Water Uptake by Cotton Roots During Fruit Filling in Relation to Irrigation Frequency

J. W. Radin,* J. R. Mauney, and P. C. Kerridge

ABSTRACT

Yield of irrigated cotton (Gossypium hirsutum L.) increases as the interval between water applications is decreased, even if the total amount of water applied is unchanged. Experiments were undertaken to compare season-long water relations of high-frequency dripirrigated cotton (1- to 2-d intervals) to cotton irrigated at approximately 2-wk intervals. The crop was grown at two locations in central Arizona on a Mohall sandy loam (fine-loamy, mixed, hyperthermic Typic Haplargid) and an Avondale clay loam (fine-loamy, mixed, hyperthermic Typic Torrifluvent) soils. In 2-yr trials at each location, irrigation frequency had inconsistent effects on midday leaf water potential (\Psi_w) during vegetative growth. When the crop developed a heavy fruit load, however, Ψ_w of plants on the longer cycles was much lower than that of drip-irrigated plants, even after irrigation when ample soil moisture should have been available. Plant hydraulic conductances, estimated from regressions of single-leaf transpiration rate against Ψ_{un} were high in both treatments early in the season. Hydraulic conductance decreased greatly during fruiting in plants on long irrigation cycles but less so in drip-irrigated plants. Late in the season, after fruit maturation and during plant regrowth, conductances were again high and similar in the two treatments. The results imply that during heavy fruiting, mild water stress associated with long irrigation cycles triggers deterioration of the root system that is very slow to be reversed. High-frequency drip irrigation, by preventing cyclical stress, apparently minimized this deterioration during fruit filling.

RIP IRRIGATION (frequent delivery of small amounts of water to match current demand) has found wide acceptance for production of high-value crops (Bresler, 1977; Howell et al., 1980). Its use has largely been limited to crops with high cash return because of the cost of installing and maintaining a delivery system. Recently, though, drip irrigation has found favor as a method to deliver water to cotton, especially in areas of relatively high water costs in which irrigation efficiency is paramount (Wilson et al., 1984). An estimated 40% of cotton in Israel in 1985 was drip-irrigated (Halevy and Kramer, 1986). In the southwestern USA, drip irrigation increases yields of cotton on light or shallow soils in which water storage is inadequate to supply the crop over an extended irrigation cycle (Howell et al., 1980; Wilson et al., 1984; Bucks et al., 1988). Some recent reports, however, indicate substantial yield increases under other circumstances as well (Briggs et al., 1983; Wuertz and Tollefson, 1987). Henggeler (1988) concluded that yields increase by 1.5 to 2% for each day subtracted from the irrigation cycle, independently of soil conditions.

There are several possible causes of yield increases with increasing irrigation frequency. Bucks et al. (1988) found significant diurnal plant water stress toward the end of a long irrigation cycle. Daily drip irrigation alleviated this stress, allowing the crop to approach its

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production potential for more days of the season. An altogether different view is that of Carmi and Shalhevet (1983) and Ben-Porath (1985). They reported that simulation of drip irrigation by artificial restriction of rooting volume (small pots) caused a more favorable partitioning of biomass among plant organs, leading to a more compact structure, greater fruiting efficiency, and enhanced earliness. They advanced the hypothesis that hormonal changes due to root volume restriction could be responsible for improved fruiting efficiency of drip-irrigated cotton.

A third possible mechanism for effects of drip irrigation on yield involves altered plant water relations. Water encounters significant resistance to flow as it passes through the plant, particularly in the root system (Fiscus, 1983). If drip irrigation were to decrease root resistance, such a shift could promote water extraction and thus give rise to the same growth changes as those ascribed to improved irrigation efficiency. Studies reported here were undertaken to test for direct effects of drip irrigation on plant water relations and transport resistances.

