Drought Response of Low and High Maintenance Landscape Roses

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Abstract

Acclimation to drought was studied in the low-maintenance (Rosa hybrida) 'Ferdy' and 'Pink Meidiland', and the high-maintenance 'Double Delight' and 'Paradise'. All plants were acclimated to drought with five consecutive, 4-day drought cycles, followed by a 2-day recovery period after the fifth drought cycle. Low-maintenance cultivars experienced less drought stress, as evidenced by higher leaf water potential, whole plant transpiration rate (Ev), relative water content, and leaf conductance on the final day of drought stress cycles. Morphologically, the low-maintenance cultivars had greater leaf cuticle weight than high-maintenance cultivars. Differences in the density and size of stomata and epidermal cells were not related to drought response. Low-maintenance cultivars had a smaller evaporative surface (smaller total leaf areas, smaller individual leaves, and reduced shoot dry weights). However, root : shoot ratios (root dry weight : top dry weight) and leaf area ratios (total leaf area : total plant dry weight) were comparable. Drought acclimation caused a greater reduction in osmotic potential of low-maintenance roses during the recovery period. Apparently, drought resistance in the low-maintenance roses was associated with increased cuticle thickness, reduced evaporative surface, and smaller individual leaves.

Index words: Rosa hybrida, water relations, osmotic potential, cuticle, cell size

Species used in this study: rose (Rosa hybrida L., 'Ferdy', 'Pink Meidiland', 'Double Delight' and 'Paradise').

Significance to the Nursery Industry

Roses are highly valued in the landscape for their beauty and fragrance. However, many rose cultivars require extensive maintenance as they are susceptible to diseases and do not always maintain their desirable characteristics during adverse environmental conditions. If low-maintenance cultivars which maintain growth and flowering characteristics when water is limiting could be identified, the use of roses in landscaping might increase. In this study, the low-maintenance rose cultivars 'Ferdy' and 'Pink Meidiland' experienced less drought stress as evidenced by higher leaf water potential, whole plant transpiration rate, relative water content and leaf conductance than the higher-maintenance hybrid tea roses 'Double Delight' and 'Paradise'. Drought resistance in the low-maintenance roses was associated with increased cuticle thickness, reduced evaporative surface, and smaller individual leaves.

Introduction

Cultivar differences in drought susceptibility have been observed in greenhouse roses (Rosa hybrida) (23), but research concerning potential drought resistance mechanisms of landscape roses is limited (7, 12). Several cultivars marketed as exhibiting disease tolerance, drought resistance and winter hardiness have recently been released. These cultivars are considered low-maintenance since less pesticide, fertilizer, irrigation and pruning are necessary to maintain a desirable plant than with most cultivars currently used for landscaping. Research is needed to determine physiological and morphological differences between the low- and high-maintenance cultivars that might indicate potential drought resistance mechanisms.

Various morphological and physiological changes in response to water stress appear to confer some measure of drought resistance (15). Decreased stomatal density has been associated with reduced transpirational water loss (17) and increased osmotic adjustment for greater turgor maintenance and growth under lower tissue water status in roses grown in a growth chamber (1). Mycorrhizae-inoculated rose plants had a greater root : shoot ratio and transpiration rates than nonmycorrhizal plants (11).

The objectives of this study were: 1) to determine the effect of drought acclimation on water relations of low- and high-maintenance landscape roses, and 2) to determine physiological and morphological mechanisms of drought resistance among these cultivars.

