

DIURNAL CIRCADIAN VARIATION IN PHOTOSYNTHESIS IN *Dracaena sanderiana* UNDER CONTRASTING TEMPERATURE AND LIGHT

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ABSTRACT

Dracaena sanderiana is prominent and in-demand cut foliage in the global ornamental industry. It is important to know how this species perform under variable environmental conditions. This study was conducted to examine the stress responses of *Dracaena sanderiana* under contrasting temperature and light conditions by using chlorophyll fluorescence (ChlF) transient analysis technique. *D. sanderiana* cuttings were held in distilled water and subjected to two different light levels, *i.e.*, $22,500 \pm 2,000$ lux and 750 ± 200 lux allowing two distinct temperature levels. The chlorophyll fluorescence data were collected through OJIP analysis using a portable fluorometer (FluorPen, FP 110). The measurements were recorded four times a day (9 am, 12 pm, 3 pm, and 6 pm) and the data were collected continuously for four days commencing from the first day of treatment application. The major parameters derived from the OJIP analysis, including specific energy fluxes per reaction center (ABS/RC, TR/RC, ET/RC, and DI/RC), flux ratios (maximum quantum yield of primary photochemistry- ϕ_{Po} , electron transport efficiency - ψ_o , and quantum yield of electron transport - ϕ_{Eo} and maximum quantum yield of non-photochemical de-excitation- ϕ_{Do}), and performance index (PI) were recorded. ChlF data showed a clear unimodal diurnal variation in plant performances of *D. sanderiana* at $22,500 \pm 2,000$ lux. The circadian variation was reported for all measured ChlF parameters except the ψ_o , TR/RC, and ET/RC. Based on these circadian variations of ChlF, it can be concluded that *D. sanderiana* displays a facultative CAM pathway as an adaptation to the stressed conditions. Thus, this species can be used in indoor landscaping.

1. INTRODUCTION

Dracaena sanderiana is one of the most popular cut foliage among the world ornamental industry (Beura et al., 2007). It is a perennial herb that belongs to the family Agavaceae and in general terms, it is called 'Lucky Bamboo'.

When a plant is developing in non-ideal conditions, plant stress may occur. If the stress surpasses the plant tolerance limitations, ultimately it can cause plant death. Plants have distinct mechanisms to overcome and survive under this stressful condition. They have been adapted to their environmental conditions with modified physiological processes.

Crassulacean acid metabolism (CAM) is the most adapted photosynthetic pathway for stress conditions among those three mechanisms of C₃, C₄, and CAM particularly when water is scarce and light and temperature are high. CAM plants, receive CO₂ from the environment mostly at night when the stomata are opening and then assimilate it to the level of glucose during the following light period (K. Winter & Smith, 1996).

CAM can function in a variety of ways: (a) obligate CAM, (b) facultative or inducible CAM, (c) CAM-cycling, (d) CAM-idling (Herrera, 2009). Facultative CAM explains the employment of CAM photosynthesis in plants usually under drought, salinity, photoperiod, nutrient deficiencies that would otherwise use C₃ or C₄ photosynthesis (K. Winter & Smith, 1996). When stress is removed, the up-regulation of CAM is entirely reversible in its purest form (Klaus Winter & Holtum, 2014).

Chlorophyll fluorescence (ChlF) is a non-invasive, rapid technique to identify the status of photosynthetic apparatus in plants (Ariyaratna et al, 2020). It is a subtle reflection of the primary reaction of photosynthesis. They reveal details about the structure and function of the photosynthetic apparatus, such as electron transport near photosystem II, the size of the antenna system, the time it takes to establish light adaptation and the redox state, etc. (Buschmann & Buchanan-Bollig, 1983).

During the transition from day to night and vice versa, the daily pattern of fluorescence kinetics can cause rapid variations in photochemical quenching (qP), non-photochemical quenching (NPQ), and quantum yield of photosystem II, electron transport (PSII). During the day, the course of PSII and NPQ is influenced by air temperature, whereas the maximal quantum efficiency of PSII photochemistry (Fv/Fm) shows a light-dependent response (Adams et al., 1989). If the photosynthetic mechanism in plants can easily be identified using a simple technique like ChlF, the plants can safely be used in the light-limiting indoor environments. Therefore, this study was conducted to examine the stress responses of *Dracaena sanderiana* under contrasting temperature and light conditions by using chlorophyll fluorescence (ChlF) transient analysis technique.

