

Drought effects on water flow, photosynthesis and growth of potted grapevines

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Summary

In two consecutive years and under different environmental conditions, leaf gas exchange, sap flow and trunk diameter were measured to estimate transpiration of grapevine. Daily maxima of sap flow were lower than estimations obtained by gas exchange measurements. Sap flow was delayed with regard to variation of irradiance. For irrigated plants the correlation between transpiration rates of single leaves as determined by gas exchange and instantaneous sap flow was high ($r^2=0.84$). However, the correlation of sap flow with the total daily water consumption was even higher ($r^2=0.98$) and close to 1:1. At various water states, leaf photosynthetic rate was also correlated with sap flow ($r^2=0.78$); the correlation coefficient increased to $r^2=0.91$ when the daily balance was compared. Plant growth, estimated from linear variable displacement transducers was closely related to the daily sap flow.

Key words: *Vitis vinifera* L., sap flow, photosynthesis, trunk diameter, water stress, water recharge, hydraulic conductivity.

Abbreviations: A = net photosynthesis, $\Delta\Phi$ trunk = increment in trunk diameter, E = transpiration, g = stomatal conductance, LVDT = linear variable displacement transducer, PFD = photon flux density, SHBM = stem heat balance method, SWC = soil water content, Ψ_{PD} , Ψ_{MD} = predawn and midday leaf water potential.

Introduction

Effects of environmental factors on whole-plant transpiration and photosynthesis are often derived from intensive single-leaf measurements. This approach has limitations due to the large variation of single-leaf values across the canopy, and possibly to uncertainties due to the specific conditions in the gas exchange cuvettes as compared to the ambient air (ANSLEY *et al.* 1994; GOULDEN and FIELD 1994; SMITH and ALLEN 1996).

The use of sap flow meters or linear variable displacement transducer sensors (LVTDS) seems to be a promising alternative to overcome these limitations (SMITH and ALLEN 1996; LINK *et al.* 1998). Sap flow measurements give reliable,

direct estimates of plant or shoot water loss without disturbing the leaf environment (SCHULZE *et al.* 1985; STEINBERG *et al.* 1990; ANSLEY *et al.* 1994; BRAUN and SCHMID 1999 b). On the other hand, LVTDS enable continuous measurements of the trunk diameter, which can be related to plant growth, water use and water status (KLEPPER *et al.* 1971; KOZLOWSKY 1972; GARNIER and BERGER 1986; SCHOCK *et al.* 1988; KATERJI *et al.* 1994). Shrinking and swelling of extensible plant tissues provide indirect information on transpiration streams during the day which are related to changes in the water content and turgor potential of their cells.

Previous work of our group has shown that water stress of grapevines at the leaf level reduces photosynthesis, due to both, stomatal closure and metabolic impairment (FLEXAS *et al.* 1998; 1999; 2002; ESCALONA *et al.* 1999; FLEXAS 1999). Photosynthesis and transpiration were also shown to be reduced at the whole-plant level in grapevines and other crops by means of trunk sap flow and LVDT measurements (HIGGS and JONES 1984; HUGUET 1985; SCHOCK *et al.* 1988; MYBURGH 1996; LOVISOLO and SCHUBERT 1998; ESCALONA 1999). In grapevines, sap flow measurements have also been used to determine stem morphology, plant water consumption and irrigation scheduling (BRAUN and SCHMID 1999 a; LASCANO *et al.* 1992; EASTHAM and GRAY 1998; GINESTAR *et al.* 1998; BRAUN and SCHMID 1999 b; CALÓ *et al.* 1999).

The main objective of the present work was to study the effects of drought on water transport and storage in grapevines by means of combined measurements of gas exchange, trunk sap flow and trunk diameter. Sap flow measurements possibly may be used to predict total plant photosynthesis and growth, then may facilitate regulation of deficit irrigation programs.

Material and Methods

Plant material and treatments: Six one-year-old vines, cv. Tempranillo grafted on R-110 rootstock, were grown under favorable conditions as described earlier (FLEXAS 1999), planted in pots (60 l) containing a 20:80 v/v mixture of organic matter and sandy loam. In the three months prior to starting measurements the plants were maintained at field capacity by periodically watering with 50% Hoagland solution (approximately $2.5 \text{ l pot}^{-1} \text{ d}^{-1}$). A 2-cm layer of perlite

was extended over each pot to diminish direct soil evaporation. At the onset of experiments shoot length was about 1.5 m and the average total leaf area was about 0.5 m².

