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Canopy Temperature Depression as an Effective Physiological Trait for Drought Screening

Parvaze Ahmad Sofi, Asmat Ara, Musharib Gull and Khalid Rehman

Abstract

Water stress is a major production constraint in agriculture worldwide. Efforts to breed for drought tolerance are invariably hampered by the amount of time required to phenotype a large number of individuals and poor or inconsistent correlations and multiple mechanisms involved. Canopy temperature depression has emerged as a potential surrogate in view of substantial natural variation in crops as well as its correlation with yield. Based on the experimental findings two types of ideotype models based on CTD have been proposed as isohydric (“water saving”) and anisohydric (“water spending”). The isohydrics have advantage in the harsher environments, whereas the anisohydrics perform better under moderate/mild drought situations. Water savers have a shallow root system with intermediate root growth and thin roots. They are early and have high water use efficiency, reduced transpiration and limited leaf area and canopy biomass development and superior photosynthate remobilization to pod and grain. Contrary to this, water spenders have a vigorous and deep rooting system with rapid root growth and a thicker root system. Such genotypes are early and have highly effective water use, moderate transpiration and fast leaf area and canopy biomass development, moderate sink strength and superior photosynthate remobilization to pod and grain formation.

Keywords: drought stress, physiology, canopy temperature depression

1. Introduction

The world is currently experiencing the combined effect of population growth and climate change leading to an unsustainable use of food and water resources. The population is going to touch 9.8 billion, and demand for food and feed crops is expected to almost double by 2050 [1]. Climate change models predict an increase in temperatures and increased frequency of severe events such as droughts and floods [2]. Higher temperatures may increase precipitation but also increase evaporation from crops, land, and surface water. An increase in the frequency of droughts and floods that invariably lead to crop failures can have a devastating effect on food availability and consequently accessibility. As per the current IPCC projections, the 20-year extreme annual daily maximum temperature will likely increase by about

1–3°C by the mid-twenty-first century and by about 2–5°C by the late twenty-first century, depending on the region and emission scenario [3]. Based on historical data collected in Africa on more than 20,000 trials between 1999 and 2007, each “degree day” spent above 30° is likely to reduce crop yields by 1% under optimal conditions and that penalty is going to increase up to 1.7% under water-limited conditions [4]. The impact of a climate change is not only about the projected increase in temperature, but it also affects the magnitude and distribution of rainfall, as well as availability of water at critical times of the crop growth [5]. While as the total amount of rain has recorded an increase in Africa over the last few years, the erratic and unpredictable nature of the drought and floods cycle has also increased [6].

Globally, rainfed agriculture is practiced in 80% of the total agricultural area and generates 62% of the world’s staple food (FAOSTAT, 2011). In view of the current global water scarcity scenarios, climate change implications, and increases in demand for nonagricultural water use, the expansion of the area under irrigation, especially in developing countries, does not seem to be a realistic proposition to address food security challenges. Drought is one of the major production constraints in agriculture worldwide. It principally affects crops cultivated under rainfed conditions, which represent 80% of the total cultivated area worldwide. It is estimated that cultivation on the earth is only possible on 16% of the potentially arable area due to limited availability of water [7, 8]. Africa is strongly affected by drought almost every 12 years, but drought intensified during the years 2009–2011, during which, the wheat yields reduced by 45% in Kenya [9]. Similar trends have also been reported from Australia where drought reduced wheat yields by 46% in 2006 [10]. Around 17% of the global cultivated area was affected by drought during the period 1980–2006 [11]. **Tables 1** and **2** depict the proportion of cultivated areas implicated by drought stress and estimated yield reductions reported in various crops.

2. Breeding for drought tolerance

Breeding for drought tolerance is a sustainable option to reduce the risk of crop failure by improving the ability of crop plants to extract water from the deeper soil strata through better root architecture, by decreasing the amount of crop water demands (improving water use efficiency), or by improving a crop’s ability to survive longer periods without water, thereby ultimately increasing yields in rainfed environments. However, breeding for drought tolerance is complex because

Region	Crop species	Proportion of the cultivated area affected by drought
Africa	Wheat	80%
Eastern Asia	Maize	50%
Europe	Maize	60%
North America	Wheat	47%
Oceania	Barley	70%
South America	Maize	50%
South Asia	Wheat	65%
Southeast Asia	Rice	65%

Table 1.