MATERIALS AND METHODS

Cotton was grown at two experimental sites in Arizona. In 1984 and 1985, 'Deltapine 62' was grown at the Maricopa Agricultural Center of the University of Arizona. The soil was a Mohall sandy loam. Crops in adjacent fields were irrigated either by gravity flow in sloping furrows or by a subterranean drip irrigation system. Each treatment was replicated three times in a split-plot design, with irrigation regimes as the main plots and days of sampling as the subplots. Rows were spaced 1 m apart, and each plot was four rows wide by 12.2 m long. All plant samplings and measurements were made on an interior row. Cultural practices in the furrow-irrigated treatment were similar to normal commercial practices in the area. Cotton was planted on Day 114 and Day 105 in 1984 and 1985, respectively, with a final plant population of approximately 100 000 ha⁻¹. Generally, 200 mm of water was applied with each irrigation. Total irrigation plus rainfall during 1984 and 1985 was approximately 1640 and 1740 mm, respectively. A total of 168 and 213 kg N ha⁻¹ was applied in the 2 yr.

The drip-irrigated treatments are described elsewhere in detail (Mezainis, 1985; Tucker et al., 1986). Evapotranspiration (ET) was estimated from Erie et al. (1982) to determine the irrigation requirement, and water was supplied to the plants on 1- or 2-d intervals. The drip-irrigated treatments selected for study in 1984 and 1985 received 117 and 100% of estimated ET, respectively (total applied = approximately 1200 and 1030 mm). Total N applied through the irrigation system was 224 kg ha⁻¹ in 1984 and 75 kg ha⁻¹ in 1985. These N rates were adequate to support full yield in both years (Tucker et al., 1986).

Experiments in 1986 and 1987 were at the Western Cotton Research Laboratory, Phoenix, AZ. The soil at this location is an Avondale clay loam. Comparisons in these years were between biweekly flood irrigations in level basins and surface drip irrigations. 'Deltapine 61' cotton was planted in raised beds within the level basins on Day 90 in 1986 and Day 98 in 1987. Each treatment was replicated four times,

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but the experimental design was otherwise as described above. Plots were four rows wide, with a row spacing of 1 m. In the flood-irrigated treatments, irrigations were 150 mm usually applied at 2-wk intervals. The total water applied (including rainfall) was approximately 1460 and 1470 mm in 1986 and 1987, respectively. Urea (about 168 kg N ha⁻¹) was applied in each year.

The drip-irrigated plots were watered daily with an amount of water calculated from pan evaporation with an adjustment for leaf area (Kimball et al., 1986). Total water added (irrigation plus rainfall) was approximately 1340 and 1460 mm in 1986 and 1987, respectively. In 1986, N was added in only very small quantities (10 kg ha⁻¹). In 1987, N (88 kg ha⁻¹ total) was added weekly through the drip system.

Leaf $\Psi_{\rm w}$ (xylem pressure potential) was determined with a pressure chamber. Procedures for excision, transport, and handling of leaves were described earlier (Radin et al., 1985). All leaves used for these measurements were recently expanded mainstem leaves in full sunlight and were collected in early afternoon (1230 to 1430 h). In all cases, duplicate leaves were randomly selected from each replicate plot. Effects of irrigation regime and day of year on midday $\Psi_{\rm w}$ were assessed by analysis of variance, with each year considered as a separate experiment. The LSD for comparison of irrigation regimes within any single day was calculated according to Cochran and Cox (1950). Comparisons within an irrigation regime were by Duncan's multiple range test.

Stomatal conductances were determined with a LI-COR LI-1600 porometer (LI-COR, Lincoln, NE). Again, measurements were made in early afternoon on the most recently expanded mainstem leaves in full sunlight. Total leaf conductance was the sum of the conductances from each side. Within each replicate, readings were on randomly selected duplicate or triplicate leaves. Data were analyzed as described for midday $\Psi_{\rm w}$.

Plant hydraulic conductances were estimated as slopes of regressions relating transpiration rate to leaf Ψ_w (Bates and Hall, 1982; Fiscus, 1983). Transpiration rates of single leaves were determined with the LI-1600 porometer in the transpiration mode. On several days during the season, rates were obtained at four or five intervals beginning before dawn and ending at midday. Duplicate leaves in each plot were selected as described above. Immediately after measurement of transpiration, the leaves were excised and were stored under dark humid conditions for transport to the laboratory. Leaf water potentials were determined in the laboratory after transpiration measurements were finished. Tests showed that an excised leaf could be stored for several hours without significant change in its water potential. For each date and treatment, the relationship between transpiration rate and $\Psi_{\rm w}$ was determined by linear regression analysis. In 1986, readings across replicate plots were combined because not all replicates were measured each time. In 1987, transpiration and Ψ_{w} were determined in each replicate plot at each time interval. Regressions were calculated separately for all four replicates of each treatment, and the slopes of these regressions were analyzed as described for midday $\Psi_{\rm w}$.