Materials and Methods

Plant culture. One-year-old plants of low-maintenance, nongrafted Rosa hybrida 'Ferdy' and 'Pink Meidiland', and 2-year-old plants of the high-maintenance 'Double Delight' and 'Paradise' grafted onto Rosa setigera Michx. 'Dr. Huey' understocks were planted in 7.6 liter (2 gal) pots containing a medium of composted pine bark : sand (4:1 by vol) amended with 4.2 kg/m³ (7.1 lb/yd³) 18N-2.6P-10K (18-6-12) Os- mocote slow release fertilizer (Sierra Chemical Co., Mil- pitas, Calif.), 3 kg/m³ (5.1 lb/yd³) each of gypsum and dolomitic limestone, and 74.2 g/m³ (2 oz/yd³) fritted trace elements (W.R. Grace, Fogelsville, PA). The low-maintenance roses are commercially propagated by stem cuttings.
(own-rooted); whereas, the high-maintenance plants are commercially grafted for landscape purposes. These cultivars are commercially marketed and planted as 1- and 2-year-old plants, respectively. Plants were established for two months in a greenhouse under long-day photoperiods obtained by a 2-hr night interruption with supplemental incandescent lighting with 12 μmol m⁻² s⁻¹ at plant height. The maximum PPF was 900 μmol m⁻² s⁻¹ at plant height, and minimum/maximum air temperatures were 18/30°C (64/86°F). After the 2-month establishment period, plants were drought acclimated beginning November 23, 1987 with five consecutive 4-day drought cycles in which plants were irrigated to contain container capacity every 4 days. Following the fifth drought cycle, plants received a 2-day irrigation recovery period, and the experiment was terminated on December 12, 1987. The length of these drought cycles was determined by a preliminary experiment in which water was withheld until plants were unable to recover overnight from water stress, as determined by measuring leaf water potential (Ψₑ) with a Scholander-type pressure chamber (20) (Soil-moisture Equipment Corp., Santa Barbara, Calif.). At the end of day 4 of each cycle and prior to rehydration and the initiation of the subsequent cycle, predawn and high-maintenance plants were −0.25 and −0.74 to −1.10 MPa, respectively. Plants were used for this study were one day shorter than those identified in the preliminary study to assure plant survival throughout the experiment despite limited moisture supply.

Plant water status measurements. Leaf water potential (Ψₑ) of the two uppermost fully-expanded leaves was measured on five plants per treatment with a Scholander-type pressure chamber between 1300 and 1600 HR on the first and third day of each cycle. A leaf was enclosed in a polyethylene bag and Ψₑ determined. Leaf conductance (gₑ) was determined on similar leaves at the same time with a LiCor 1600 steady state diffusive porometer (LiCor, Inc., Lincoln, Neb.). Predawn Ψₑ was also determined between 0400 and 0600 HR following all afternoon Ψₑ measurements.

During the final stress cycle of the study, whole-plant transpiration (E) was determined gravimetrically (10). On the day 1 of cycle 5, plants were irrigated and allowed to drain, and containers of five plants per treatment were enclosed in polyethylene bags, and bags were secured around the plant crown (stem-root junction). Plants were weighed daily at 1000 and 1630 HR. From these data and leaf areas measured at harvest, E was determined using the procedures of Graham et al (10).

Leaf relative water content (RWC) was determined on days 1 and 4 of the first, third and fifth stress cycles immediately after afternoon Ψₑ and gₑ measurements were complete. Relative water content was measured on three samples in each cultivar and block, resulting in 15 observations per cultivar. Relative water content was determined by weighing a 1 cm (0.4 in) diameter leaf disc immediately after removal from the plant to determine fresh weight (FW). Leaf discs were then floated on distilled water for 2 hr, blotted dry and weighed to obtain a turgid weight (TW). Dry weights (DW) were determined after oven drying at 95°C (203°F) for 24 hr and RWC was calculated by the equation:

\[ RWC = \left( \frac{(FW - DW)}{(TW - DW)} \right) \times 100. \]

Osmotic potential (Ψₒ) at full turgor (Ψₑ ≈ 0.1 MPa) was determined after plants were watered to container capacity for two consecutive days at the completion of the fifth drought cycle. Ten leaf samples per cultivar were frozen at −30°C (−22°F) in a Revco ULT 1786 A-O-B freezer (Rheem Manufacturing Co., Asheville, N.C.). Leaves were thawed and allowed to equilibrate to room temperature [22°C (72°F)] for approximately 1 hr in water-proof envelopes, and Ψₒ was measured psychrometrically from expressed sap with a C-52 chamber coupled with a PR-55 psychrometer microvoltmeter (Wescor, Inc., Logan, Utah).

Cuticle isolation and epidermal wax determination. At the termination of the experiment, eight leaf samples were taken from fully expanded leaves from the newest growth of drought acclimated and nonstressed plants. Individual leaf areas were determined. Leaves were then placed in a solution of 1.589 g (0.056 oz) ZnCl₂ per ml concentrated HCl at 22°C (72°F) (13). Solutions were changed daily until cell debris was removed from the cuticles (about 1 month). Cuticles were weighed to obtain total cuticle and epidermal wax weight per cm² of leaf area. Isolated cuticles were dried for 20 min changes of acetone to remove water, then six 20-min changes of chloroform at 22°C (72°F) with constant agitation (18). Cuticles were again weighed to determine wax and isolated cuticle weights.

