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Cavitation and Transpiration Profiles of Cut Roses under Water Stress

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Summary

Maintenance of stomata activity during post-harvest period is one of the key factors keeping water status of cut roses in balance, thereby determining their vase life. In order to study their stomata function and stomata adaptation ability to water stress, transpiration and cavitation rate of cut roses (*Rosa hybrida* 'Candid Prophyta') were measured simultaneously. Rose stems with an ultrasonic sensor fixed at the peduncle were placed in a gas exchange chamber. Transpiration as well as acoustic emissions were recorded under fluctuating 3 h light-dark rhythm or under continuous light, respectively in dehydration experiments. When starting the experimental procedure roses showed a strong dependence of transpiration rate on light-dark rhythms, indicating a stomata function. The first cavitations appeared after 5 light-dark cycles in this experiment. Parallel to an increase of cavitation rate the transpiration rate declined. Exposure of rose stems to air led first to a short increase of the transpiration rate (Iwanoff effect), which then progressively decreased during the following 3 h dehydration period. With a time lag of a few minutes to the increase of transpiration the cavitation rate increased rapidly as well, and reached its maximum within the following 20 minutes of dehydration. Thereafter the cavitation rate started to decline nearly parallel to the transpiration rate, and stayed on a low level within the rest of the rehydration period. In most cases replacing the roses back into water increased the transpiration rate only partially caused by the long after effect of water stress on stomata function. A strong relationship between cavitation occurrence and transpiration rate was observed also during their following vase life. Furthermore, simultaneous measurements of cavitations and transpiration rate has been shown to be a very helpful aid in studying water stress management of cut roses.

Key words. acoustic emissions – dark-light change – dehydration – gas exchange – postharvest life – *Rosa hybrida* – stomata

Introduction

The water management of cut roses is one of the most intensively studied topics in post-harvest literature of ornamentals. The exposure of cut stems to air (Van Doorn 1990), the bacterial or physical occlusions of xylem vessels (Van Doorn and Dhont 1994; van Doorn and Reid 1995), and climatic conditions stimulating evapotranspiration (Van Doorn 1997; Doi et al. 2000) are the dominant factors worsening the water balance, and thus the post-harvest potential of cut flowers. To quantify vase life limitations by means of a prognosis model, not only these factors, but also the mechanisms controlling water uptake, water transport and water loss have to be understood well. In this connection, the adaptation ability of these mechanisms to water stress is of special importance. Therefore, the objective of this paper is to investigate stress responses of cut roses by using gas-exchange and ultrasonic acoustic techniques.

Stomata function

It is generally considered, that entire plants regulate transpiration by stomatal conductance in order to prevent water stress. However, there is still a lack of understanding what exactly drives stomata regulation (Sperry 2000). Especially in cut flowers little is known about stomata and their controlling function during post-harvest life. De Stigter (1980) has shown, that during the first 24 h after cutting transpiration and water uptake of cut 'Sonia' roses were identical or very similar to roses before cutting or to those that remained intact. During the following days both, transpiration rate and water uptake of cut roses dropped sharply. In earlier experiments Mayak et al. (1974) showed a relationship between low stomatal closure and short vase life of 'Golden Wave' roses.

Information about velocity of stomata reaction under water stress can be found at van Doorn and Reid (1995). After exposure of freshly cut shoots to air, stomata of all tested cultivars ('Frisco', 'Sonia', 'Madelon' and 'Cara Mia') closed nearly completely, and stomatal conductance decreased from about 300 mmol m^{-2} s^{-1} to about zero within 3 h. The observed differences in water stress tolerance of these cultivars were not related to their transpiration characteristics, except 'Frisco'. The considerably lower water loss of 'Frisco' roses during dehydration was attributed to its lower cuticular transpiration (van Doorn

and Reid 1995). In addition to the hydraulic status of the flowers stomata function of cut roses is also controlled by photoperiod and production conditions. Doi et al. (1999) observed a pronounced rhythm of transpiration with 'Bridal Pink' roses under light-dark change and found that even during dark phases roses kept a transpiration rate of about 15–20 % of that of light phases.

Considering production conditions, cropping season (Slootweg et al. 2001) and air humidity seem to have a particularly strong effect on stomata function (Mortensen and Fjeld 1995; Torre et al. 2003). Torre et al. (2003) have observed a failure in stomata response to water stress with cut roses which have been grown under high relative humidity (RH=90 %) in comparison to roses from a moderate RH (70 %).