Crop development was followed during the season by weekly destructive harvests. In 1984 and 1985, 1-m sections of a row were harvested, but in 1986 0.3-m sections (three plants) were harvested. All plants within the randomly selected sections were brought to the laboratory for determinations of leaf area and boll numbers. Leaf areas were measured with a LI-COR LI-3100 leaf area meter. Boll numbers were normalized to 1-m² ground area and analyzed as described for midday $\Psi_{\rm w}$ (except for data from 1985, when plant samplings were on different days in the two irrigation treatments and thus were not comparable).

RESULTS

With relatively long irrigation intervals, the leaf Ψ_{w} of cotton tended to rise and fall with the availability of soil water. This pattern is illustrated for 1987 in Fig. 1. Two observations are noteworthy. First, leaf $\Psi_{\rm w}$ sometimes fell below -2.0 MPa toward the end of a cycle, indicating stress (Grimes and Yamada, 1982; Guinn and Mauney, 1984; Radin et al., 1985). Second, the degree of recovery of leaf Ψ_w after irrigation depended upon time of season. Before Day 185, recovery was complete within a few days of irrigation, with the $\Psi_{\rm w}$ rising to match that of the drip-irrigated plants (Fig. 1). After Day 185, though, leaf ψ_w did not increase after irrigation to the same degree. A similar pattern was seen in all years, with the midseason "recovery" $\Psi_{\rm w}$ 0.2 to 0.7 MPa below the $\Psi_{\rm w}$ of drip-irrigated plants on the same day (Fig. 2 to 4, upper panels). In 1984 and 1986, measurements very late in the season again showed convergence of postirrigation leaf $\Psi_{\rm w}$ in the two treatments, but in 1985 and 1987 there was no convergence during the observation period (Fig. 1 to 4). The effect of irrigation treatment (I) on postirrigation midday $\Psi_{\rm w}$ was significant (P < 0.05) only in 1986 and 1987, the 2 yr that the tests were run at Phoenix. In all 4 yr, the effects of the day of year (D) and of the $I \times D$ interaction were significant (P < 0.01 and P < 0.05, respectively).

One possible reason for the lower postirrigation $\Psi_{\rm w}$ in plants on long cycles could be a greater rate of transpiration. Measurements of midday stomatal conductances in 1984 did not support this contention. Except for Day 165 early in the season, conductances of furrow-irrigated plants did not exceed those of dripirrigated plants (Table 1). Furthermore, the leaf area index of the furrow-irrigated crop was slightly less than that of the drip-irrigated crop (not shown). As a result, it seems unlikely that water fluxes through furrow-irrigated plants could be larger than those of drip-irrigated plants.

The cotton crop often undergoes a developmental phenomenon known as "cutout" (Mauney, 1986). When fruiting begins, vegetative growth slows and may

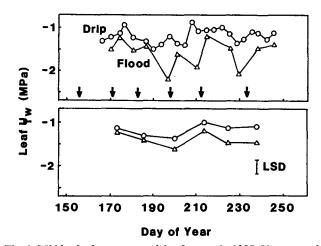


Fig. 1. Midday leaf water potentials of cotton in 1987. Upper panel: all measurements included. Lower panel: values shown only for selected dates that closely followed irrigation or rainfall. Arrows show times of flood irrigation. Vertical bars indicate LSD (0.05) for within-day comparisons.

eventually stop. As the fruit load increases, the retention rate of young fruits also declines sharply (Guinn and Mauney, 1985). In all years, divergence of $\Psi_{\rm w}$ in the two irrigation treatments occurred when the crop was carrying 80 to 100 bolls $\rm m^{-2}$ ground area. This was also approximately the time when boll number became constant, especially in 1984 and 1986 (Fig. 2 to 4, lower panels). Additionally, in 1986 the late-season convergence of $\Psi_{\rm w}$ in the two treatments approximately coincided with emergence from cutout and entry into a second cycle of fruiting. In 1984, late season convergence of $\Psi_{\rm w}$ was not associated with emergence from cutout.

