Should plants keep their (canopy) 'cool' or allow themselves to grow 'warm' under stress: It is a Hobson's choice and plants survive by doing a balancing act

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Should plants keep their (canopy) 'cool' or allow themselves to grow 'warm' under stress: It is a Hobson's choice and plants survive by doing a balancing act

V. R. Sashidhar, S. J. Ankegowda, Mahesh J. Kulkarni, M. N. Srinivas, T. G. Prasad, U. Nagalakshmi and R. Devendra*

Two drought postponement strategies are put into operation in plants when the soil starts to dry. Ironically, one results in 'cooler' canopies (maintains transpiration (T) by keeping stomata open) and the other initiates a cascade of events leading to closure of stomata and the consequent 'warming' of canopies. The 'dilemma' of plants is which of these two strategies to operate at what time and for how long. Our studies suggest that it is a Hobson's choice for plants as both processes have distinct advantages and disadvantages. In this paper we discuss why, how and when the plant makes the choice between these two strategies when it is undergoing a long drought in the field. We also briefly discuss the metabolic costs involved in adapting either of these strategies and the balancing act a plant does, not to just survive, but maximize carbon gain in a difficult catch 22 situation.

THE well-known stomatal physiologist Rascke said: 'Land plants are in a perpetual dilemma throughout their lives. Assimilation of CO_2 from the atmosphere requires intensive gas exchange and the prevention of excessive water demands that the gas exchange be kept low.' Transpiration (T) has often been called as a 'necessary evil', 'necessary' because it 'cools' the leaf below air temperature and 'evil' because it accelerates the rate of loss of soil water; which is often limiting particularly in the semi-arid tropics[1]. If we accept the fact that the process of transpiration keeps leaf temperatures below air temperatures, it is also necessary to ascertain by what degree the leaves become warmer or hotter if this process is curtailed. In fact plants could well be regulating the process of transpiration in concert with their ability to tolerate different temperatures. For example, plants growing in deserts where the temperatures often reach 50°C have the option of either curtailing T or maintaining a moderate level of T (ref. 1). The former strategy would result in shoot temperatures rising perilously close to lethal temperatures, while the latter would still keep shoot temperatures at least a few degrees below the air temperature. We present evidence to show that plants adopt either of these strategies, presumably in tune with their own adaptation to high temperatures.

The authors are in the Department of Crop Physiology, University of Agricultural Sciences, GKVK, Bangalore 560 065, India.

*For correspondence. (e-mail: vrsashi@yahoo.com)

Strategy I: Programmed to keep their cool under stress

In a field study which we conducted for four consecutive years (1993–96), with two hundred genotypes of finger millet, it was observed that the plants stayed 'cool' amazingly even 16 days after imposing a long duration of drought in the field (Figure 1). This suggested that the plants had developed a strategy to maintain a certain level of transpiration. This is possible only by elongating their roots further to tap water available in deeper layers. Data on a few selected genotypes in separate studies showed that these 'stay cool' genotypes tend to produce significantly longer roots when a drought stress was imposed (Figure 2). What is the adaptive strategy involved here and how common is it? Data from the literature show that the first option whether it be the millets or many desert species, is to stay cool, i.e. the Crop Canopy Air Temperature Difference (CCATD) is negative (Table 1). This means that the plant decides to expand or divert its metabolic energy to maintain T. The metabolic costs involved are enormous because the only way it can do so is to send its roots deeper. This means diversion of energy meant for shoot growth to produce longer roots (Figure 3). Separate studies in selected pot-grown plants differing in CCATD in the field have confirmed this observation. This strategy to maintain a high water uptake through a better root system is considered the most effective dehydration postponement trait[2,3].

Strategy II: Programmed to grow 'warm' under stress

Stomatal closure by ABA-mediated root to shoot signalling leads to warming of canopies. Root to shoot signalling is now widely accepted as another dehydration postponement trait[4,5]. Inherent in this strategy is a system of communication which will signal the stomata to restrict opening to avoid excessive water loss. In this system a message synthesized by the roots which are the first to sense the water deficit, leaves the roots, uses the xylem as a conduit, reaches the stomata and restricts the water loss as classical 'first line of defence'[6]. We had in an earlier paper reported the advantages and disadvantages of two types of root to shoot signal communication; the electrical versus the chemical signal[7]; ABA with its specific mode of action on the stomata is widely accepted as the predominant signal. The level of this hormone increases up to 50 times in the xylem sap of stressed plants[4–7].