Cavitations

Continuing transpiration of plants after exposure to air and/or bacterial blockages of basal parts of the stems often result in cavitations or embolization of their xylem conduits (e.g. Durkin 1980; Evans et al. 1996), which frequently reduces their vase life. After mild stress, blockages seem to be temporary only and do happen in the lowermost parts of the shoots only (Van Doorn 1990). The breakage of water columns due to cavitations of vessels is accompanied by an emission of acoustic signals which have been measured either in audible (e.g. Crombie et al. 1985) or recently in ultrasonic frequencies (e.g. Tyree and Dixon 1983; Tyree and Sperry 1989; Milburn 1993). A strong relationship between the number of acoustic signals and the loss of stem hydraulic conductivity (Lo Gullo and Salleo 1991; Salleo et al. 2000) along with the chance of a continuous non-destructive observation of plants has added the acoustic emission method to the monitoring of the plant water status (Lo Gullo and Salleo 1991).

Acoustic emission signals have been reported with cut flowers under water stress (Dixon and Peterson 1989; Van Doorn and Jones 1994; van Doorn and Suiro 1996; Bleeksma and van Doorn 2003). Usually a high cavitation rate is associated only with strong water stress of plants (Dixon et al. 1988; Van Doorn and Jones 1994), and often depends on the cultivar (van Doorn and Suiro 1996). A causal relationship was described between a high number of cavitated vessels and inhibition of water uptake (Van Doorn and Jones 1994; van Doorn and Suiro 1996). Nevertheless, information about interactions between transpiration and cavitation processes during post-harvest life are still missing in literature, especially in cut flowers under water stress. Furthermore, until now there are no cavitation and transpiration profiles available, showing the dynamics of these processes under changing climatic conditions.

Therefore, the main objectives of this paper are 1) proving a controlling ability of stomata during post-harvest life of cut roses; 2) studying a relationship between cavitation occurrence and transpiration rate and 3) testing the actual acoustic emission signals as indicators of water stress.

Materials and Methods

Plant material

To study the relationship between cavitation occurrence and transpiration rate in cut roses (*Rosa hybrida*) flowers from own production as well as imported products have been examined. Roses of 60 cm lengths and bud development stage 2 (after Vbn 2001) were kept overnight in a cooler (4°C, darkness) to achieve a certain rehydration level. At the start of each experiment, the stems were cut in air to a length of 40 cm and kept individually in vials with 100 ml of tap water (water hardness of 2.32 mmol l^{-1}) for the whole duration of tests. The submerged part of the stems was defoliated.

To test stomata control of roses under water stress in some experiments flowering stems were kept dry for 3 h by placing them in dry vials. This dehydration was carried out under the same climatic condition as cavitation, transpiration and water potential measurements, at a temperature of 20 °C, water vapour saturation deficit of 10.5 hPa and lightning at a level of 60 or 120 µmol m^{-2} s^{-1}, for continuous lighting or a fluctuating 3 h/3 h rhythm according to the experiment, provided by two high-pressure mercury lamps (HQI, Osram).

Cavitation measurement

Acoustic emissions were recorded continuously at the flower peduncle (Spinarova and Hendriks 2005), 3 cm below the sepals. The sensors were attached to rose stems by rubber bands, and as a coupling media silicone paste was used. Ultrasonic acoustic emissions (UAE) were measured with a digital two channel acoustic emission device (AMSY4, Vallen-System GmbH, Icking, Germany). The 8 piezoceramic sensors per each channel of the instrument (VS150-M), with a frequency range of 100 to 450 kHz, were recording signals in intervals of 4 s. To avoid background noise, which was around 38 dB_{AE}, only UAE data above 40 dB_{AE} were considered for analysis. For each treatment 4–7 single rose stems were tested. One further rose with an attached UAE sensor was always used for parallel transpiration measurement additionally. As numerous experiments have shown, acoustic emissions correspond with cavitation occurrences in xylem (Tyree and Sperry 1989), and hence, we will use both terms as synonyms.