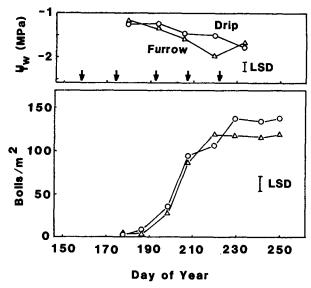


Fig. 2. Midday leaf water potentials (upper panel) and fruit load (lower panel) of cotton plants in 1984. Measurements were made when soil moisture was adequate to support full transpiration. Arrows show times of furrow irrigation. Vertical bars indicate LSD (0.05) for within-day comparisons.

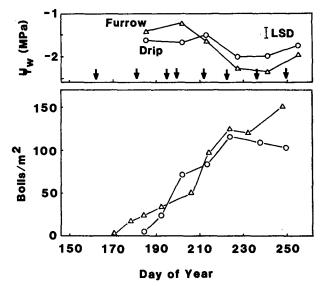


Fig. 3. Midday leaf water potentials (upper panel) and fruit load (lower panel) of cotton plants in 1985. Measurements were made when soil moisture was adequate to support full transpiration. Arrows show times of furrow irrigation. Vertical bar indicates LSD (0.05) for within-day comparisons.

Seasonal changes in plant water relations were studied in more detail in 1986 and 1987. In 1986, the postirrigation $\Psi_{\rm w}$ of the two crops diverged beginning around Day 190 (Fig. 4). As in 1984, this time coincided with the cessation of fruit set. In 1986, measurements were carried out long enough to observe the second flush of fruit set after maturation of the first fruits. Fruit set resumed in drip-irrigated plants around Day 240; the leaf $\Psi_{\rm w}$ of the two treatments was again similar when measured on Day 245 (Fig. 4). Hydraulic conductances of plants were estimated from relationships between single-leaf transpiration and leaf $\Psi_{\rm w}$ (Bates and Hall, 1982). Regressions were calculated with leaf Ψ_w as the independent variable and water flux (J) as the dependent variable, i.e., with the equation in the form $J = \Delta \Psi_w/R$ in which R is the hydraulic resistance. The slope of such a regression yields the hydraulic conductance (= 1/resistance). In drip-irrigated plants in 1986, conductance on Day 183 (before cutout) was very high. Conductance declined somewhat during the season, reaching its lowest value of 34 mmol m^{-2} s⁻¹ MPa⁻¹ on Day 245 (Fig. 5). In plants on longer irrigation cycles, though, conductance

Table 1. Midday stomatal conductances of cotton leaves in 1984. Measurements were made following irrigation or rainfall, when soil moisture was adequate to support rapid transpiration.

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	Day of year	Stomatal conductance, mm s ⁻¹	
		Drip irrigation	Furrow irrigation
	165	18.8c†	23.2d
	180	40.2a	33.4b*
	194	32.7b	32.2b
	206	40.7a	42.8a
	220	42.5a	18.0e**
	234	36.2b	27.7c*

^{*,**} Significantly different from drip-irrigated plants on the same day (P < 0.05 and P < 0.01, respectively).

 $[\]dagger$ Means within a column not followed by the same letter are significantly different (P < 0.05).

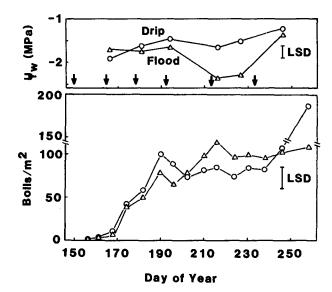


Fig. 4. Midday leaf water potentials (upper panel) and fruit load (lower panel) of cotton plants in 1986. Measurements were made when soil moisture was adequate to support full transpiration. Arrows show times of flood irrigation. Vertical bars indicate LSD (0.05) for within-day comparisons.

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followed a different seasonal pattern. In this case, it was >34 mmol m⁻² s⁻¹ MPa⁻¹ both early and late in the season, but was less than half that value on Day 218 during cutout (Fig. 5).

