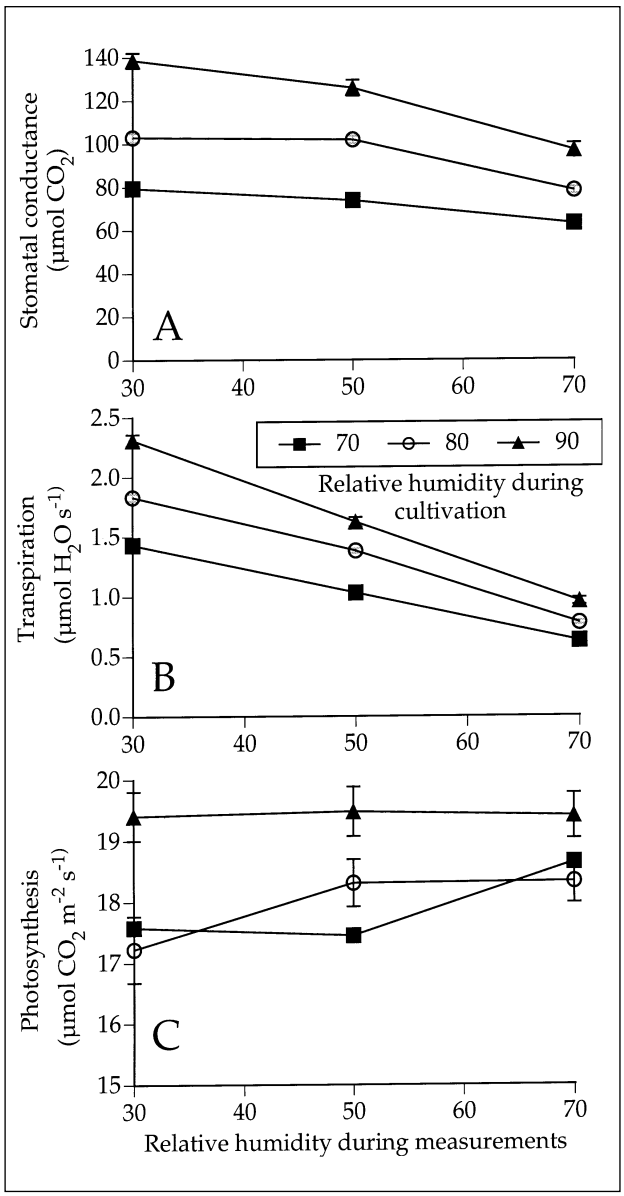


Fig. 1. Physiological responses of leaves of roses when subjected to reduced RH during measurements in situ. A: stomatal conductance (g_s), B: transpiration (T) and C: Net photosynthesis (P_n). (N=12), SE is indicated in figure if larger than legend.
Physiologische Reaktion von Rosenblättern, die für die in situ-Messungen einer geringeren RH ausgesetzt sind. A: Stomataleitfähigkeit (g_s), B: Transpiration (T) und C: Nettophotosynthese (P_n). (N=12), SE ist eingezeichnet, wenn er größer als das Symbol ist.

Stomatal resistance (g_r) measured with a porometer showed a pattern similar to that of the gas exchange measurements, i.e. highest in low RH conditions and lowest in high RH. No difference in g_r due to Ca/K ratio could be observed (Table 1).

Water loss from detached leaves showed a distinctive pattern. High RH-grown plants had a significantly greater water loss (Table 2) irrespective of time after harvest. The leaves detached from high RH plants lost almost 30% more water, reaching 50% after 6 h. Dry matter content did not differ between treatments.

Nutrient composition

RH did not affect nutrient concentration of the leaves, while reducing the Ca/K ratio resulted in a higher leaf nutrient content of N, P, Mg and K and a lower Ca content (Table 3). The nutrient composition of the petals showed the same pattern of nutrient composition, but the uptake of Ca did not increase to such a high degree. There was no significant interaction between RH and Ca/K ratio.

Discussion

Plants grown under high RH have a reduced capacity to adapt to decreases in RH, i.e. in conditions similar to those the plants would be exposed to during the post-harvest phase. This corresponds to findings for other ornamental plants, where water consumption of the whole plant was closely related to RH during growth (MORTENSEN 2000). The stomatal responses were simi-

Table 2. Water loss (% of total water content) from detached rose leaves after 2, 4 and 6 hours as influenced by RH and Ca/K ratio during growth (n=4, ±SE).
Wasserverlust (% des Gesamtwassergehalts) von Rosenblättern 2, 4 und 6 Stunden nach dem Abtrennen in Zusammenhang mit RH und Ca/K-Verhältnis während der Kultur (n=4, ±SE).

% RH	Ca/K	2 hours	4 hours	6 hours	% dry weight
70	Low	22.3±1.3	29.2±1.3	36.2±1.1	27.3±0.8
70	Medium	20.8±0.4	28.5±0.7	36.8±0.9	29.1±0.8
70	High	20.2±1.5	28.9±1.2	37.7±1.3	30.3±1.2
80	Low	25.4±2.2	33.5±2.6	41.6±2.9	26.3±0.4
80	Medium	22.9±0.7	31.4±0.9	38.9±0.7	28.3±1.0
80	High	23.6±0.4	32.1±0.3	40.1±0.3	31.5±1.9
90	Low	31.8±2.5	43.5±2.4	53.6±1.8	25.4±0.6
90	Medium	32.0±1.4	45.3±1.8	56.3±1.6	26.7±1.3
90	High	30.6±0.5	43.2±0.2	54.4±0.2	26.9±1.3
Sign. level					
RH		***	***	***	*
Ca/K		ns	ns	ns	**
RH x Ca/K		ns	ns	ns	ns

Table 3. The effect of relative air humidity and Ca/K ratio on the mineral concentration in leaves and flowers of pot roses expressed as % of nutrient in dry matter plant tissue (n=4).
Wirkung von relativer Luftfeuchte und Ca/K-Verhältnis auf die Mineralstoffkonzentration in Blättern und Blüten von Topfrosen ausgedrückt als % Nährstoff in der Pflanzentrockenmasse (n=4).