Transpiration measurement

To measure cavitations and transpiration of cut roses simultaneously, the upper part of a rose stem, equipped with the UAE sensor on its peduncle, was fixed in a gas-exchange chamber (15 l). The base of the stem was kept outside the chamber in a vase with tap water. The transpiration of the cut rose was measured continuously with a gas-exchange measuring station (Walz GmbH, Effeltrich, Germany). A bypass humidity control system was used to hold steady water saturation deficiency in the gas-exchange chamber and to calculate the transpiration rate. Details were described by Von Willert et al. (1995). Temperature in the chamber was 20 °C, a relative humidity 50–60 % and light conditions as described above.

Supporting measurements

In addition to recording of cavitation events and transpiration rate, flower development (after Vbn 2001) and water stress symptoms (wilting of leaves and petals, bent neck) were recorded. At the beginning/end of the experiments and before/after dehydration of cut roses, the

water potential of the peduncle (5 cm below flower) was measured with a Scholander pressure chamber (Model 1003, PMS Instrument Co., Corvallis, Oregon, USA). After the gas-exchange and cavitation measurements, the leaf area of the observed roses was scanned with LI-3100 Area Meter (LI-COR Inc., Lincoln, Nebraska, USA).

Statistics

Experiments with simultaneous measurement of acoustic emissions and transpiration in the gas-exchange chamber were repeated at least 4 times for each treatment. Due to a strong dependence of UAE- and transpiration data on morphological and geometrical characteristics of rose stems, only data from representative stems instead of mean data are presented.

Results

Light-dark change

Photoperiod is the most important factor controlling stomata function. As seen from the graph (Fig. 1), the transpiration rate of 'Candid Prophyta' rose was following very closely the light-dark rhythm, even with unnatural light cycles (3 h/3 h light-dark rhythm, light level 120 µmol m^{-2} s^{-1}). Furthermore, the transpiration rate was not constant but increasing up to a level of about 1.75 mmol m^{-2} s^{-1} during the first 5 light cycles, and then decreasing again. During dark periods, a relevant transpiration of about 10 to 20 % of that of light periods could be observed. At the beginning, amplitudes between light and dark transpiration rates were less expressed than at the later stage of the experiment, possibly the stomata adapted to the experimental conditions.

The cavitation profile follows the light-dark rhythm as well (Fig. 1). First cavitations did not occur before 18 h after the beginning of experiment (6 light-dark cycles), and increased consecutively to a maximum level of about 500 hits h^{-1} when the transpiration rate was already decreasing. This maximum with an pronounced light-dark rhythm lasted only 3 light cycles. Then the cavitation rate dropped down to a level of about 100 hits h^{-1} with rather small differences between light and dark phases. A detailed study of the light phases showed that the cavitation onset was always a few minutes later than the start of the transpiration.

Roses under water stress

With cut flowers, the exposure of the cut surface to air is one of the hardest water stress situations. To examine the correlation between occurrence of cavitations and stomata function under such conditions, a rose with UAE-sensor was placed in a gas-exchange chamber. After adaptation to the chamber climate, water was taken off the stem base for a 3 h dehydration phase, while transpiration and cavitation rates were recorded (under light level 60 µmol m^{-2} s^{-1}, continuos light). As seen from the graph (Fig. 2), the transpiration rate was increasing for about 20 min after exposure to air and then continuously decreased from 1.1 to 0.4 mmol m^{-2} s^{-1} during the whole dehydration period. The replacement of the rose back into water increased the transpiration rate almost to its original level.

With a time lag of a few minutes to transpiration, the cavitation rate increased rapidly, and reached its maximum of about 2000 hits h^{-1} within the next 20 min of dehydration. Then the cavitation rate decreased nearly parallel to the transpiration rate and stayed on a low level (200 hits h^{-1}) within the rest of the rehydration period.

