

PINUS ELDARICA MEDW. (= P. BRUTIA SUBSP. ELDARICA) STOMATAL
CONDUCTANCE RESPONSE TO ENVIRONMENTAL FACTORS AND LEAF WATER
POTENTIAL¹

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Abstract.--Studies conducted in southern New Mexico determined environmental and leaf water potential effects on Pinus eldarica stomatal conductance (KL). Irrigated, three-year-old trees within a 0.8-ha stand planted on a 2.8 by 2.8 m spacing were studied from August through October 1983. The major environmental variable controlling KL was absolute humidity difference leaf-to-air. Photosynthetic photon flux density did not consistently effect KL during mid-day. Stomatal conductance prior to 0900 or 1000 hrs. and after 1900 hrs. (MDT) was apparently photoactively controlled. Leaf water potentials at pre-dawn and at mid-day were analysed within the context of hydroactive KL control.

Additional keywords: diffusion porometer, infrared thermometer, absolute humidity difference, photosynthetic photon flux density

INTRODUCTION

Information on transpiration rates is an integral part of understanding water consumption by forests, plantations or crops. Forest transpiration models are generally derived from an energy balance approach or from direct measurements. Dissadvantages with both approaches are the requirement of expensive instrumentation, and difficulties associated with measuring large geographic areas and the canopies of mature trees.

Models that predict transpiration combine physical constants with empirically-determined leaf temperature, vapor pressure of the air, and water vapor conductance from the leaf-to-air (Whitehead and Jarvis, 1981). Stomatal conductance is, however, necessary to adequately predict transpiration over large areas. Stomatal conductance is routinely determined with portable, steady-state diffusion porometers. Because porometers are expensive and are tedious to operate, researchers have sought alternative approaches to predict transpiration. Infrared thermography (IF) is one alternative technique being studied.

Infrared thermography can be applied as a remote sensing technique to detect disease outbreaks in crops and forests occupying large areas and, to determine forest water yield relationships to thinning practices. Plant canopy temperature, determined with handheld IF thermometers, have been combined with vapor pressure deficit measurements of air and net radiation levels to schedule crop irrigations (eg. Jackson et al. 1981, Idso et al. 1981). Handheld IF thermometers are also used to correlate remote data

¹ This work was supported in part by New Mexico Water Resources Research Institute, grant numbers 1345648 and 14236. New Mexico State University Extension Service Scientific Paper No. SP-269.

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recorded for large, forested areas with on-site measurements of individual species or trees.

Understanding stomatal responses to environmental variables is central to understanding transpiration. Stomatal closure enables plants to control water use. Stomatal conductance is controlled by several environmental and plant variables that include light, leaf and air temperature, relative humidity, tissue age, water status, wind speed and, sometimes, CO₂ concentration or plant nutrient status. Kaufmann (1982), however, determined that stomatal conductance among sub-alpine forest trees was related mainly to light, humidity, temperature and water status.

This study attempted to develop techniques to reliably predict irrigation needs of Pinus eldarica Medw. plantations grown in southern New Mexico. The major objective of this study was to describe P. eldarica stomatal responses to environmental variables and water stress.

EXPERIMENTAL PROCEDURE

P. eldarica stomatal conductance (KL) was studied on 3-year-old trees within a 0.8 ha irrigated plantation in Las Cruces, NM. Trees were 1.5 - 2.0 m tall and spaced on 2.8 X 2.8 m centers. Stomatal conductance was determined with a steady-state diffusion porometer (Licor, Inc. Li-1600) fitted with a cylindrical chamber (1600-02A). Because of chamber configuration, the leaf temperature thermocouple did not contact the leaf surface. Leaf temperature (LT) was, therefore, measured with an IF thermometer (Everest Interscience, Model 210). Leaf temperatures measured within the canopy agreed within +/- 0.3 C of canopy temperature. The thin-wire, LT thermocouple reading was used as air temperature (AT). The thin-wire, LT thermocouple was adjusted potentiometrically to equal AT measured by a calibrated Assman-type ventilated psychrometer. The psychrometer was in the center of the plantation in a shaded, well-ventilated shelter. Diffusion porometer cuvette temperatures were within +/- 0.75 C of the thin-wire LT thermocouple values. Cuvette temperature readings were within +/- 0.5 C of the LT thermocouple reading before diffusion resistance (DR) and transpiration (TR) measures. This minimized cuvette temperature changes affecting relative humidity (RH) measurements. Leaf water potential was determined at pre-dawn (leaf_PD) (0430-0600 hrs MDT) and mid-day (leaf_MD) (1200-1330 hrs MDT) with a pressure bomb (PMS Co.). Air temperature, RH, photosynthetic photon flux density (PPFD), DR, and TR were measured with the steady-state diffusion porometer during mid-day (1215-1330 hrs. MDT).