A first experiment was conducted in 1996 in a glasshouse under environmental conditions similar to those outdoors. Measurements were made during two consecutive days (a sunny and a cloudy day, respectively) using 4 well-watered plants. Irrigation was then stopped and measurements were repeated 10 d later.

A second experiment was conducted in 1997, using 6 out-door-grown vines. During this experiment, different levels of drought were achieved by varying the irrigation regime (FLEXAS 1999).

Environmental conditions, plant water status and leaf area: Leaf temperature, leaf-to-air vapour pressure deficit and photon flux density (PFD) incident on the leaf surfaces were measured within the chamber of a Li-6400 infrared gas exchange analyser (Li-Cor Inc., Nebraska, USA). In the second year weather conditions (air temperature, relative humidity, wind speed, irradiance and precipitation) were registered in a weather station (Delta-T Devices, U.K.) placed in the experimental field.

Leaf water potential was measured with a Scholander chamber (Soil moisture Equipment Corp., USA) at predawn (6:00 h) and approximately at noon (13 - 14:00 h). Values from two different leaves per treatment were averaged. Soil water content (SWC) was measured with Time Domain Reflectometry (TDR, Trime-Sytrunk, IMKO, Switzerland), previously calibrated for the soil used in this experiment.

The total leaf area of each plant was calculated several times during the experiment using a previously obtained correlation with the length of the main leaf lamina. This correlation allowed rapid estimation of the total leaf area of each plant.

Gas exchange measurements: CO₂ assimilation rates (A), stomatal conductance (g) and leaf transpiration (E) of the 6th-8th leaf from the top were measured using a portable gas analyser (Li-6400, Li-Cor, USA). During the first experiment, diurnal changes of gas exchange parameters were monitored on a single leaf averaging measurements every 30 min. The leaf was oriented to the sun. During the second experiment, measurements were taken at fully expanded leaves in their natural position; 8 times per day, from predawn to sunset, measurements at 6 different leaves per treatment were averaged. Total daily net photosynthesis and transpiration were calculated as the integral of each diurnal cycle, assuming the measured value to be representative of the interval between two consecutive measurements.

Sap flow measurements: Sap flow was determined by the trunk heat balance method (Dynagauge, Dynamax, USA). Gauges suitable for trunk diameters from 0.9 to 1.1 cm (SG 10 type) were applied. The power input to the heater was set to recommended values and no damage of the shoot was observed during the measurements. The value used for thermal conductivity of the trunk (Kst) was 0.42 W m⁻¹ K⁻¹ (STEINBERG *et al.* 1990). The sheath conductance constant (Ksh) was calculated for each gauge as a mean value recorded between 3 and 6 a.m., assuming no sap

flow. Signals were logged every 10 s and averaged over 30 min.

During the first experiment, diurnal courses of sap flow were recorded for 4 different plants (corresponding to different degrees of soil water depletion) together with gas exchange measurements. During the second experiment, sap flow of 6 plants submitted to different water availabilities, was continuously recorded over the 30-d experiment.

The sap flow data were related to the leaf area in order to compare them with leaf gas exchange, assuming that all the leaves had rates similar to those used for gas exchange measurements. This was likely during these experiments, provided that all the leaves were fully exposed and non-senescent at the time of experiments.

To test the gauges for proper operation, sap flow per h and per d was compared with gravimetric measurements of water loss of the same potted plants. A highly significant correlation was obtained between sap flow and weight loss ($r^2 = 0.94$, $P < 0.001$), which was close to 1:1. Sap flow data were recalculated according to this correlation, even the differences between recorded and calculated values were <9 %.

Measurements of trunk diameter: Changes in the diameter of trunks were continuously recorded during the 30 d of the second experiment, using linear displacement transducers (LVDTs) (Solartron Metrology, UK). Six sensors made of INVAR (64 % Fe, 36 % Ni), a material whose dilation is negligible (0-2 µm) under common temperature ranges, were installed in the plants where sap flow sensors were placed. Data were logged every 15 min with a CR10X data-logger module (Campbell Scientific Logan, USA). Daily growth of the trunk was calculated as the difference between two successive daily maxima of the trunk diameter.