Stomata and cell density and area measurements. Stomata and epidermal cell densities and areas of drought acclimated and nonstressed leaves were determined from the terminal leaflet of the newest fully expanded mature leaf. Acetate replicas of abaxial and adaxial leaf surfaces (19), were mounted on glass microscope slides. A Zeiss 9901 binocular light microscope (Dexter Instrument Co., San Antonio, Texas) connected to a Panasonic WV 3240 video camera (Matsushita Electric Ind., Co., Yokohama, Japan) and NEC Autocolor TV receiver (NEC Home Electronics, Elk Grove Village, Ill.) were used to determine leaf epidermal cell densities and areas from all treatments. The TV receiver was calibrated with a stage micrometer, and the number of stomata, abaxial and adaxial epidermal cells per mm² was determined in 12 samples per treatment. A grid was attached to the TV receiver, to determine cell sizes in 20 samples per treatment (21).

Plant biomass measurements. Upon completion of the study, plants were harvested and, and leaf number and area (LiCor-3100 Area Meter, LiCor, Lincoln, Neb.), shoot and root dry weight, root : shoot ratio (root dry weight : top dry weight) and leaf area ratio (LAR) (total leaf area : total plant dry weight) were determined in 5 plants per cultivar.

Statistics. The experimental design was a randomized complete block with five blocks and two plants per block for plant water status and biomass measurements. Analysis of variance procedures were performed on all data, and mean separations were determined by Student Newman Keul or LSD Procedures. The experimental design utilized for cuticular wax, stomatal and cell density, and cell area measurements was a split-plot. Main plots were cultivars and subplots were drought stress treatments. Treatment replications are indicated in each section. Data were subjected to analysis of variance procedures with mean separation by Student Newman Keul Procedures.

Results

Plant water status. On day 1 of the first cycle (low drought stress), the high maintenance 'Paradise' had a higher $g_1$ than any of the other cultivars (Fig. 1A). By cycle 3, day 1 (low stress), there was no difference in $g_1$ among the cultivars. However, all four cultivars had acclimated to drought and had lower $g_1$ relative to cycle 1, day 1. During high stress (day 4 of cycles 3 and 5), the low maintenance 'Ferdy' and 'Pink Meidiland' had higher $g_1$ (Fig. 1A) and E than 'Double Delight' and 'Paradise' (Table 1).

Preadawn $\Psi_1$ followed the same trend as afternoon (pm) $\Psi_1$, hence only pm $\Psi_1$ is reported. High maintenance roses had lower (more negative) $\Psi_1$ than low maintenance roses during high stress (day 4 of cycles 3 and 5), while 'Ferdy' and 'Pink Meidiland' maintained a comparable $\Psi_1$ during the low and high stress days of a given cycle (Fig. 1B).

The RWC mirrored $\Psi_1$ data in that 'Ferdy' and 'Pink Meidiland' had a higher RWC than 'Double Delight' and 'Paradise' during high stress (day 4 of cycles 3 and 5) (Fig. 1C). 'Ferdy' and 'Pink Meidiland' had a lower (more negative) $\Psi_1$ than the high maintenance 'Double Delight' during the 2-day recovery period following the fifth drought cycle (Table 2).

Cuticle and epicuticular wax characteristics. There were no differences between drought acclimated and nonstressed leaves in cuticle and epicuticular wax characteristics. 'Ferdy' and 'Pink Meidiland', however, had greater cuticle weights than the high-maintenance cultivars 'Double Delight' and 'Paradise' (Table 3). Wax weight was not significantly different among the cultivars.

Table 1. Whole plant water loss (mmol m$^{-2} s^{-1}$) of low-maintenance ('Ferdy', 'Pink Meidiland') and high-maintenance ('Double Delight', 'Paradise') roses 2 and 4 days after irrigation during the fifth drought stress cycle.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Day 2</th>
<th>Day 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferdy</td>
<td>3.31 b</td>
<td>3.01 b</td>
</tr>
<tr>
<td>Pink Meidiland</td>
<td>5.75 a</td>
<td>5.27 a</td>
</tr>
<tr>
<td>Double Delight</td>
<td>1.04 c</td>
<td>0.87 c</td>
</tr>
<tr>
<td>Paradise</td>
<td>1.41 c</td>
<td>1.16 c</td>
</tr>
</tbody>
</table>

'Mean separation within columns by Student Newman Keuls Procedure, 5% level; n = 5.