	Leaves					Flowers				
	N	**P**	**K**	**Ca**	**Mg**	**N**	**P**	**K**	**Ca**	**Mg**
% RH:										
70	3.60±0.04	2.48±0.11	35.4±4.7	10.2±1.3	2.61±0.10	2.14±0.05	2.18±0.06	23.1±2.5	1.45±0.14	1.90±0.07
80	3.75±0.05	2.46±0.10	33.7±4.3	9.8±1.2	2.63±0.10	2.22±0.06	2.19±0.07	21.8±2.4	1.35±0.13	1.95±0.08
90	3.65±0.05	2.54±0.13	33.5±4.3	9.7±1.2	2.62±0.08	2.17±0.05	2.23±0.05	20.0±1.9	1.17±0.11	1.86±0.06
Ca/K:										
Low	3.82±0.05	2.99±0.04	53.3±1.2	4.5±0.2	2.35±0.05	2.35±0.02	2.41±0.03	31.2±0.9	0.75±0.02	2.11±0.04
Medium	3.67±0.04	2.35±0.03	31.5±0.3	11.5±0.2	2.69±0.06	2.19±0.04	2.15±0.03	20.5±0.7	1.68±0.07	1.98±0.05
High	3.51±0.02	2.14±0.07	17.8±0.7	13.7±0.5	2.82±0.10	2.00±0.04	2.04±0.05	13.3±0.03	1.54±0.07	1.62±0.03
Sign. level										
RH	**	ns	ns	ns	ns	ns	ns	**	***	ns
Ca/K	***	***	***	***	***	***	***	***	***	***
RH x Ca/K	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

lar to those found for cut roses, where the stomata actually ceased their regulatory function (MORTENSEN and FJELD 1998). The threshold levels for these detrimental effects of stomatal response tend to be at approximately 85 % RH for up to 12 h daily.

The results are consistent with a mechanism for stomatal responses to RH that is based on the rate of water loss from the leaf. Stomata may not directly sense and respond to either the water vapor concentration at the leaf surface or the difference in water vapor concentration between the leaf interior and the leaf surface (MOTT and PARKHURST 1991). However, stomatal responses that caused reductions in transpiration at low RH were not accompanied by decreases in P_n, indicating that heterogeneous (patchy) stomatal closure does not occur.

Low RH during growth caused low leaf conductance and low rates of transpiration and CO_2 assimilation in rice (KAWAMITSU et al. 1993). The responsiveness of leaf conductance to vapor pressure deficit was affected by RH during growth and also reduced the CO_2 assimilation at high internal CO_2 partial pressure. In this experiment, we found no effect of RH on dry weight of the plants (MORTENSEN et al. 2001)

Studies in soybean have indicated that the increase in total transpiration rate and decrease in P_n in response to increasing VPD is controlled by cuticular conductance at low VPD and stomatal conductance at high VPD, while g_s is affected by cuticular transpiration (ZOU and KAHNT 1988). This is in correspondence to other results, where atmospheric water content mainly controlled g_s (FERREIRA and KATERJI 1992).

Low RH caused stomatal closure, and reduced both transpiration and internal CO_2, while high VPD at low RH increased transpiration. This suggests that stomatal closure might play a role in adjusting transpiration and intercellular CO_2 through lower RH rather than through higher VPD (LIU et al. 1997). The transpiration rates in tea, coffee and cocoa declined as VPD increased above 1.0–1.5 kPa, whereas in sunflower the transpiration rate increased, although non-linearly, with rising VPD (HERNANDEZ et al. 1989).

The lower RH conditions resulted in increased transpiration, but we did not find increases caused by the humidity, except for an increased uptake of Ca and K in flowers since the elements follow the sap flow.

The nutrient composition of the plants is strongly affected by the Ca/K ratio. The patterns in leaves and petals are identical, and the increasing Mg content with decreasing Ca/K ratio reflects competition between the divalent cations. The increased Ca content corresponds to results with miniature roses, showing that an increased Ca content in the nutrient solution increased the Ca content in the plant and subsequently resulted in better post-harvest quality (RASMUSSEN STARKEY and ANDERSSON 2000).

Interactions with other cations strongly influence Ca uptake, and cation antagonism by K, Mg and NH_4 can substantially depress Ca uptake, but this is not evident with respect to the leaves. However, in the petals, where a low transpiration is prevalent, it is not unusual to find higher Ca content in connection with low RH. The different pattern in Mg uptake increased concentration with increased Ca/K of the leaves, and decreased concentration of the flower with increased Ca/K is puzzling, but was also seen by TORRE et al. 2001.

The high Ca/K level, which resulted in a marked lower K content of the leaves and flowers, did not result in a significant reduction in the stomatal regulation nor in the water loss of the detached leaves, which might have been expected, since K is linked to the regulatory mechanism. The K level, however, might not have been sufficiently low to cause disruption in regulation of the stomata.

The results show that the effects of humidity and Ca are complex and the negative effect of high humidity, in terms of stomatal responses, cannot be alleviated solely by increased Ca concentration. Increased Ca content of flowers, however, is well known to improve post-harvest performance, e.g. by better tolerance to grey mould, but strong fluctuations in RH are needed to secure functional stomata.

The experiment was funded by the Norwegian Research Council and by the Ministry of Food, Agriculture and Fisheries, Denmark in connection with the OPKOT research programme.

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Eingereicht: 09.04.02/11.07.02

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