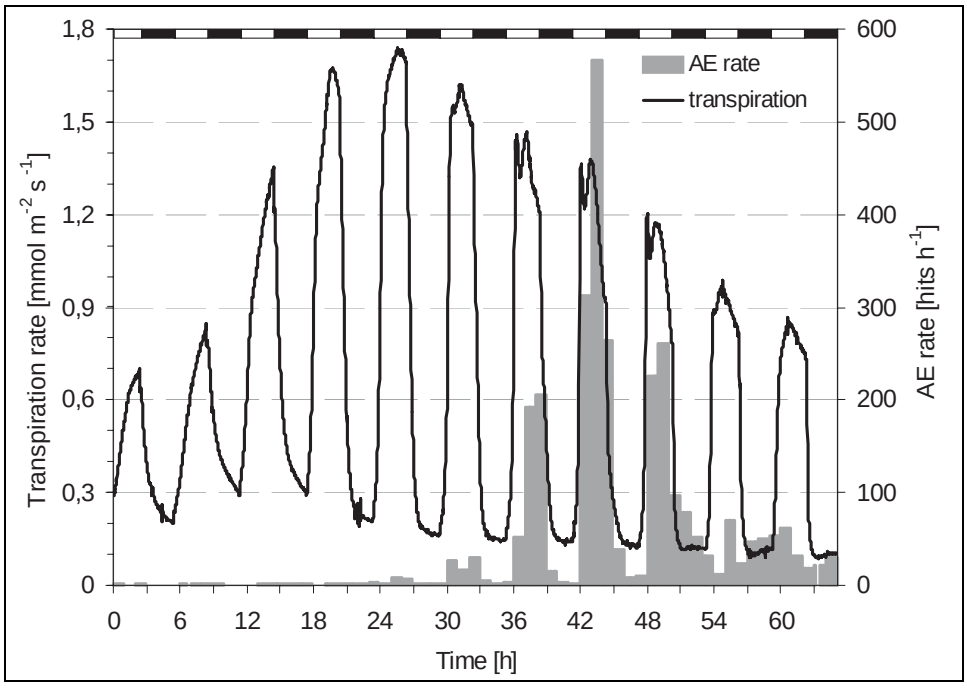


Fig. 1. Acoustic emission (AE) and transpiration profiles of cut rose 'Candid Prophyta' during 3 h/3 h light-dark change. AE and transpiration data are from a representative single rose stem.

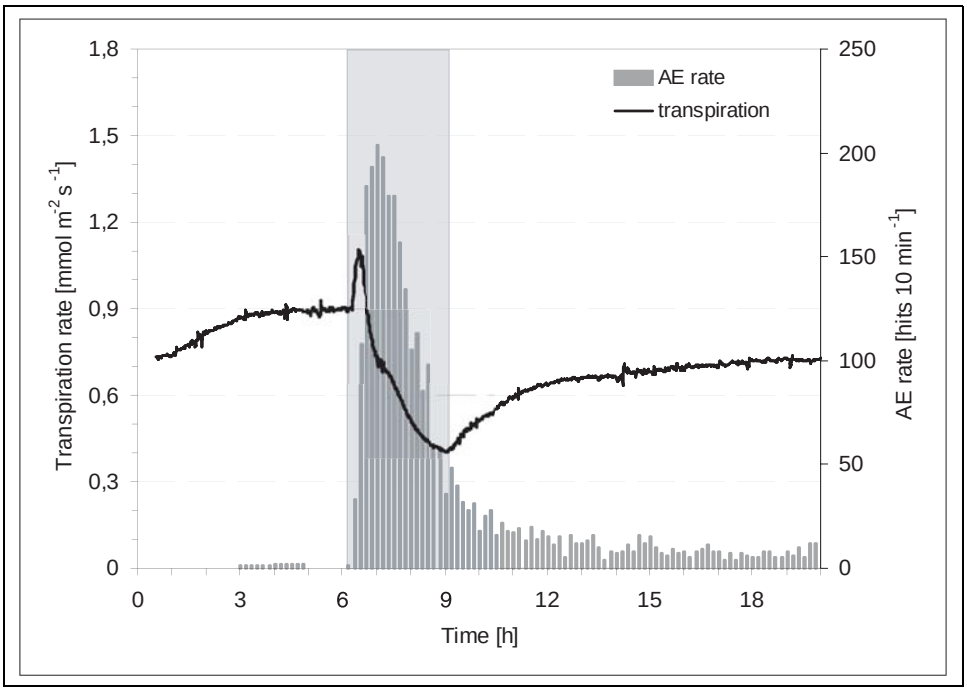


Fig. 2. Occurrence of acoustic emission (AE) and transpiration rate of cut rose 'Candid Prophyta' during 3 h dehydration and following rehydration (gey part of the graph shows dehydration period). Profiles are from a representative single rose stem.