Proportion of the cultivated area affected by drought in different regions and for different crops (source: [12]).

Crop	Yield reduction	References
Barley	49–57%	[13]
Chickpea	78%	[14]
Groundnut	55–72%	[15]
Maize	43–80%	[16]
Oat	79%	[17]
Potato	89%	[17]
Rice	42–66%	[18]
Brassica	39%	[17]
Rye	52%	[17]
Bread wheat	57%	[17]
Durum wheat	74%	[19]
Pigeon pea	42%	[20]
Green gram	71%	[20]
Black gram	74%	[20]

Table 2.
Impact of drought stress on yield reduction in different crops.

it involves quantitative inheritance and environmental influence [21]. Efforts to breed for drought tolerance are invariably hampered by the amount of time required to phenotype a large number of individuals and poor or inconsistent correlation between a phenotype and yield under drought conditions due, in part, to multiple mechanisms involved. Various authors have investigated the genetic basis of drought tolerance in common bean and reported that both additive and nonadditive gene actions are involved in drought tolerance [22, 23]. Schneider et al. [24] reported a strong genotype x environment interaction in the expression of identified quantitative trait locus (QTL), such that potential for marker-assisted selection in breeding for drought tolerance was also inconclusive. Selection based solely on yield performance confounds the complexity of breeding for drought as yield is a highly complex trait with low heritability especially under stress conditions. Therefore, it is imperative to identify less complex traits related to the drought that will improve upon selection for drought tolerance and separate these traits into major components which may help further understanding of the genetic basis.

A better understanding of the relationship between below- and aboveground traits will contribute to improved productivity under drought stress. Root traits including structure and their spatial distribution of root system in different soil horizons are essential for yield improvement because of its high heritability under drought stress [25–27] and high correlation with yield traits [28]. However, extensive use of roots as the target traits for developing climate resilience suffers from the difficulties associated with studying roots, especially under field conditions. The shoot traits are easy to measure and quantify; however, it has to be linked with root traits with the perspective of improving drought tolerance. In the following sections, we discuss some of the potential aboveground traits that have been shown to be correlated with improved drought tolerance as well as better grain yield under stress. Currently, there is a huge shopping list of relatively unranked traits that have been proposed to be used as surrogates for drought tolerance response. Canopy temperature depression has emerged as a potential surrogate in view of substantial natural variation in crops as well as its correlation with yield under both stress and nonstress conditions [29].

3. Canopy temperature (CT) and canopy temperature depression (CTD)

Plant water balance is a direct measure of drought response of crops. In fact, the transpiration is the main cause of changes in leaf temperature, and there is a direct relationship between leaf temperature, transpiration rate, leaf porosity, and stomatal conductance [30]. As long as the plants continue to transpire through open stomata, the canopy temperatures could be maintained at metabolically comfortable range; otherwise, higher temperature would slow or retard the vital enzymatic activities and consequently the overall metabolism. The closure of stomata for a considerable period of time, especially during the periods of higher evaporative demands driven by high temperature and vapor pressure deficit, is known to increase the leaf temperature [31] and hamper plant's ability to maintain a relatively cooler canopy during grain filling period as an important physiological adaptation for stress [22]. Canopy temperature differences have been shown to correlate well with the transpiration status in rice, potatoes, wheat, and sugar beet. Deviation of temperature of plant canopies from the ambient temperature, also known as canopy temperature depression = air temperature (T_a) – canopy temperature, has been recognized as an indicator of overall plant water status [33] and facilitates in evaluation of plant response to stresses like high temperature [34] and drought [35, 36]. CTD is positive when the canopy is cooler than the air, and this value has been associated with yield increase in different crops [37, 38]. The thermal imagery system is a powerful tool as it can capture the temperature difference of plant canopies quite rapidly.