Results and Discussion

The experiments were performed during a typical Mediterranean summer, with average maximum PFDs of about 1500 µmol m⁻² s⁻¹, midday temperatures around 32 °C, and VPDs ranging from 2 to 3 kPa. Soil water content ranged between 20 % (irrigation) and 8 % (most severe drought), while pre-dawn leaf water potentials ranged between -0.01 MPa and -0.66 MPa. This range has been observed for Tempranillo under field conditions (FLEXAS *et al.* 1998). Midday leaf water potentials showed similar values regardless of treatment, which agrees with field observations on this cultivar (FLEXAS *et al.* 1998; FLEXAS 1999) and others (CHONÉ *et al.* 2001).

During both experiments there was a significant decrease of daily sap flow under water stress conditions (*e.g.* Fig. 1 A). This is a widely reported response of plants to soil water depletion, usually associated to decreased stomatal conductance, which in turn is triggered by ABA synthesised in roots and/or to decreased leaf water potential (SCHULZE 1986; CHAVES 1991; TARDIEU and SIMONNEAU 1998). There was also a concomitant decrease in transpiration and stomatal conductance (data not shown). It seems unlikely that leaf water potential triggered stomatal closure here, as grapevines showed isohydric behaviour, with similar values

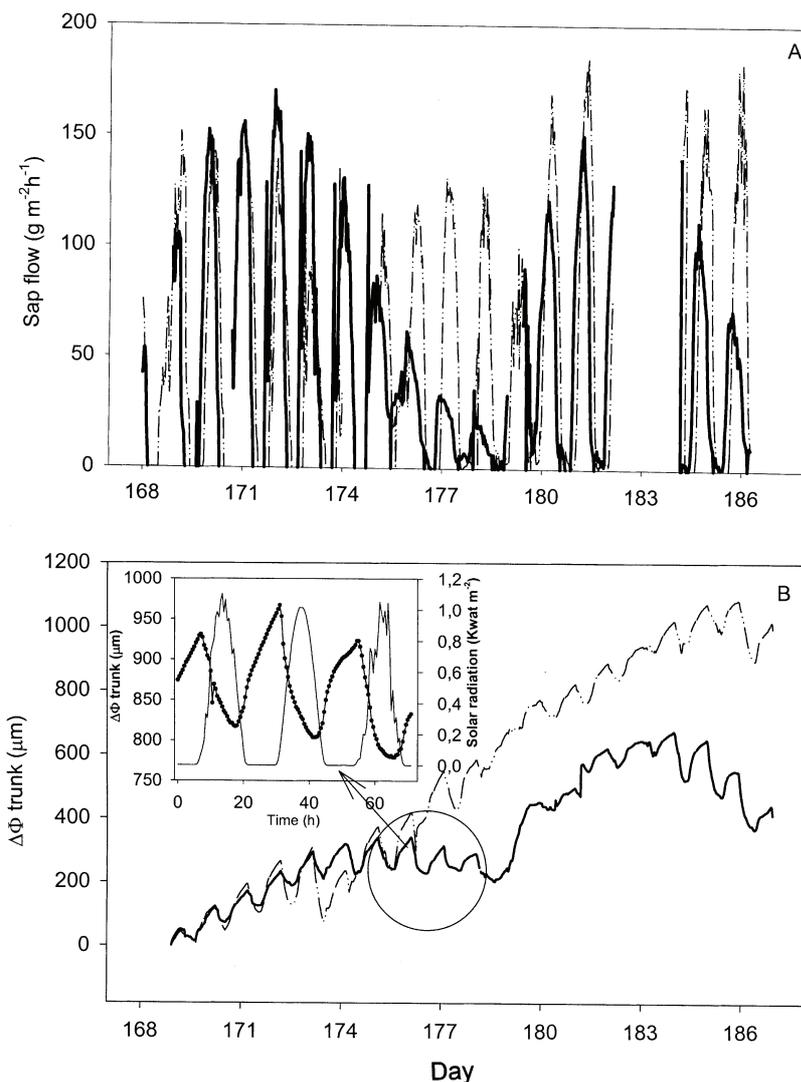


Fig. 1: Continuous recordings of sap flow (A) and trunk diameter (B) of grapevine plants submitted to two consecutive cycles of water stress. The insert shows a detail of trunk diameter changes. Data are means from two plants per treatment (dotted lines, irrigated; solid line, non-irrigated).