The plantation was planted as a randomized complete block experimental design; a subset of the main study was used here. The measurements were replicated by sampling two alternate blocks within the plantation on consecutive days at 3-day intervals from Aug. 10 through Nov. 8, 1983. At least three measurements were made on each of two saplings sampled from each treatment. Sampling was restricted to current-year, expanded needles from the second flush behind the apical bud located mid-crown on south-facing lateral branches. Leaf_MD measurements were restricted to needle fascicles on the lowest portion of the defined flush and branch, to minimize defoliation effects. Needles for pre-dawn measurements were harvested from an alternate, lateral branch of similar size and appearance. Pressure chamber measurements were made within 1 minute of needle harvest and followed a procedure modified for conifer needle fascicles (Johnson and Nielsen, 1969). The inflow rate of the chamber was set at 200 psi min⁻¹ (Kaufmann, 1968).

Porometer measurements were made on conifer needles as described above. Three two-needled leaves were placed parallel and horizontally flat across the 5.7 cm wide chamber aperture so needle taper did not alter surface area. Needle surface area within the chamber (8.27 cm^2 ; $\text{SE} = 0.007$) was determined by visual methods. Individual needles in the chamber were separated by about 5 mm to facilitate air flow around each needle. Care was taken not to shade conifer needles during measurements. The instrument-mounted PPF sensor was held horizontally beside the canopy to obtain radiation measurements; these were taken before and after each three porometer measurements.

All diffusion resistance measurements were corrected for LT and boundary layer resistance by the following procedure:

$$\text{DAH} = [\text{RHO sat @ } T_1] - [(\text{RH}\%)^1 (\text{RHO sat @ } T_c)] \quad (2)$$

where T_1 = leaf temperature (C)

T_c = air temperature (C)

RHO sat = saturation water vapor density at LT or AT ($\mu\text{g cm}^{-3}$)

DAH = absolute humidity difference ($\mu\text{g cm}^{-3}$)

thus DR is;

$$\text{DR} = (\text{DAH } \text{TR}^{-1}) - R_b \quad (3)$$

where R_b = boundary layer resistance (s cm^{-1})

Because the steady-state diffusion porometer computes DR using a fixed R_b value appropriate for broad-leaved plants, an R_b value derived for conifer needles was used to correct the data. This value (0.036 s cm^{-1}) was determined for artificially-prepared spruce needles by Beardsell et al. (1972).

RESULTS AND DISCUSSION

Kaufmann (1982) identified DAH and PPF to be the major variables controlling KL in non-stressed forest trees. He also reported that KL was affected by leaf water potential (leaf P) in water-stressed trees, and by the previous nightly minimum AT. Figure 1 illustrates the relationship of KL to DAH. When DAH exceeded $15 \mu\text{g cm}^{-3}$, KL was near 0.20 cm s^{-1} with little further reduction observed. When DAH was less than $15 \mu\text{g cm}^{-3}$, KL varied between 0.20 and 1.80 cm s^{-1} .

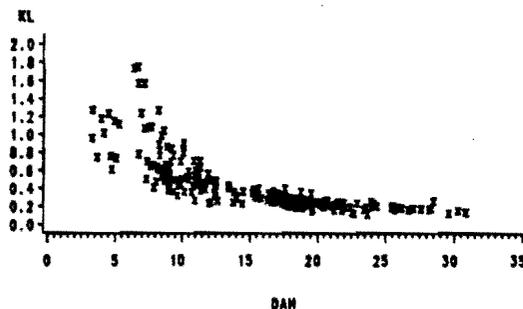


Figure 1 The relationship between *P. eldarica* stomatal conductance ($\text{KL} = \text{cm s}^{-1}$) and absolute humidity difference leaf-to-air ($\text{DAH} = \mu\text{g cm}^{-3}$).