2. METHODS

2.1. Experimental set-up

The experiment was conducted in a glasshouse at the Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Sri Lanka, under two different environmental conditions, including high light intensity (22,500±2,000 lux; maximum temperature 48 °C; average RH of 42%) and low light intensity (750±200 lux; maximum temperature 31°C; average RH of 53%). The healthy cuttings of *Dracaena sanderiana* with leaves in the same maturity level were collected and cut ends were immediately immersed in water and kept under shade until separated into treatments.

The distilled water (150 mL) was filled into cleaned glass bottles. *D. sanderiana* cuttings were recut using disinfected sharp secateurs and placed in glass containers. Treatments were laid out in a Completely Randomized Design (CRD) with 02 glass containers (technical

replicates) with 03 shoots (biological replicates). Two sets of treatments were placed in two different places. For ChlF data collection a single leaf was chosen per treatment and three ChlF readings were collected from the three different places of the same leaf.

2.2. Making measurements

ChlF data were recorded using a portable fluorometer (FluorPen, FP 100). The measurements were recorded four times per day (9 am, 12 pm, 3 pm, and 6 pm) and the data collection was conducted continuously for four days using the selected leaf throughout the experiment as replicates. The leaf was not dark-adapted and the cells were exposed to a $3000 \mu\text{molm}^{-2}\text{s}^{-1}$ saturating light pulse and ChlF was captured. Performance Index (PI), Specific energy fluxes (per RC) for absorption (ABS/RC), trapping (TR0/RC), electron transport (ET0/RC), and dissipation (DIO/RC) and Flux ratios or yields such as the maximum quantum yield of primary photochemistry (ϕPo), electron transport probability (ψo), and the quantum yield of electron transport (ϕEo) were measured.

2.3. Data analysis

The data were subjected to ANOVA in completely randomized design (CRD) using statistical analysis software (SAS, version 9.4, SAS Institute Inc., Cary, NC, USA). The significance of differences between the mean values was determined by Duncan's Multiple Range Test (DMRT) at $p \leq 0.05$. Tests for homogeneity of variance were performed on all parameters and, where applicable, LSDs suitable for comparing means of three replicates were determined.

3. RESULTS AND DISCUSSION

3.1. Results

3.1.1. Performance Index

As depicted in Figure 1, at any given time of day, the performance index [PI (ABS)] in low light (750 ± 200 lux) was significantly higher ($p \leq 0.05$) than that of high light ($22,500 \pm 2,000$ lux) in *Dracaena sanderiana*. In high light conditions, it showed a clear unimodal diurnal rhythmic variation of PI (ABS), with the peak occurring at 6 pm.

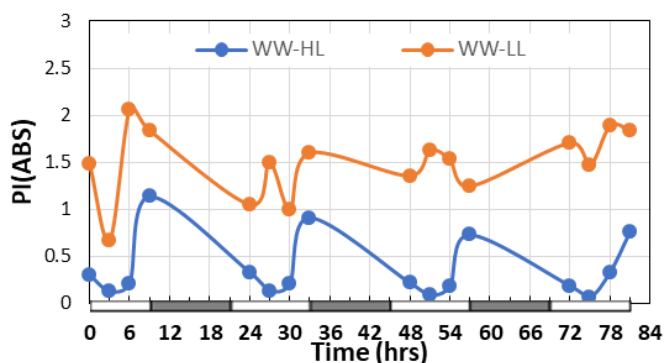


Figure1: Performance index under high light (WW-HL) and low light (WW-LL) conditions.

3.1.2. Measurements of flux ratios

When comparing the treatments, the maximum quantum efficiency of primary photochemistry of PS II [Φ_{Po}] was significantly higher at the point ($p \leq 0.05$) in the low light condition (750 ± 200 lux) compared to that of high light condition ($22,500 \pm 2,000$ lux) at any given time of the day (Fig. 2A). However, there are some non-significant points between high and low light levels as well (e.g. 33rd hr, 57th hr). The maximum quantum efficiency of primary photochemistry of PS II [Φ_{Po}] was strongly affected by the day-night transition in *D. sanderiana* under high light levels and Φ_{PSII} showed a clear unimodal circadian variation at the transition times but more importantly, the highest values were reported at 6 pm in the night time because of the photosynthetic physiology of *D. sanderiana*. But in low light conditions there was no such clear rhythm observed (Fig.2A).