of midday leaf water potential in both, irrigated and water stressed plants. ABA signalling could be the cause for reduced conductance and transpiration, since it has previously been reported as an important conductance modulator in grapevines (CORREIA *et al.* 1995). Also, in isohydric species such as grapevines, reductions of sap flow are likely to be due to decreased xylem conductivity as inferred, from the Hagen-Poiseuille formulation of sap flow itself, since the isohydric behaviour implies small variations in $\Delta\Psi$. Decreased hydraulic conductivity in water-stressed grapevines has been described by SCHULTZ and MATTHEWS (1988).

Trunk growth also reflected the effects of water stress. Fig. 1 B shows daily variations on trunk diameter for an irrigated and a water-stressed plant. Trunk diameter decreased during the day and increased at night. These variations are the sum of at least two components: trunk growth, and shrinking and swelling of the xylem vessels. The irrigated plants showed a progressive growth of the trunk diameter, since the difference between two consecutive daily

peaks was always positive. Total trunk growth during the 20 d of the experiment was about 1.1 mm, and the maximum daily growth was around 100 μm . Similar results were obtained by MYBURGH (1996). In water-stressed plants the pattern was similar to that of irrigated plants at the beginning of the experiment, as well as after irrigation at the end of the first drought cycle. At water deficiency, however, the daily growth stopped for several days. These variations paralleled the decrease in sap flow. With prolonged water stress, the difference between two consecutive daily peaks was negative.

Variations in trunk diameter showed two different phases, defined by a change of slope (Fig. 1 B, insert). The first one, which occurred during the first 4 h of the night, was coincident with the remaining sap flow period after sunset (see below). The magnitude of trunk diameter variation during this phase decreased with increasing drought, from around 29 μm (irrigation) to 17 μm (most severe water stress). The second phase, which started after sap flow cessation and

which consisted of stepwise trunk diameter increases of about 30 μm , was less affected by drought (data not shown). The different effects of water stress on these two phases strongly suggest that water stress mainly affected the pattern of water recharge at night, with a smaller effect on total daily trunk growth.

A high degree of similarity was observed between daily courses of transpiration rates as measured either by sap flow or by gas exchange (Fig. 2), although a certain displacement between the two curves can be observed. During a typical sunny day (Fig. 2 A), maximum transpiration values were recorded between 12:00 and 14:00 h, but in the morning flux estimated by gas exchange was always higher than sap flow. On average, the course of sap flow showed a 45 min delay with respect to leaf gas exchange readings. For a cloudy day (Fig. 2 B) the transpiration rates estimated by both methods were considerably lower. However, during a short sunfleck interval at 15:00 h, the transpiration rate increased to values similar to those observed under sunny conditions. Again, during the sunfleck, reactions of gas exchange were higher than those of sap flow. When the plants were subjected to water stress (Fig. 2 C), transpiration rates were reduced throughout the day. Early in the morning, a transpiration peak was recorded by gas exchange; it was not reflected by the sap flow pattern, which showed a gradual but sustained decrease during the day. Later in the evening, even though leaf transpiration stopped, sap flow was still measurable, possibly showing the capacity of the plant water deficit.

A displacement between gas exchange and trunk flow values, the first showing a higher peak transpiration, has also been found in other studies (SCHULZE *et al.* 1985; GREEN *et al.* 1989; GUCCI *et al.* 1990; STEINBERG *et al.* 1990). As shown by the present results, such a displacement is accompanied by the maintenance of a certain water flux in the evening (when leaf transpiration is very low) and at night. The sap flow remaining after sunset has been described as a good estimate of the recharge volume (PHILLIPS *et al.* 1996). It is clear however, that sap flow of irrigated plants was higher than transpiration in the evening, after 18h (Fig. 2 A). Such a difference may indicate that recharge starts before sunset, which is consistent with the observed afternoon recovery of leaf water potential in field-grown grapevines (DÜRING and LOVEYS 1982; BARCELÓ *et al.* 1998). If this afternoon recharge flux (sap flow minus leaf transpiration) is added to the nocturnal recharge, absolute values of recharge were approximately 230 g plant^{-1} under irrigation.