The roses kept under climatic conditions similar as in the chamber showed stem water potential of about −0.14 MPa before exposure of the stem to air, and about −1.2 MPa after 3 h of dehydration. Replacing flower stems back into water for about 12 h (under light) led to increase of their water potential to −0.75 MPa. With roses, which had been stored in a cooler 3 days longer, no increase of transpiration and no change of water potential was observed after 12 h of rehydration (data not shown).

Water potential

Water potential measurements are the standard method for the quantification of water stress in plants. To ascertain interactions between water potential and occurrence of cavitations each 5 min stem water potential was measured on separate 'Candid Prophyta' roses (during a parallel dehydration experiment). During the 3 h of exposure to air the water potential of shoots was decreasing (becoming more negative) continuously, and reached the level of −1.5 MPa (Fig. 3). The acoustic emission rate (hits 5 min^{-1}) was increasing rapidly to its maximum within the first hour of dehydration. During the next 2 h the cavitation rate was continuously declining. At the time of highest cavitation (and transpiration rate), water potential was not lower than about −0.5 to −0.8 MPa in this experiment. The cumulative signal rate was following the curve of water potential all the time of dehydration.

Discussion

Effects of light-dark change

On cut roses kept under short time light-dark rhythm simultaneous measurements of transpiration and UAE have shown a strong dependence of transpiration rate on photoperiod. This indicates a normal stomata function at the beginning of rose vase life, well corresponding with early findings of De Stigter (1980). With a 3 h light-dark change the transpiration rate increased successively, and reached its maximum of about 1.75 mmol m^{-2} s^{-1} after about 5 cycles. At that time transpiration rate during the dark phase was about 10–15 % of that of the light phase. These data are in a good agreement with a pronounced transpiration rhythm of cut roses 'Red Sandra' (Son et al. 1997) and 'Bridal Pink' (Doi et al. 1999), following a diurnal change and keeping night transpiration of about 10–20 % of that during day time.

An iterative increase and decrease of the transpiration rate during an experimental period was obtained also by Doi et al. (1999) using a 12 h photoperiod. In their experiments transpiration rates have shown an increasing tendency until the 4th light phase and then a decrease well corresponding to an exceeding water uptake by transpiration. In our experiment, the decrease of the transpiration rate was accompanied by the appearance of first cavitations. During the first 5 light cycles no or only few cavitations could be obtained, probably due to a positive water balance at the beginning of the vase life period. With increase of transpiration, water balance may have become disturbed and first cavitations occurred. According to the theory of Tyree and Ewers (1991) these cavitations may act as a hydraulic signal initiating stomatal closure under water stress, and may explain the observed reduction of the transpiration rate.

The cavitation rate reached its maximum in about 3 cycles after the start and then declined again. This can be interpreted either by a feed back to closure of stomata, and a subsequent reduction of water stress, or by the limited number of vessels which can become cavitated or embolized. Due to experimental conditions (entire rose with flower in gas-exchange chamber) it cannot be distinguished, if the high transpiration rate during the dark phase (about 10–15 % of that of light phases) was mainly caused by limited closure of stomata or by high cuticular