Figure 2 illustrates the relationship of leaf_{PD} and leaf_{MD} to KL. A decline in both curves occurred at $KL = 0.20 \text{ (cm s}^{-1}\text{)}$ and indicates that stomata closed as a result of turgor loss in guard cells, causing partial stomatal closure. Alternatively, water vapor density may not have been saturated within the stomatal cavity. The latter would be a result of an evaporation rate from the mesophyll surfaces exceeding the recharge rate (ie. dehydration). Two types of stomatal response by forest species to water status have been cited: (1) a gradual response, where KL increases to a daily maximum and gradually declines thereafter in response to low humidity, causing dehydration of guard cells that results in partial stomatal closure (Lange et al., 1971); and (2) an abrupt response, where KL increases to a maximum level, then declines precipitously to a lower level, and is attributed to total or partial stomatal closure caused by soil water deficit (Dougherty et al., 1976). Many researchers have observed threshold leaf_P where stomatal closure resulting from limited soil water content is attributed as the underlying cause for abrupt stomatal response (Hinckley et al., 1978). Many threshold leaf_P values are cited for different species. Using this definition, P. eldarica threshold leaf_P would apparently be -0.8 and -2.0 (MPa) at pre-dawn and mid-day, respectively (Fig. 2). However using the above threshold leaf_P definition, assumes that soil water deficit solely causes hydroactive stomatal closure. To fit the definition, KL would achieve a daily maximum, then decline abruptly and continually through remainder of the day. We will demonstrate that P. eldarica stomata did not strictly conform to either response type or threshold leaf_P definitions.

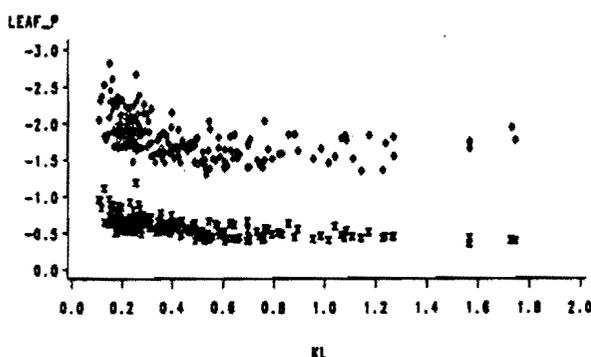
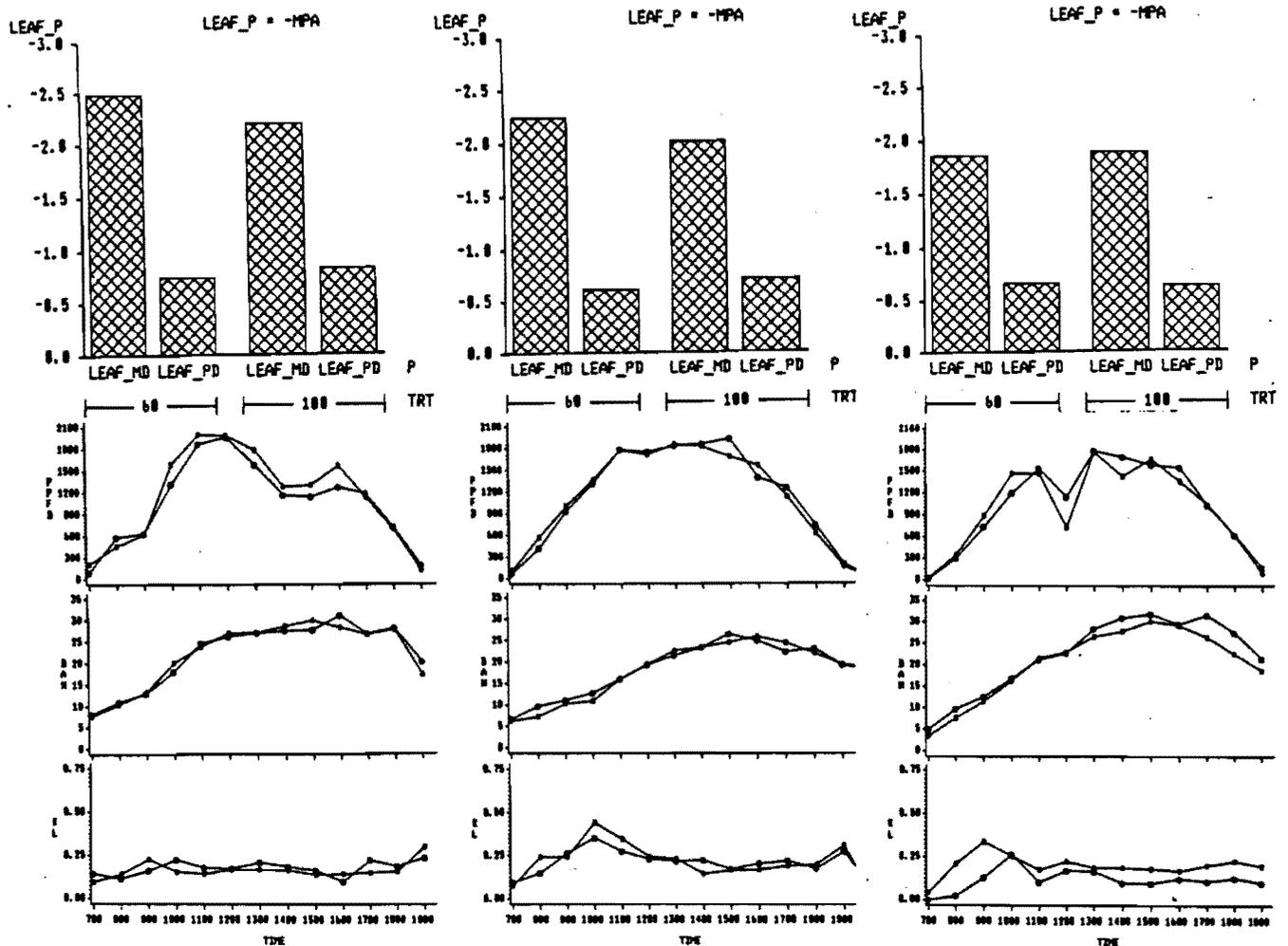