Under water stress, sap flow exceeds transpiration before noon (after 11h) (Fig 2 C), even though sap flow and transpiration data are very low. Under these conditions absolute values of recharge were only 130 g plant^{-1} . A decrease of the absolute recharge under drought is consistent with the idea of increased xylem cavitation, which has been shown in water-stressed grapevines (SCHULTZ and MATTHEWS 1988) and would help to explain the decreased hydraulic conductance and sap flow. It is also consistent with the described reduction of the first phase of nocturnal trunk diameter variation under water stress (Fig. 1 B, insert).

Despite the small differences between these two approaches, a good correlation between the transpiration val-

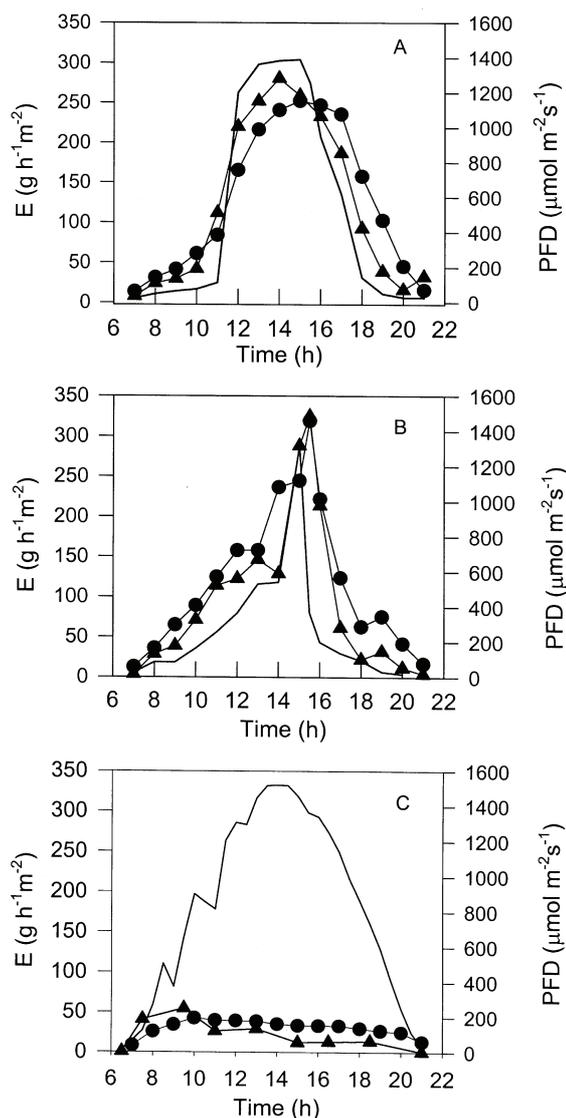


Fig. 2: Diurnal courses of transpiration (E) measured by sap flow (circles) and gas exchange (triangles) of irrigated plants on a sunny (A) and a cloudy day (B), and plants under drought conditions (C). The solid line represents photosynthetic photon flux density (PPFD).

ues estimated by both methods was observed (Fig. 3 A). When these two methods for estimating transpiration were compared on a daily basis the correlation was even closer (Fig. 3 B), thus supporting the validity of sap flow measurements for the estimation of total plant transpiration. It remains to be tested if the relationship still holds under field conditions, with more complex canopies and highest LAI, when many leaves never receive direct radiation (ESCALONA 1999).

It is well known that there is a high correlation between stomatal conductance (and, thereby, transpiration) and net CO_2 assimilation (CHAVES 1991). Since sap flow measurements accurately reflect whole-plant transpiration, some correlation between leaf photosynthesis and sap flow is expected and has indeed been observed. Although some scattering was present when plotting instantaneous values of A and sap flow (Fig. 3 C), the correlation was distinctly improved by using integrated daily balances (Fig. 3 D). Thus,