Table 2. Osmotic potential ($\Psi_o$) of low-maintenance ('Ferdy', 'Pink Meidiland') and high-maintenance ('Double Delight', 'Paradise') rose plants following a 2-day recovery period after 5 drought stress cycles; $\Psi_o$ = -0.1 MPa.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>$\Psi_o$ (MPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferdy</td>
<td>-2.0 b</td>
</tr>
<tr>
<td>Pink Meidiland</td>
<td>-1.9 b</td>
</tr>
<tr>
<td>Double Delight</td>
<td>-1.3 a</td>
</tr>
<tr>
<td>Paradise</td>
<td>-1.6 ab</td>
</tr>
</tbody>
</table>

Mean separation by Student Newman Keuls Procedure, 5% level; n = 5.

Table 3. Leaf epicuticular wax and cuticle weight of drought acclimated and nonstressed low-maintenance ('Ferdy', 'Pink Meidiland') and high-maintenance ('Double Delight', 'Paradise') rose plants.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Wax</th>
<th>Cuticle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferdy</td>
<td>1.03 a</td>
<td>1.53 a</td>
</tr>
<tr>
<td>Pink Meidiland</td>
<td>1.22 a</td>
<td>1.26 a</td>
</tr>
<tr>
<td>Double Delight</td>
<td>1.05 a</td>
<td>0.82 b</td>
</tr>
<tr>
<td>Paradise</td>
<td>0.87 a</td>
<td>0.87 b</td>
</tr>
</tbody>
</table>

'Mean separation within columns by Student Newman Keuls Procedure, 5% level. Means followed by the same letter are not significantly different; n = 24 for wax weight and n = 16 for cuticle weight.
Table 4. Plant biomass, root : shoot (R/S) ratio and leaf area ratio (LAR) of low-maintenance ('Ferdy', 'Pink Meidiland') and high-maintenance ('Double Delight', 'Paradise') rose plants after five 4-day stress cycles.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Leaf number</th>
<th>Individual leaf area (cm²)</th>
<th>Leaf area (cm²)</th>
<th>Shoot dry weight (g)</th>
<th>Root dry weight (g)</th>
<th>R/S ratio</th>
<th>LAR (cm² g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ferdy</td>
<td>703 a</td>
<td>3.9 c</td>
<td>2597 b</td>
<td>48.5 b</td>
<td>80.7 b</td>
<td>1.7 a</td>
<td>22.0 a</td>
</tr>
<tr>
<td>Pink Meidiland</td>
<td>118 b</td>
<td>12.8 b</td>
<td>1470 c</td>
<td>28.2 b</td>
<td>36.8 c</td>
<td>1.3 a</td>
<td>22.6 a</td>
</tr>
<tr>
<td>Double Delight</td>
<td>122 b</td>
<td>40.9 a</td>
<td>4984 a</td>
<td>114.0 a</td>
<td>123.2 a</td>
<td>1.2 a</td>
<td>21.1 a</td>
</tr>
<tr>
<td>Paradise</td>
<td>102 b</td>
<td>41.7 a</td>
<td>4163 a</td>
<td>101.1 a</td>
<td>91.7 ab</td>
<td>0.9 a</td>
<td>21.9 a</td>
</tr>
</tbody>
</table>

Mean separation within columns by Student Newman Keuls Procedure, 5% level; n = 5.

Stomata and cell densities and areas. There was no consistent trend in stomatal density or cell area, nor were there significant cultivar × drought interactions in stomatal or cell densities or areas (data not presented).

Plant biomass. High-maintenance plants had a greater leaf area, larger individual leaves, and greater shoot dry weight than low-maintenance roses; however, all cultivars had similar root : shoot ratios and LAR (Table 4). There were no differences in root dry weight between 'Ferdy' and 'Paradise'. 'Ferdy' had the greatest leaf number (smallest sized leaves of all cultivars); however, its leaf area was still less than the high-maintenance cultivars. 'Pink Meidiland' had the smallest root dry weight and leaf area and was the least vigorous cultivar in this study. Leaf abscission did not occur in any of the cultivars during the drought and recovery cycles.