In 1987, the measurements were repeated. Plants irrigated on long cycles again showed significantly lower hydraulic conductances than drip-irrigated plants on Day 202 and Day 216, although in this year the differences between treatments were considerably smaller than in 1986 (Table 2). Values again converged toward the end of the season on Day 244. Ir-

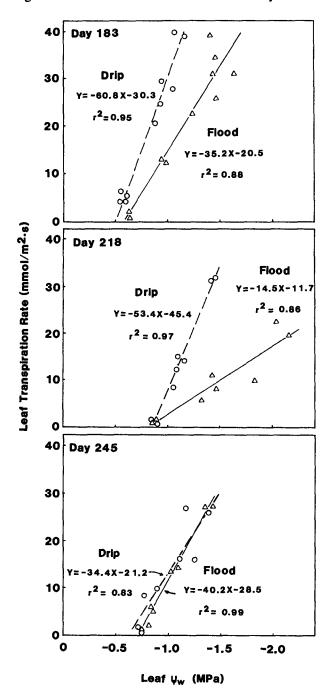


Fig. 5. Regressions relating single-leaf transpiration rate of cotton to leaf water potential on 3 d in 1986. All measurements were taken within 4 d following irrigation or rainfall to minimize soil moisture stress. Each point represents measurements within a single replication.

rigation regime had no significant effect on hydraulic conductance, but both day of measurement and the I \times D interaction had significant effects (P < 0.01 and P < 0.05, respectively). All of these data were acquired 4 d following an irrigation, so differences did not simply reflect the depletion of water from the root zone. Rather, the pattern indicates that water transport properties depend strongly upon stage of crop development.

DISCUSSION

Experiments reported here were carried out in plots devoted to other investigations as well. "Irrigation treatments imposed upon the crop include not only different irrigation regimes, but also different fertilization schemes and other cultural practices. The results are discussed here solely in terms of the differences in irrigation, but these other uncontrolled factors may also have contributed to the results. Of particular interest is the difference in N application rates in 1986. Several criteria indicate that the drip-irrigated crop was not substantially deficient in N at any time. Although leaf N concentration was slightly low (28 g kg⁻¹) on Day 210, petiole NO₃-N and leaf photosynthetic rate were not significantly increased by fertilization in adjacent plots. The seed cotton yield in 1986 was similar to the long-term average on this field (Kimball et al., 1986) and exceeded the yield on the same field in 1987, despite the increased N application in that year (B.A. Kimball, personal communication,

Two important effects of high-frequency drip irrigation can be identified. First, frequent replenishment of water prevents the cyclical water stress that can occur with longer irrigation intervals. In a study of drip-irrigated cotton in Arizona, Bucks et al. (1988) concluded that drip irrigation benefits yields by timely delivery of water to alleviate soil moisture stress. Although they reported no other important effects on crop water relations, their observations were confined to the first half of the season. Our data during the first half of the season (Fig. 1 to 4) are consistent with those of Bucks et al. (1988).

A second important effect of drip irrigation is seen when the crop approaches cutout. At this stage of growth, plants irrigated on long cycles apparently develop a decreased ability to withdraw water from the soil. Data obtained on Day 218 of 1986 illustrate this

Table 2. Hydraulic conductances of cotton plants in 1987. Conductances were estimated from slopes of regressions relating single-leaf transpiration rate to leaf water potential. Measurements were made 4 d following irrigation, when soil moisture was adequate to support rapid transpiration.

Day of year	Hydraulic conductance, mmol m ⁻² s ⁻¹ MPa ⁻¹	
	Drip irrigation	Flood irrigation
174	28.8c†	26.8c
188	37.8b	43.8a*
202	26.5d	21.9d*
216	39.4a	30.8b**
244	26.0d	27.8c

^{*,**} Significantly different from drip-irrigated plants on the same day (P < 0.05 and P < 0.01, respectively).