Figure 2 The relationship between P. eldarica leaf water potential (LEAF_P = MPa) at pre-dawn (star) and mid-day (diamond) and stomatal conductance ($KL = \text{cm s}^{-1}$).

Figures 3 A, B and C show hourly KL, DAH, PPFD, and leaf_{PD} and leaf_{MD} on three dates before and after irrigation on Aug. 27, 1983. The figures compare the high 100 (46 cm water) and the low 60 (17 cm water) irrigation treatments. Data in these figures indicate KL was photoactively controlled before 0900 or 1000 hrs. and after 1900 hrs. (MDT). The data demonstrate the effect of high evaporative demand (Fig. 3A) suppressing KL; DAH increased to near $30 \text{ (}\mu\text{g cm}^{-3}\text{)}$ as KL decreased to $0.10 \text{ (cm s}^{-1}\text{)}$ in the 100 treatment at 1600 hrs. High DAH similarly affected both the 60 and 100 treated trees. Stomatal conductance at 1900 hrs. increased from previous mid-day low values, following a decline in DAH. Minimal effects of reduced PPFD caused by cloud cover were detected in the DAH and KL data at 1300 to 1500 hrs. Saplings in either irrigation treatment did not reach threshold leaf_{PD} levels. Leaf_{MD} were, however, above the threshold at -2.5 and -2.2 in the 60 and 100 treatments, respectively.



Figures 3 A, B and C Hourly stomatal conductance ($KL = \text{cm s}^{-1}$), absolute humidity difference leaf-to-air ($DAH = \mu\text{g cm}^{-3}$), photosynthetic photon flux density ($PPFD = \mu\text{mol m}^{-2} \text{s}^{-1}$) and leaf water potential ($LEAF_P = \text{MPa}$) at pre-dawn ($LEAF_{PD}$) and mid-day ($LEAF_{MD}$) of *P. eldarica* on Aug. 21, Aug. 26 and Sept. 3, 1983. The trees received 5.1 and 10.7 cm water in the 60 (squares) and 100 (circles) irrigation treatments on Aug. 27, 1983.