Discussion

Plant water status and osmotic potential. 'Ferdy' and 'Pink Meidiland' did not reach the same level of water stress as the high-maintenance roses. Predawn Ψₛ of low- and high-maintenance plants ranged from -0.25 to -0.34 MPa and -0.74 to -1.10 MPa, respectively, at the end of a stress cycle and prior to rehydration and the initiation of the next cycle. It would have been ideal to test the four cultivars produced from similar propagation systems and of initial equal evaporative surface. Unfortunately, the two low-maintenance and two high-maintenance cultivars were morphologically distinct with quite different growth habits. Furthermore, the low-maintenance roses are commercially propagated by stem cuttings (own-rooted), whereas the high-maintenance plants are grafted for landscape purposes. The high-maintenance roses are commercially produced and marketed as 2-year-old plants, whereas an advantage of the low-maintenance cultivars is their production and planting in the landscape as 1-year-old plants. Precautions were taken to work with equal medium substrate volumes and to assure that no plant became root-bound in containers during the course of the experiment.

All cultivars responded to drought acclimation as indicated by lower g and Ψₛ, from the initiation of cycle 1 through the low stress of cycle 5, day 1. During high stress (day 4 of cycles 3 and 5), gₛ, E, Ψₛ, and RWC were higher in the low-maintenance 'Ferdy' and 'Pink Meidiland'. This is in part explained by their lower total evaporative surface, smaller individual leaf size with increased boundary layer resistance, and hence reduced evaporative demands. Greater drought acclimation may have occurred with the low-maintenance roses which maintained comparable E rates through high stress (cycle 5, day 4), while E of the high-maintenance roses declined. Drought acclimation has been reported in mycorrhizal-inoculated 'Ferdy' plants (11).

Another response to drought acclimation and possible contributing factor to the greater drought resistance of the low-maintenance cultivars was the lower (more negative) Ψₛ at full turgor (Ψₛ = -0.1 MPa) compared with the high-maintenance 'Double Delight' during the 2-day recovery period following the fifth drought cycle. While osmotic adjustment was not measured during high stress (day 4 of cycles 3 and 5), it may have occurred. Osmotic adjustment is a physiological mechanism of drought tolerance (14) and has been associated with glasshouse roses grown in a growth chamber study (1). Osmotic adjustment allows for maintenance of turgor at lower Ψₛ, thus avoiding wilting and enabling cells to create a larger driving force for water uptake (24). The values for Ψₛ in the low-maintenance 'Ferdy' and 'Pink Meidiland' under glasshouse conditions were similar to those measured by pressure-volume (PV) curve for drought acclimated Rosa hybrida 'Samantha' under growth chamber conditions (1). In contrast, Ψₛ values for the more stressed high-maintenance 'Double Delight' and 'Paradise' were higher (less negative) than values observed for non-acclimated plants of 'Samantha' (1).

Cuticle and epicuticular wax characteristics. Wax and cuticle weights did not differ between drought acclimated and nonstressed leaves. The low-maintenance cultivars, however, had greater cuticle weights than high-maintenance cultivars. Increased epicuticular wax and cuticle weights have been associated with improved drought resistance in several crop species (4, 6, 22). While the cuticle is not thought to induce much protection against drought (16), it is still a barrier to moisture loss and may have contributed to the higher water status of 'Ferdy' and 'Pink Meidiland'. Differences in cuticle and epicuticular wax quantities have been attributed to part in genetic factors as well as environmental conditions (2).

Stomata and cell density and area measurements. There were no significant cultivar × drought interactions in stomatal or cell densities or areas. While no differences in stomatal density occurred with the different drought treatments in this study, other studies have shown increased stomatal frequency under drought conditions (3, 8, 9). Increased stomatal frequencies have been attributed to a smaller leaf size which tends to concentrate the stomata in a smaller area (5). There have also been occasional reports of decreased stomatal frequency with drought stress conditions (3).

Plant biomass. The smaller shoot biomass and evaporative surface, and the greater boundary layer resistance associated with smaller individual leaf surfaces reduced transpirational water loss and contributed to the lower water demands of the low-maintenance cultivars. Double Delight had the largest root system, yet with its large evaporative surface, was more susceptible to drought. Root dry weight of Paradise was the same as the low-maintenance Ferdy, but was more drought susceptible with its greater evaporative surface. Due to the greater evaporative surface and a trend for a reduced root: shoot ratio, Double Delight and Paradise would not be expected to maintain as favorable a water balance as the low-maintenance roses, which agrees with some of our field observations.

In summary, the low-maintenance cultivars maintained a better water status by the avoidance mechanisms of reduced evaporative surface, greater leaf cuticle weight, and possibly by the tolerance mechanism of osmotic adjustment.

Literature Cited