Root to shoot signalling leading to an initial restriction of the stomatal opening and finally in the stomatal closure should therefore result in positive CCATD or warmer canopies. In opuntia shoot temperatures are often 20–25°C higher than the air temperature[1]. In the same study and under similar environmental conditions, six other desert species still maintained slightly cooler canopies although the soil only a few centimeters away was 12 to 28°C higher than the air temperature. Long-duration droughts of forty days in rainfed cotton resulted in canopy temperatures of at least 10°C higher than the irrigated control[8]. However, we know that a negative CCATD is maintained in a majority of field-grown crops well into drought even up to the 16th day after drought (Figure 1, Table 1). How does this happen? This is where the second part of dehydration postponement comes in, i.e. maintenance of root elongation under stress to tap water available in deeper layers. This mechanism is as complex as it is intriguing. There is good evidence from a wide range of crops to show that root elongation is indeed maintained at low water potentials[9,10]. Root osmotic adjustment is the central mechanism responsible for this phenomenon[14].

Table 1. Strategy I. Field studies involving different species where the plants adopted to 'stay cool'

Crop	Duration of drought	Reference
Six desert species	Long duration	1
Sorghum	Long duration	12
Wheat	Short duration	13
Soybean	Long duration	14

In these types, the crop canopy air temperature difference was negative. This means that the canopy temperature is several degrees lower than the air temperature, thereby giving a negative CCATD value. However, the soil temperature is much higher than air. In the desert study, soil temperatures were more than 20°C higher. Astonishingly the leaf temperatures were a few degrees cooler than air.