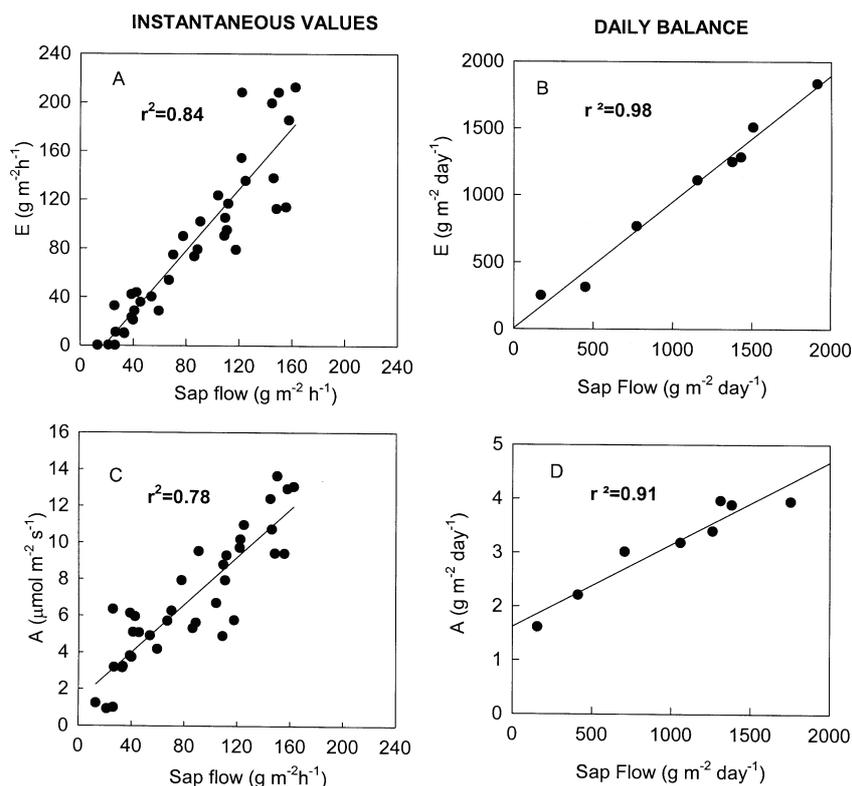


Fig. 3: Relationship between instantaneous values of sap flow and E and A (left: A, C); relationship between the daily balance of sap flow and the daily balance of E and A (right: B, D). Measurements correspond to diurnal courses at varying water status.

as sap flow correlates with photosynthesis, and whole plant photosynthesis is the main determinant of plant growth (FARQUHAR and SHARKEY 1994; LAWLOR 1995), some correlation between sap flow and plant growth is expected. To test this correspondence we used the increment of trunk diameter between consecutive days as an indicator of growth (GRACIA *et al.* 1999). A close relationship between daily trunk growth and daily sap flow was observed (Fig. 4) which supports the hypothesis that sap flow measurements could also be a promising tool for estimating plant growth, at least in periods of important vegetative growth, *i.e.* from flowering to veraison. These results encourage further studies on these relationships in the field, with a more dense and complex canopy.

In summary, the present results show that sap flow and trunk diameter measurements could be interesting approaches to estimate total plant water consumption under different environmental conditions. Also, they may serve to estimate total plant photosynthesis and growth, and to develop regulated deficit irrigation programs with the aim to maximise water use efficiency.

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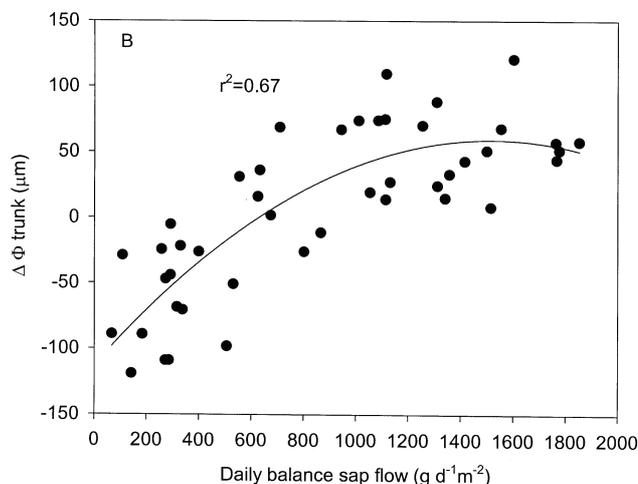


Fig. 4: Correlation between daily trunk growth (estimated as the difference between the peaks on two consecutive days) and daily sap flow.

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