A distinct circadian or rhythmic pattern was not found in this electron transport efficiency as already noted in PI (ABS) or maximum quantum efficiency of primary photochemistry of PS II either in low light or high light (Fig. 2B). But it is apparently shown that higher values were reported under low light conditions rather than high light levels. The maximum quantum yield of non-photochemical de-excitation [ϕ_{Do}] was found to be significantly higher ($p \leq 0.05$) in high light conditions than in low light levels at any given time of the day (Fig.2C). A clear unimodal circadian oscillation of ϕ_{Do} was identified in high light settings, with the specialty being the minimum value reported at 6 pm whereas other parameters (maximum quantum efficiency, performance index) performed well at that time.

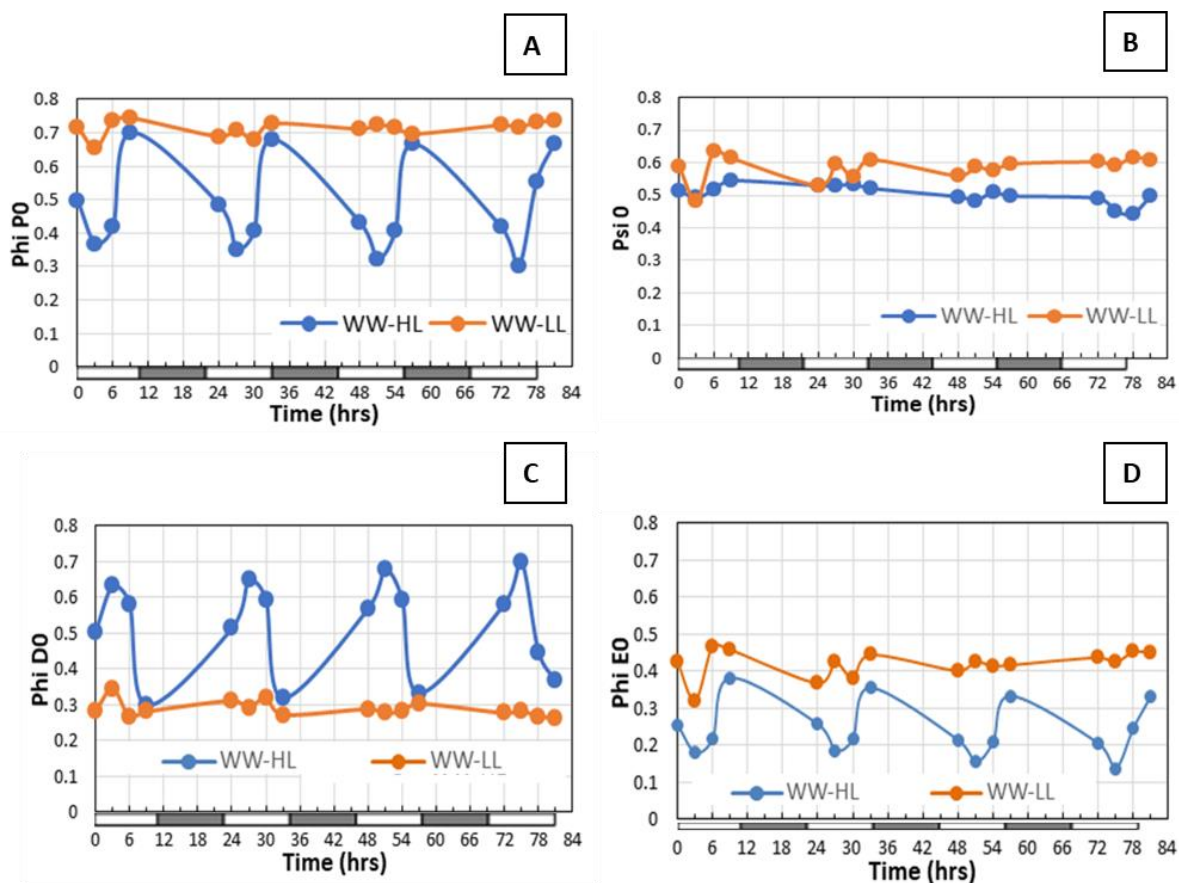


Figure 2: Maximum quantum yield of primary photochemistry under high light (HL) and low light conditions (LL), electron transport efficiency under high light (HL) and low light (LL) conditions, quantum yield of non-photochemical de-excitation under high light (HL) and low light (LL) conditions and quantum yield of electron transport under high light (HL) and low light (LL) conditions.