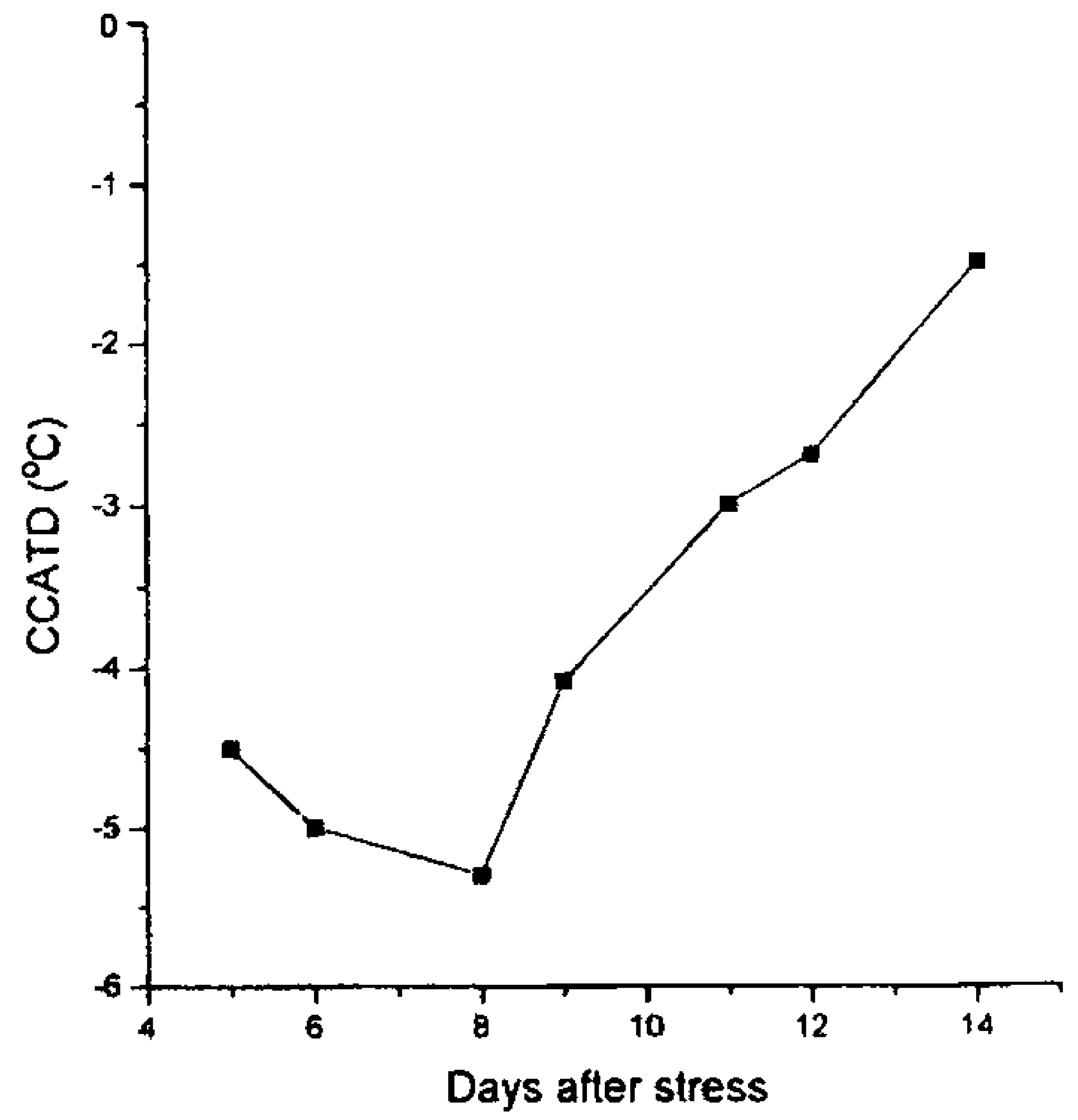

Figure 1. Average crop canopy air temperature difference of 200 genotypes of finger millet in the field which maintained a negative CCATD (canopy temperature lower than air, i.e. cooler canopy) on all days during a 16-day drought imposed in the field. Plant canopies can be at temperatures ranging from 7 to 8°C (– 7 to – 8°C display of CCATD on the infra-red gun; Figure 5). CCATD values decrease from more negative to less negative values, eventually reaching 0°C, the threshold at which the stomata close. Then canopies become warmer. Finger millet genotypes were a few degrees cooler even on 16th day, i.e. the stomata were partially open.