Stomatal conductance on Aug. 26, 1983, a day characterized by maximal soil water deficit before irrigation on Aug. 27, demonstrated both gradual and abrupt stomatal response types (Fig. 3B). A KL peak occurred near 1000 hrs. and suggests an abrupt response type. However, KL also declined gradually as DAH increased through the day, and recovered late in the day as DAH declined. High $PPFD$ indicate clear skies predominated throughout the day. While $leaf_{PD}$ in either irrigation treatment did not exceed threshold $leaf_P$, $leaf_{MD}$ in the 100 and 60 treatments (-2.1 and -2.3 MPa, respectively) were at or exceeded the assumed threshold. Comparing the data collected on this date to the previous date (Fig. 3A), $leaf_{PD}$ were similar, but $leaf_{MD}$ were less negative. Evaporative demand as measured by DAH was less on Aug. 26 ($DAH = 26 \mu\text{g cm}^{-3}$) than on Aug. 21 ($DAH = 30 \mu\text{g cm}^{-3}$). Stomatal response, evidenced by late day KL increase, was apparently related to DAH and unrelated to plant water stress caused by a soil water deficit. This stomatal response was

observed in trees receiving either irrigation treatment. Trees in the 60 treatment demonstrated a greater KL peak at 1000 and 1900 hrs. than trees in the 100 treatment. Late day KL increase is atypical of soil water deficit-induced stomatal closure. Thus, the data suggest that stomata responded in a manner commonly found among desert plant species.

Figure 3C, shows relationships between KL, DAH and PPFD for both irrigation treatments. This figure illustrates the effect of the Aug. 27, 1983 irrigation (10.7 and 5.1 cm water for the 100 and 60 treatments, respectively) on the above relationships. Leaf_PD did not approach threshold levels, and leaf_MD in both irrigation treatments were at -1.8 (MPa). This is below the assumed threshold leaf_P. While DAH increased to near 30 ($\mu\text{g cm}^{-3}$) during the 1500 hr. measurement, KL dropped to 0.20 (cm s^{-1}) in the 60 treatment. Previously, KL in the 60 treated trees peaked at 0.35 (cm s^{-1}) during the 0900 hr. measurement. Late day KL recovery was evident in this treatment. Trees in the 100 treatment demonstrated an additional stomatal response, not related to DAH, PPFD or leaf_P. Heavy irrigation apparently effected stomatal behavior as evidenced by the shift in KL relative to KL in the 60 treated trees at 0700 to 1000 hrs. regardless of DAH level. Furthermore, KL in the 100 treated trees was consistently lower than those in the 60 treatment for the remainder of the day. Kozlowski (1984) discusses plant responses to soil flooding and indicated, in flood intolerant species, stomata close within a day or two after flooding and remain closed for an extended period of time. In this study, greater soil water content yielded less negative leaf_P but did not yield greater KL by trees in either the 60 or 100 treatments. Regardless of treatment, KL responded to DAH while PPFD had little affect.

Lange et al. (1971) demonstrated the effect of humidity on stomatal response. Stomata rapidly closed when Polypodium vulgare epidermal strips were transferred from moist to dry air, but opened when exposed to the reverse process. These researchers concluded that the direct cause of abrupt stomata closure was the rapid loss of turgidity among dehydrated guard cells and surrounding epidermal cells because leaf_P affects were eliminated. Prunus armeniaca KL decreased as VPD leaf-to-air increased, while leaf_P became less negative (Schulze et al., 1972). Thus, epidermal and mesophyll tissues were shown to respond independently. In contrast, P. eldarica KL decreased and leaf_P became more negative as DAH increased (Fig. 4). This suggests an intimate link between epidermal and mesophyll tissues, and demonstrates a negative feedback mechanism cited by Mansfield and Davies, (1981). In this study, dehydration from leaf epidermal and mesophyll cells could have increased as DAH increased, causing a concomitant reduction in both leaf_P and KL.