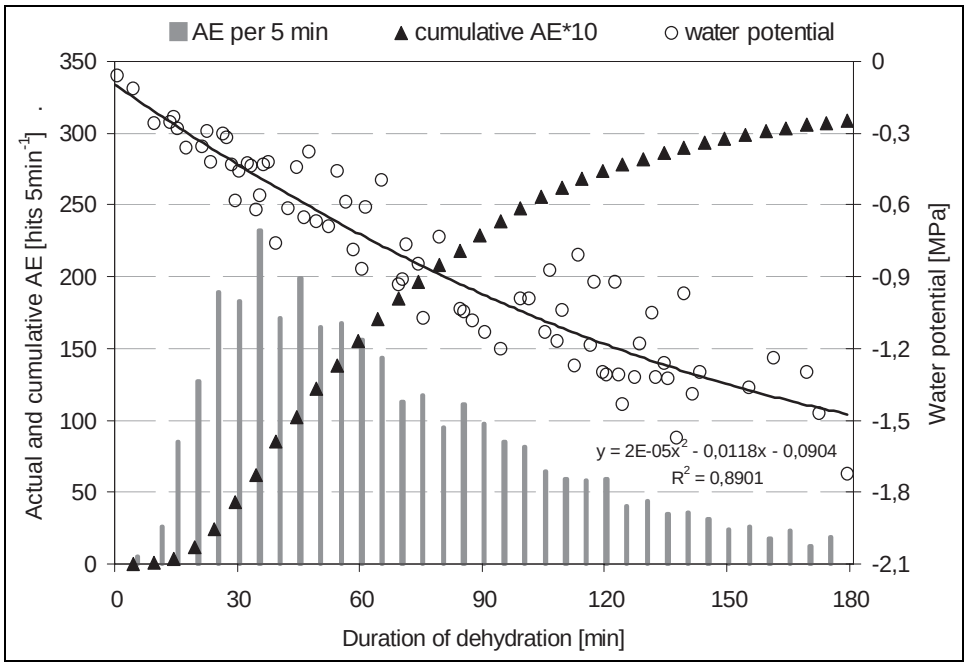


Fig. 3. Water potential and acoustic emission (AE) rate during 3 h of dehydration of cut rose 'Candid Prophyta'. AE profiles are from a representative single rose stem; water potential measurements were done with 60 roses, each dot represents a single rose.

transpiration of petals and leaves. An ABA additive as a stomata closing agent to the vase solution did not reduce relevantly the transpiration rate during darkness. This supports the assumption that cuticular transpiration is the main reason for high night transpiration and indicates a relevant water loss of cut roses during their vase life.

Effects of water stress

Exposure of cut rose stems to air has led to an increase of the transpiration rate for a period of short time followed by its progressive decrease during the 3 hour dehydration period. The increase is known in literature as Iwanoff effect (in: LÖSCH 2001) describing a passive opening of stomata by a strong initial release of tension after detaching leaves or stems. With a time lag of only a few minutes after exposure to air the cavitation rate increased rapidly and reached its maximum within the first hour of the dehydration phase. Measurements of water potential of roses under similar climatic conditions have shown that the water potential during the appearance of the first cavitations was not lower than − 0.2 to −0.3 MPa. And even at the time of the highest cavitation rate, it did not reach values lower than − 0.8 MPa. This indicates that with cut roses a high cavitation rate can occur also at a higher water potential than is described in literature (e.g. DIXON et al. 1988, VAN DOORN and JONES 1994, VAN DOORN and SUIRO 1996). However, VAN DOORN and SUIRO (1996) observed acoustic emissions shortly after beginning of the dehydration period and at a relatively high water potential (about −0.4 MPa), too. But, in their experiments a high cavitation rate was obtained much later, depending on the cultivar from 1 to 20 h after exposure to air, and at much lower water potentials (between −1.7 to −3.8 MPa). Possible explanations for these differences are either a different susceptibility of cultivars to cavitations, or more probably due to differences in sensor positions. In our experiments sensors were placed at the peduncle which has been proved to be usually much more sensitive to cavitations (SPINAROVA and HENDRIKS 2005) than basal parts of stems used by VAN DOORN and SUIRO (1996).

In addition to that, at the beginning of vase life measurements of acoustic emissions at the peduncle have a lower risk for detecting signals induced by stem shrinking or tissue fractures. That is one of the reasons, why UAE measurements at this position seem to be especially suitable for the observation of water stress with cut roses. Later on, when visible symptoms of rose wilting appear also on the peduncle, acoustic emissions should no longer be associated with cavitations only.

Long time observations of cut roses exposed to air have further shown, that, depending on stress conditions, the transpiration rate often stays on a low level for a long time, or only slightly increases after mild stress. In most experiments the initial transpiration level was not regained even during 24 h of rehydration following water stress. These observations are in a good agreement with current knowledge on stomata function after water stress (e.g. HU et al. 1998). For a relevant increase of the transpiration rate after water stress, e.g. the high ABA level has to be rebuilt, the CO_2 accumulation has to be reduced, or a relevant net import of osmotica has to be installed (in: LÖSCH 2001). Data from our experiments cannot answer the question which one of these mechanisms is controlling the late opening of stomata after drought stress.

Additionally to that, some own post-harvest experiments have shown a slight increase of vase life after moderate periods of dehydration. The obtained aftereffects of stomata closure after dehydration might be a key for better understanding such unexpected results.

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