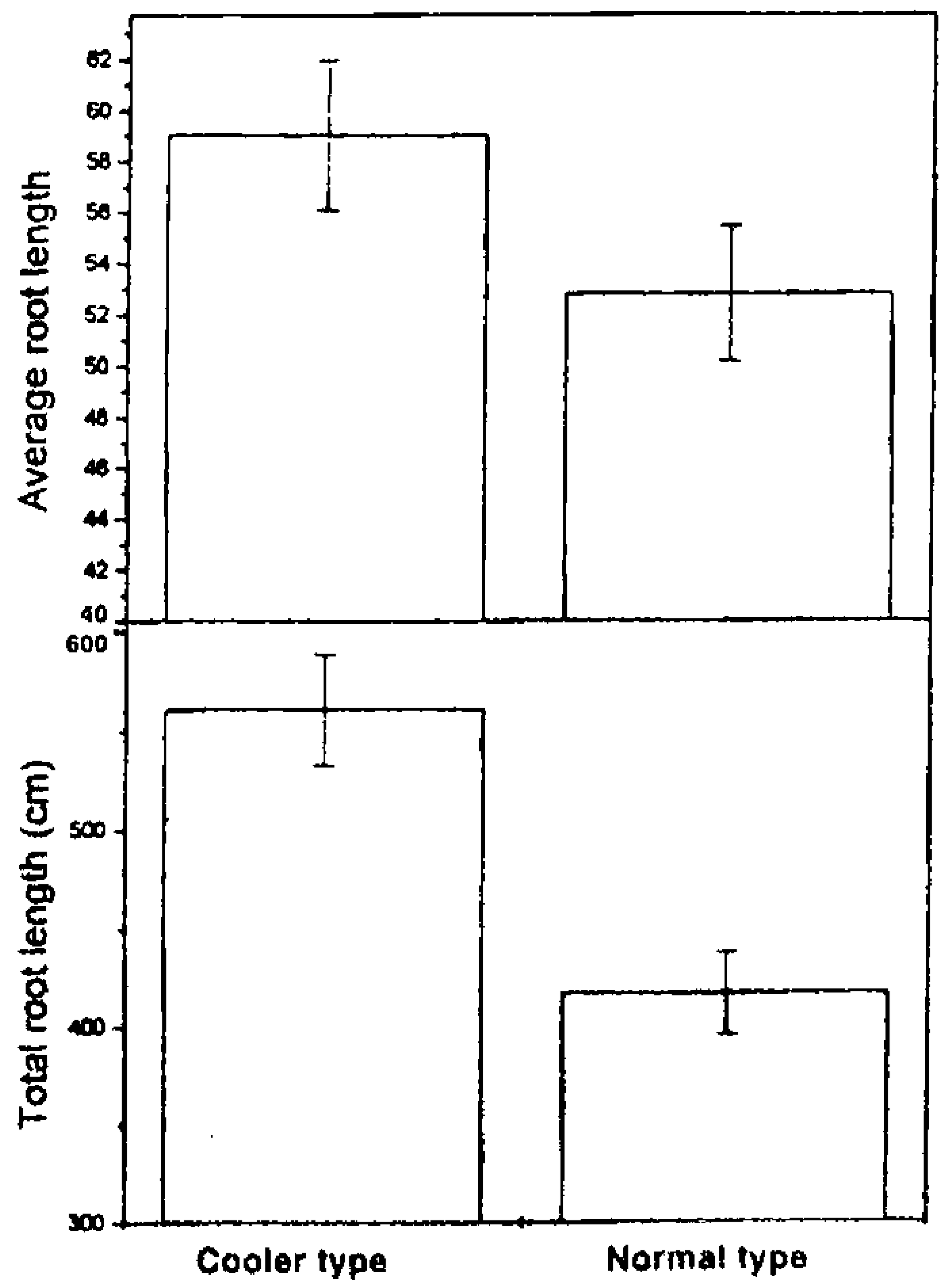

Figure 2. Average root length and total root length of cooler and normal type finger millet genotypes under stress. Total root length was calculated by multiplying average root length and total number of roots