Here the peak was observed at 12 pm in almost every treatment. However, it was not visible under low light conditions. But some points of high light were non-significant with low light levels (eg; 57th of WW).

As shown in Figure 2D, there was a significant difference ($p \leq 0.05$) in the quantum yield of electron transport under two light conditions. In low light conditions, the quantum yield of electron transport [ϕ_{Eo} or (ET/ABS)] was significantly larger than in high light conditions at any given time of day. In high light conditions, a distinct unimodal circadian fluctuation in ϕ_{Eo} was detected, with a peak at 6 pm. In low-light conditions, however, there was no discernible rhythm.

3.1.3. Measurements of Specific energy fluxes (per reaction centre)

Within each treatment, there was a significant difference ($p \leq 0.05$) in the effective antenna size (ABS/RC) under two light conditions at a given time except for some points (Figure 3A) (e.g. 9th, 24th, 33rd, and 81st hr). In high light conditions, a clear unimodal circadian fluctuation in absorption per reaction center was detected, with a peak at 12 pm. In low-light conditions, however, there was no discernible rhythm.

As shown in Figure 3B, trapping per reaction center (TR/RC) varies throughout the day; however, it is not rhythmic as a clear circadian variation. In there a significant difference ($p \leq 0.05$) can be identified in the trapping per reaction center (RC) under two light conditions at a given time. There was a significant difference ($p \leq 0.05$) in electron transport per RC between two light levels (Fig. 3C). A noticeable diurnal change in both low and high light settings could not be found in this particular energy flux called electron transport per reaction and showed the same pattern in both low and high light levels. As shown in Figure 3D, the heat dissipation per RC was significantly different ($p \leq 0.05$) between two light levels at all the times where the measurements were taken, except at the dusk (6 pm).