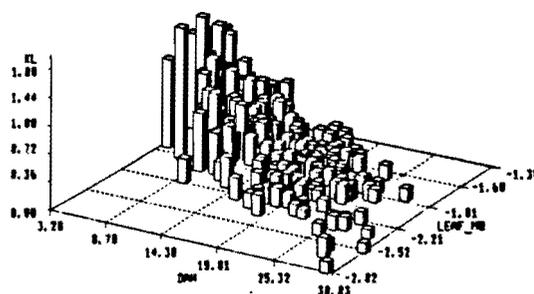


Figure 4 The relationship between P. eldarica stomatal conductance (KL = cm s^{-1}), absolute humidity difference leaf-to-air (DAH = $\mu\text{g cm}^{-3}$) and leaf water potential at mid-day (LEAF_MD = MPa).

A relationship between pre-dawn plant water potential and maximum KL has been established for forest trees (Hinckley et al. 1978). Kaufmann (1979) also related TR to pre-dawn xylem pressure potentials in *Picea engelmannii* Engelm. seedlings, and canopy TR rates of *P. sylvestris* and *Picea sitchensis* were related to leaf P (Jarvis, 1976, as cited by Whitehead and Jarvis, 1981). Stomatal conductance was related to leaf P levels among *P. sylvestris* (Whitehead, 1980) and *P. contorta* (Running, 1980). A similar relationship between KL and leaf P was shown in this study, but with considerable dependence on DAH. While the current data indicate threshold leaf P levels at pre-dawn and mid-day, the strict definition of limited soil water content should be reconsidered, particularly in regard to the similar affect that DAH can have on KL.

The relationship between KL, DAH and PPFD is shown in Fig. 5. When DAH was greater than 15 ($\mu\text{g cm}^{-3}$), KL equaled approximately 0.20 (cm s^{-1}), regardless of PPFD level. When DAH was less than 15 ($\mu\text{g cm}^{-3}$), KL increased and a slight, inconsistent interaction between PPFD, DAH and KL was detected. As PPFD and DAH decreased, so did KL. This is inconsistent with increasing KL when DAH decreased under high PPFD. The relationship under reduced PPFD is not clear, because there were not enough observations when these conditions prevailed. The relationship, however, demonstrates a mid-day photoactive stomatal response.

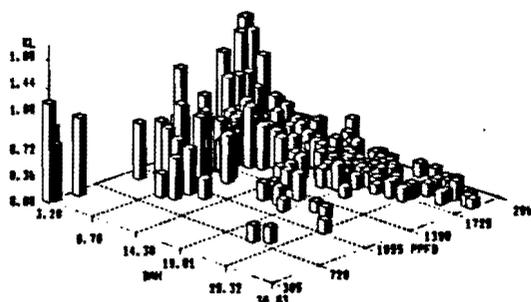


Figure 5 The relationship between *P. eldarica* stomatal conductance ($\text{KL} = \text{cm s}^{-1}$), absolute humidity difference leaf-to-air ($\text{DAH}_1 = \mu\text{g cm}^{-3}$) and photosynthetic photon flux density ($\text{PPFD} = \mu\text{Mol m}^{-2} \text{s}^{-1}$).

CONCLUSIONS

P. eldarica KL during mid-day was controlled mainly by DAH. When DAH was greater than 15 ($\mu\text{g cm}^{-3}$), KL remained near 0.20 (cm s^{-1}). When DAH was less than 15 ($\mu\text{g cm}^{-3}$), KL varied between 0.20 and 1.80 (cm s^{-1}), and indicated a photoactive response during mid-day. Data indicated photoactive stomatal response before 0900 or 1000 hrs. and after 1900 hrs. (MDT). Threshold leaf P was established at pre-dawn and mid-day (-0.8 and -2.0 MPa, respectively). The threshold leaf P definition, however, should be redefined to include the possible affect on leaf P by DAH. The most negative leaf MD values were directly related to greatest DAH. *P. eldarica* stomatal response was similar to desert plant species by exhibiting mid-morning peak KL, decreasing KL in response to increasing DAH and, finally, late day partial recovery in direct response to decreasing DAH. This type of stomatal response was observed on dates before and after irrigation and suggests that mid-day KL near 0.20 (cm s^{-1}) was the result of DAH, rather than limited soil water content.

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