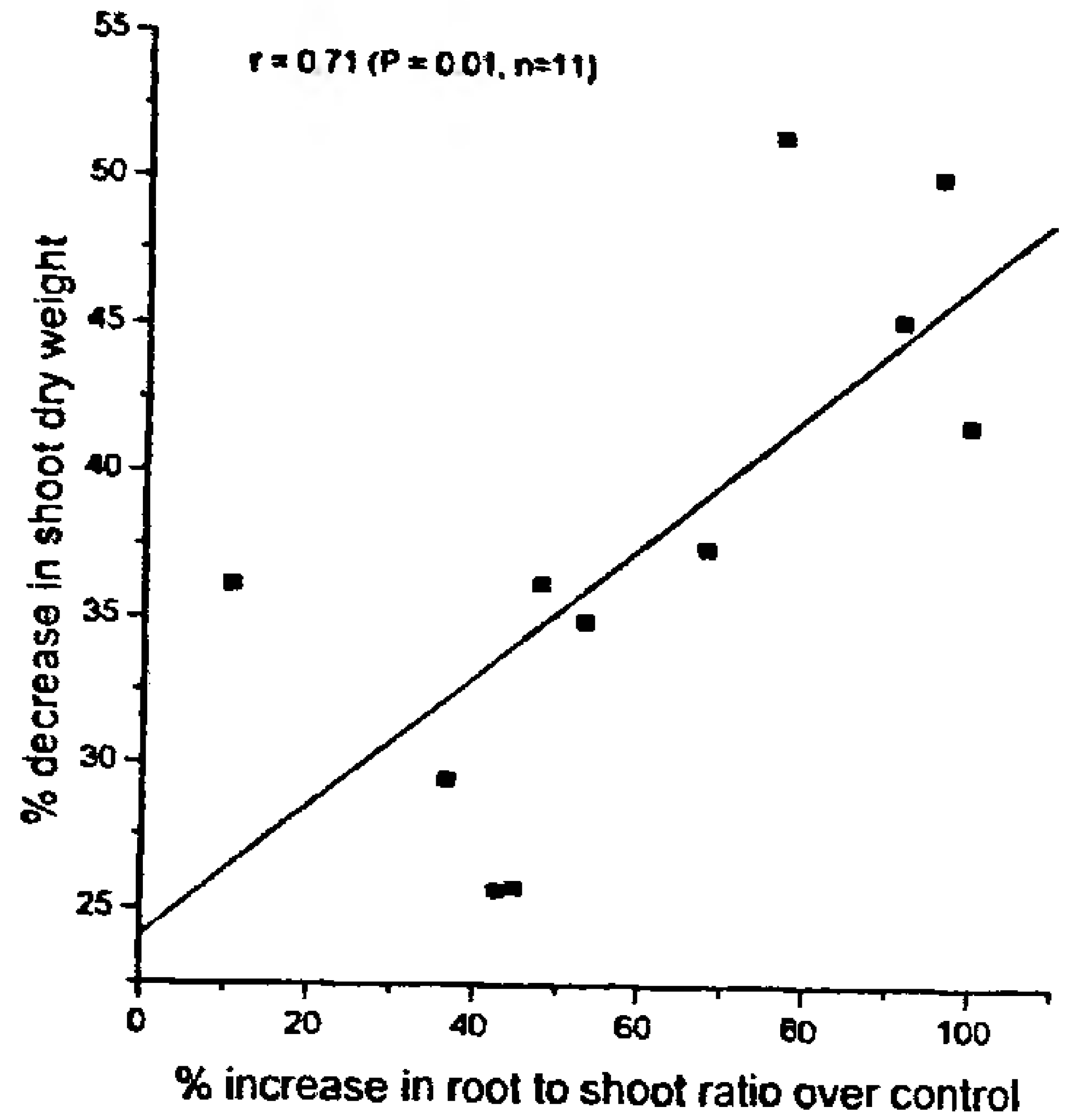

Figure 3. Relationship between root to shoot ratio and shoot dry weight under stress.

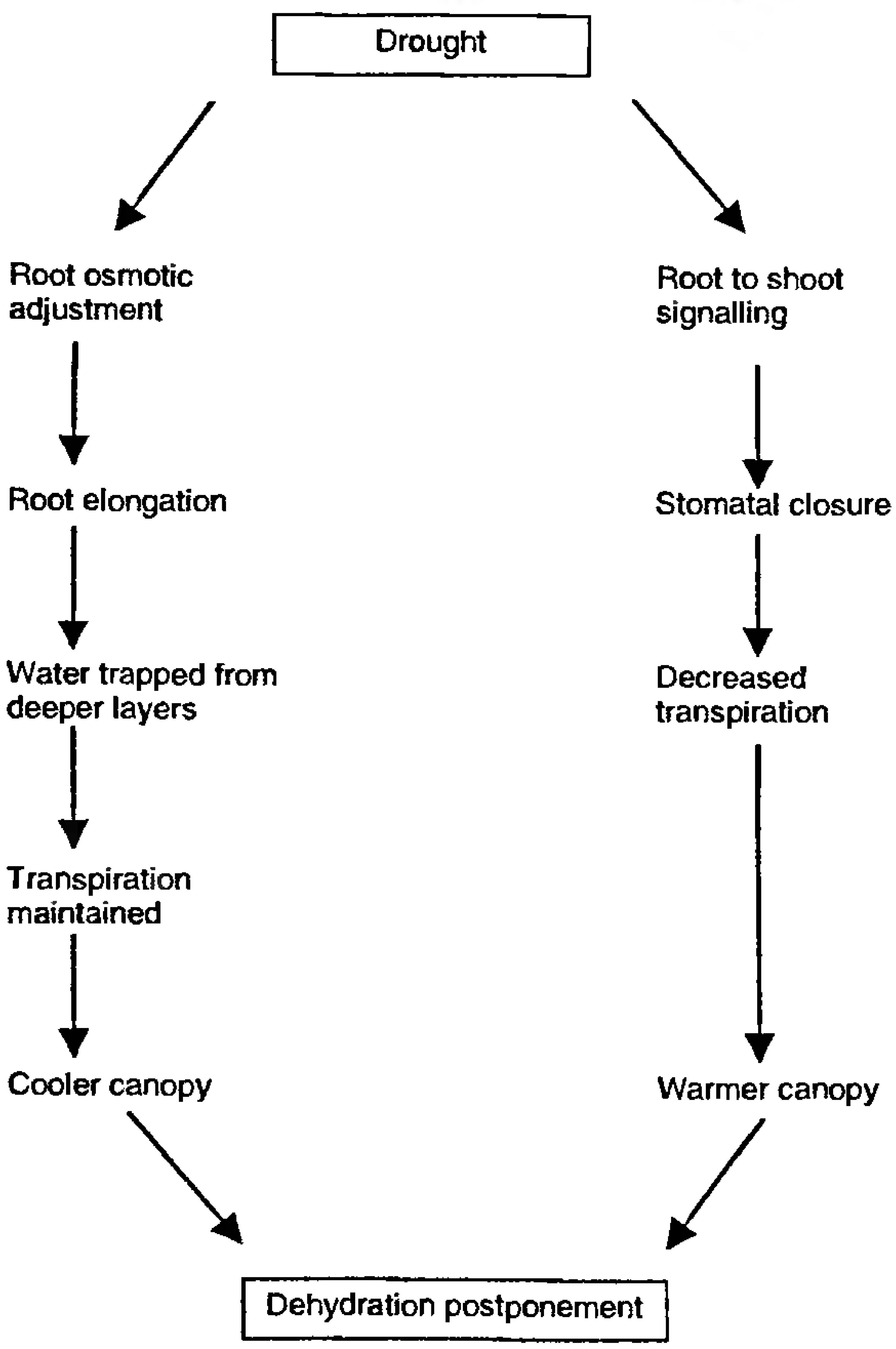

Figure 4. Flowchart showing the two divergent dehydration mechanisms that a plant can adopt. Ironically, one results in a warmer canopy and the other in a cooler canopy.