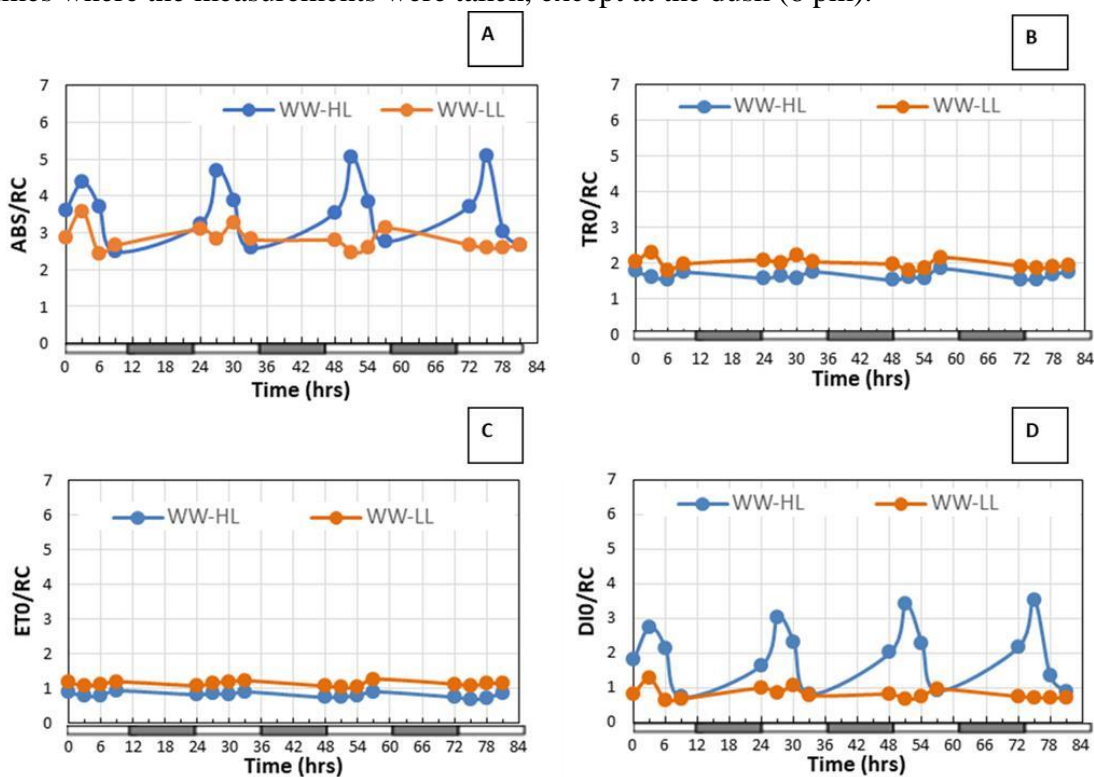


Figure 3: Effective antenna size under high light (HL) and low light conditions (LL), trapping per reaction centre under high light (HL) and low light (LL) conditions, electron transport per reaction centre under high light (HL) and low light (LL) conditions and heat dissipation per reaction centre under high light (HL) and low light (LL) conditions.

3.2. Discussion

3.2.1. Performance Index

The steep drop in PI during the night-to-day transition indicates the termination of photosynthesis due to Calvin cycle inactivation. The same observations can also be made for CAM plants. When stomata are open at night, CAM plants absorb CO₂, which is fixed by Phosphoenol Pyruvate Carboxylase (PEPC) and converted to oxaloacetate, which is then reduced to malate. During the day, malate is decarboxylated in the cytoplasm, producing large concentrations of CO₂ inside photosynthetic tissues, which is fixed by Rubisco behind closed stomata, saving significant amounts of water compared to C₃ photosynthesis. This unique CO₂ concentration mechanism permits CAM plants in warm desert environments to perform carboxylation and Calvin cycle reactions (Niewiadomska & Bilger, 2011).

Even in the low light levels, there is some variation, regardless of a significant rhythmic pattern. These circadian variations in *D. sanderiana* provide evidence for the CAM activity in this plant which is supporting the survival even under the different light and temperature stress levels in the treatment (Klaus Winter & Holtum, 2014). But it is difficult to conclude that *D. sanderiana* is a facultative CAM plant only by observing the circadian pattern in PI (ABS), therefore some other major contributing factors to PI (ABS) were also measured and the results are discussed in the next sections.

3.2.2. Measurements of flux ratios

These figures (Fig.2) showed that the circadian variation can be observed only under high light conditions which are having more levels of stress. The reason for that is *D. sanderiana* has acted as a facultative crassulacean acid metabolism (CAM) plant under stress conditions. Facultative CAM explains the optional utilization of CAM photosynthesis in plants that would otherwise use C₃ or C₄ photosynthesis, usually under drought stress salt stress, and other stressful situations. When stress is removed, the upregulation of CAM is entirely reversible in its purest form. Reversibility distinguishes facultative CAM from constitutive CAM plants' ontogenetically planned unidirectional C₃-to-CAM changes (Klaus Winter & Holtum, 2014). When it comes to electron transport efficiency in *D. sanderiana*, it does not illustrate a remarkable drop during the midday. CAM plants, on the other hand, demonstrated a faster induction of ETR than C₃ plants, as well as a faster induction of photochemical quenching during the midday. Later in the day, in CAM plants, rapid recovery of PET takes place. A higher capacity of electron sinks is associated with a faster induction of ETR in PSII during midday, which could be due to enhanced Rubisco activity as a result of increasing CO₂ concentration. A constant state of diminished PSI acceptors in CAM plants during the day appears to be mostly independent of CAM-related CO₂ level variations. This could indicate a limitation imposed by Rubisco's poor availability, which is most likely due to its deterioration. Keiller et al. (1994) observed state transition in *M. crystallinum* CAM plants during the majority of the day and received the same results.

The quantum yields of photochemical and non-photochemical quenching have a close linear relationship. Non-photochemical quenching increased proportionally in response to decreases in $\Delta F/F_m'$. For C₃ and C₄ plants, Laisk et al. (1997) found a similar pattern. The sum of $\Delta F/F_m' + Y_N$ was 0.80 ± 0.04 (mean \pm SD; n = 358). As the capacity for photochemical quenching decreased in *Clusia hilariana*, the capacity for non-photochemical quenching increased in a coordinated manner, allowing efficient control of excitation lifetimes, minimizing the formation of triplet-state chlorophylls, as well as the production of singlet oxygen and radicals (Laisk et al. 1997).