[†] Means within a column not followed by the same letter are significantly different (P < 0.05).

point (Fig. 5). For a leaf transpiration rate of 20 mmol m^{-2} s⁻¹, the leaf Ψ_w was -1.2 MPa in the drip-irrigated crop and -2.2 MPa in the furrow-irrigated crop. Nonetheless, the predawn Ψ_w was similar for the two treatments (points nearest the X-intercept of the regression). This convergence at very low flow rates indicates that the difference between treatments lies in the water transport pathway and is expressed only at high flow rates. At this time of the season, then, yield-depressing $\Psi_{\rm w}$ values are maintained after irrigation because the plants on long irrigation cycles only very slowly recover the ability to extract available soil moisture. Evidence that these observations are related to cutout includes the restoration of early season behavior late in the season after emergence from cutout (Fig. 5, Table 2). Cotton is known to be very sensitive to water stress during fruiting (Hiler and Howell, 1983). Our observations may provide a partial explanation of this increased sensitivity. Interpretation is difficult, though, because sensitivity to stress is maximal when potential ET is near its peak (Erie et al., 1982). Poor recovery from stress may also be related in part to increased water depletion before irrigation.

The measure of plant hydraulic conductance in these experiments is crude. Some assumptions underlying the method are (i) that single-leaf transpiration is proportional to the flux of water through the entire plant; (ii) that transpired water comes from the soil rather than from the stem or other water-storing tissue; and (iii) that the major resistance to flow is in the plant rather than the soil. The first assumption is justified by the fact that radiant energy driving transpiration is absorbed mostly by the upper leaves of the canopy. Regarding the second assumption, although capacitance was not measured, the extremely high transpiration rates typical of cotton in Arizona preclude a sustained role for stored water as a source. The third assumption is supported by considerable data (e.g., Blizzard and Boyer, 1980). Furthermore, most of the plant resistance arises in the roots (Blizzard and Boyer, 1980; Fiscus, 1983).

Diminished root function during fruiting has been suggested before, particularly with reference to uptake of specific nutrients (Crowther, 1934; Mauney and Hendrix, 1988). Our conclusions regarding the furrowirrigated crop are similar, except that fruiting seems to be limiting uptake of water rather than nutrients. Presumably the effect of irrigation regime was unrelated to differences in depth of rooting, as both Taylor and Klepper (1971) and Meyer and Ritchie (1980) showed that depth did not influence root resistance of cotton.

An alternative explanation of these results may lie in root responses to stress and their dependence upon carbon budgets of the plant. Cessation of vegetative growth and shedding of young bolls during cutout is believed to result from a "carbohydrate stress," i.e., the use of virtually all available assimilates by the maturing bolls (Guinn and Mauney, 1985). This carbohydrate stress also affects the root system, and the potential for root growth becomes limited during fruiting (Eaton, 1931; Crowther, 1934; Eaton and Joham, 1944). McMichael (1986) stated that the root/shoot ratio reaches a peak when fruiting begins, declining

thereafter. Water stress during fruiting greatly accelerates the root system decline (Taylor and Klepper, 1974; Browning et al., 1975). When Taylor and Klepper irrigated water-stressed cotton during cutout, the root system did not regrow, unlike its response to irrigation before cutout. As a result, leaf Ψ_w recovered extremely slowly during cutout compared to its recovery before cutout (Taylor and Klepper, 1974). In drip-irrigated plants, the frequent watering may maintain higher water absorption capacity by minimizing stress-induced turnover of roots.

Visible effects of high-frequency irrigation include later and less severe cutout. In 1984, this was evidenced as 20% more bolls on plants after the first fruiting cycle (Fig. 2), and in 1986, as an earlier resumption of rapid boll set after emergence from cutout (Fig. 4). In 1985, there was no evidence that drip irrigation benefitted crop development (Fig. 3). Reasons for this difference are not known; however, the "window" of vulnerability is brief, and yield effects should be highly dependent upon evaporative demand and cultural conditions during that period. It may be difficult to demonstrate such effects with consistency.

Most cotton producers in the southwestern USA utilize a long growing season, harvesting after the crop has matured its second flush of fruits. Our data imply that ineffectiveness of the root system during fruiting can promote an early cutout and shorten the first fruiting cycle, thereby increasing the grower's dependence upon the second cycle (cf. Fig. 2). Thus, high-frequency drip irrigation may not only save water by improved irrigation efficiency, it may also facilitate short-season cotton production (harvest after one fruiting cycle) by minimizing root system ineffectiveness. This is consistent with the experience of one major producer in Arizona (Wuertz and Tollefson, 1987). If modified irrigation practices could prevent this decline of the root system without resort to expensive drip systems, the benefits would be very substantial.

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