Figure 5. The infra-red gun measures canopy temperatures in the field. It also gives a measurement of crop canopy air temperature difference.

The paradox, however, is that both the 'strategies' that a plant could adopt – root to shoot signalling or maintenance of water uptake by increased root elongation, are called dehydration postponement mechanisms. While the former results in 'warming' of the canopy, the latter helps the plant maintain a cooler canopy for a while under drought (Figure 4).

The Hobson's choice for the plant is which mechanism should be put forth first when a drought occurs. The plant has resolved this by doing a balancing act. The roots send an early warning signal in the form of ABA by the help of which the plant is able to restrict the stomatal opening within a few days after the onset of a drought. This restriction results in a drop in the stomatal conductance by at least 25 to 30%. However, uptake of water by lower roots in contact with moist soil, still maintains a reasonably high transpiration rate as the stomata are still partially open. This results in cooler canopies or a negative CCATD. Around this time the ABA accumulated in the top roots which have undergone dehydration helps the plants to maintain root turgour and elongation possibly through osmotic adjustment. Eventually, as the drought progresses the 'second line of defence mechanisms' operate which result in increased production of ABA both in the roots and the leaves. Root elongation ceases and stomatal closure occurs. The canopy becomes warmer.

Which of these two mechanisms is more cost effective

The 'early warning defence' (strategy II) results in a penalty on growth because decreased gas exchange also means decreased rates of photosynthesis, which essentially means less growth. The latter mechanism, i.e. root elongation to tap water in deep layers, has two disadvantages: (a) there are structural costs involved, and (b) there is always the danger of a limited supply of water getting exhausted too quickly.

There is some evidence to show also that more metabolic energy is required to produce 1 g of root than 1 g of shoot[2]. Ultimately the plant tries to survive by adopting two divergent dehydration postponement mechanisms; one resulting in a 'warmer canopy' and the other maintaining a 'cooler canopy'. A plant surviving under a twenty-day drought in the field would probably have done a balancing act maintaining these two strategies, simultaneously or at different rates separated by a narrow time frame. The efficiency of the balancing act decides whether the plant survives or succumbs to the soil–plant dehydration syndrome.

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Derivatives of ultramafic rocks as decorative and dimensional stone in Rajasthan

M. S. Shekhawat

The Precambrian formations of southern Rajasthan host the unique and the largest deposits of 'green marble' in India located mainly around Rikhabdev, Kherwara, and Dungarpur areas. Field study coupled with mineralogic and petrologic studies indicate that the deep green and massive bodies of serpentinite are mainly composed of antigorite with subordinate amounts of carbonates and iron oxides. These serpentinite bodies occur as large sheet-like masses, emplaced concordantly within the Proterozoic formations of Aravalli Supergroup. These deposits are being utilized by fully mechanized, open-cast, block-bench mining methods for their extensive use as decorative and dimensional stone. About 70% of the recovered 'green marble' is being exported to various countries either in the form of well dressed blocks or in the form of finished products as slabs or tiles of suitable sizes. The highly fractured deep green serpentinites are also being exploited by small-scale, manual, open-cast mining methods to manufacture immensely popular flooring mosaic chips for civil engineering works. A very small quantity of steatitized serpentinite (steatite and chlorite schist) is also being used to manufacture different types of carved items and idols.

ULTRAMAFIC (UM) rocks, specially serpentinites have attracted the attention of geoscientists as well as common men not only because of their geologic significance but also because of their economic significance. Geologically, they reveal valuable information about the composition of the underlying mantle while, economically, they host a number of metallic as well as industrial mineral deposits. In southern Rajasthan, unfortunately, these rocks are totally devoid of metallic deposits but they host large deposits of talc[1] and world's largest deposits of amphibole asbestos[2,3]. Moreover, since the last decade, one of their metamorphosed derivatives, the massive and green serpentinite has acquired a significant recognition as a

M. S. Shekhawat is in Department of Geology, M.L. Sukhadia University, Udaipur 313 002, India. (e-mail: geo@mlsu.ac.in)