When considering the quantum yield of electron transport, even though it is persistence the same way of electron transport efficiency (ψ_o), a circadian variation can be observed here

unlike ψ_o because of the diurnal variation in absorption energy. As a result of the amount of photon energy absorbed by antenna pigment molecules is altering during the day in a unimodal rhythm, ET/ABS also shows such kind of variation.

3.2.3. Measurements of Specific energy fluxes (per reaction centre)

Similar kind of circadian variation (Fig 3.) in effective antenna size with the peak during the mid-day was observed because of having strong mechanisms in *D. sanderiana* to absorb light energy even during the high light levels at mid-day. That proves *D. sanderiana* is having a better adaptation to the stress conditions. By the visual observation of the experiment, it was noticeable that *D. sanderiana* has performed better even under these high light levels with minimum wilting. Importance of circadian variations in the photosynthetic machinery in the survival of photosynthetic organisms has been well established (e.g. Beneragama and Goto, 2010).

Skillman and Winter (1997) have studied this for the high shade tolerant CAM bromeliad *Aechmea magdalenae* in a rainforest in Panama. During phase III of CAM, these plants have a particularly high capacity for absorbing light flecks and have very high thermal energy dissipation (NPQ up to 5.5) in high light. The introduction of light flecks in phase III would accelerate malate remobilization and induce phase IV CO₂ uptake, thereby increasing overall carbon uptake. Unfortunately, no recent research on this phenomenon on *D. sanderiana* appears to be accessible (Lüttge, 2000).

Our findings also show that photochemistry in the CAM plant is better protected. Adjusting the energy distribution between photosystems can also result in *D. sanderiana*. There are two probable causes for the observed increase in ABS/RC in high light. Inactivation of some PSII RCs, or an increase in antenna size, assuming that the ABS/RC ratio is determined as the total quantity of photons absorbed by Chlorophyll molecules in all RCs divided by the total number of active RCs (van Heerden et al., 2007). When trapping energy *D. sanderiana* does not show any significant difference as a CAM plant and it performs as a general C3 plant.

The observed increase in TR₀/RC under high light and temperature could be explained by the deactivation of some PSII RCs, which therefore become non-QA-reducing centers. Down-regulation of photochemical activity, combined with a considerable increase in thermal dissipation, may play a vital role in protecting plants against over-excitation and photodamage when they are stressed by high temperatures and light conditions (Ceusters et al., 2019).

Other than that different studies revealed that thermal stresses can indeed result in damage to the OEC (Oxygen Evolving Complex) and block further electron transport. This phenomenon is mostly characterized by an increase in the specific fluxes for trapping, absorption, and dissipation during the mid-day (Ceusters et al., 2019). When considering the electron transport per reaction center (ET/RC), the same phenomenon can be applied to elucidate that variation. The heat dissipation varies during the day according to a circadian rhythm; though the amplitude is not uniform in some cases. However, on every occasion, the maximum value was recorded during the mid-day (12 pm), and the minimum value was recorded at 6 pm.

There are protective mechanisms for PSII against excessive energy through improving the thermal dissipation of the excitation energy. The relationship among dissipative processes is described by the equation $\phi_{PSII} + \phi_{NPQ} + \phi_{NO} = 1$ (Ceusters et al., 2019). The decrease in qN indicated that the radiant energy dissipation process was affected by NaCl stress. As Krause and Weis (1991) considered, lower Fv/Fm values indicated that excessive energy is dissipated as heat in the antenna complex, thus resulting in a decreased quantum yield.

4. CONCLUSION

This study has shown that there is a significant effect of two contrasting light and temperature levels on the photosynthetic apparatus of *Dracaena sanderiana* and under the high level of stress conditions *D. sanderiana* can alter its photosynthetic pathway from C3 to CAM. However, following these results, chlorophyll fluorescence transient analysis can be identified as a high-throughput technique to identify the stress physiology and analyze circadian rhythms in plants. In addition based on these circadian variations of ChlF, it can be concluded that *D. sanderiana* displays a facultative CAM pathway as an adaptation to the stressed conditions.

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