Thermal infrared imaging and infrared thermography (IRT), to measure the canopy or leaf temperature, are the twin approaches that measure the extent of evaporative cooling occurring in a crop canopy and allow a remote sensing of the plant water balance. Between these two approaches, thermal infrared imaging through an infrared camera offers several benefits compared with temperature sensors, most importantly the facility for spatial resolution and the ability to sample larger area. Most infrared cameras currently have arrays of 320×240 sensor elements, which mean that $>75,000$ individual temperature readings are recorded in a single image. This allows more precise measurements in a fraction of the time needed to perform several replicate readings per plot, which is also prone to error due to changing environmental conditions between measurements. Canopy temperature is one such integrative trait that reflects the plant water status or the resultant equilibrium between root water uptake and shoot transpiration [39]. Canopy temperature has been used successfully as selection criteria in breeding for drought-prone environments [33, 37, 40].

At ambient temperature, all objects emit far-infrared light of approximately $10 \mu\text{m}$ wavelength [41]. Detectors sensitive in the $8\text{--}14 \mu\text{m}$ wavelength bands convert this radiation into a temperature reading. Such detectors are the basis of non-imaging infrared thermometers, which yield an average temperature measurement of all objects within the field of view. Applications of these simple and affordable instruments include forest canopy studies and irrigation scheduling in field crops [42]. There are yet other thermometers based on infrared imaging that can capture images by adding a scanning system, and each point of measurement is a temperature value based on a pseudo-color value that depends on the radiation captured. The radiation is converted to visual pseudo-color images representing different temperature levels. Both the non-imaging and scanning image thermometers are now being routinely used to measure the temperatures of leaves or canopy in controlled and field conditions. In case of greenhouse or growth chamber experiments where only one or two plants are used per replication, leaf temperatures are used, whereas in case of field experiments where comparatively larger plots are used, canopy temperature is mostly used. Nowadays, unmanned aerial vehicles (UAVs) or robotic equipments fitted with sensors and cameras can be used for monitoring stress advancement in greenhouses and field trials.

Infrared thermometry was first used for scheduling crop irrigation in the 1970s [43], while the use of canopy temperature in drought screening began in the early 1980s [44]. The use of canopy temperature in Centro Internacional de Mejoramiento de Maíz y Trigo or International Maize and Wheat Improvement Center (CIMMYT) breeding research began in the early 1990s for hot, irrigated environments [45] and has also been used as a selection criterion for isolating drought-tolerant parental lines for initiating strategic crossing as well as for early generation selection under drought (i.e., from F₃ generation onward). Canopy temperature measured by non-imaging IR thermometer can markedly accelerate selection of drought-tolerant genotypes given on high operational speed (≈ 10 seconds per plot), simplicity, and relatively economically friendly measurements. It is also integrative of the whole canopy due to scoring many plants at once, thus reducing error associated with plant-to-plant variation [46]. In addition, measurements of CT on plants do not interfere with the sensitive stomata, in comparison with other methods that estimate leaf conductance such as porometry and other gas exchange approaches. These may include accurate estimation of the temperatures of different organs of a single plant or the simultaneous capture of CT of all plots in a large trial [47, 48]. Besides, canopy temperature may be related directly to the genetic potential of the root's capacity to explore soil moisture [49]; however, factors such as microelement deficiency or soil-borne disease that affect root growth may confound the relationship.

Grant et al. [50] investigated the robustness and sensitivity of thermal imaging for detecting changes in stomatal conductance and leaf water status in a range of plant species (grapevine, bean, and lupin) under greenhouse or controlled environment conditions. In particular, they compared absolute leaf temperatures and thermal indices of plant stress with stomatal conductance and water potential. Thermal imaging is successfully distinguished between irrigated and nonirrigated plants of different species, with strong correlations between thermal indices and stomatal conductance as measured with a leaf pyrometer. Factors such as leaf angle are important and should be given due consideration when using thermal imaging for indirect measurement of the level of drought stress of the tested materials (Figure 1).

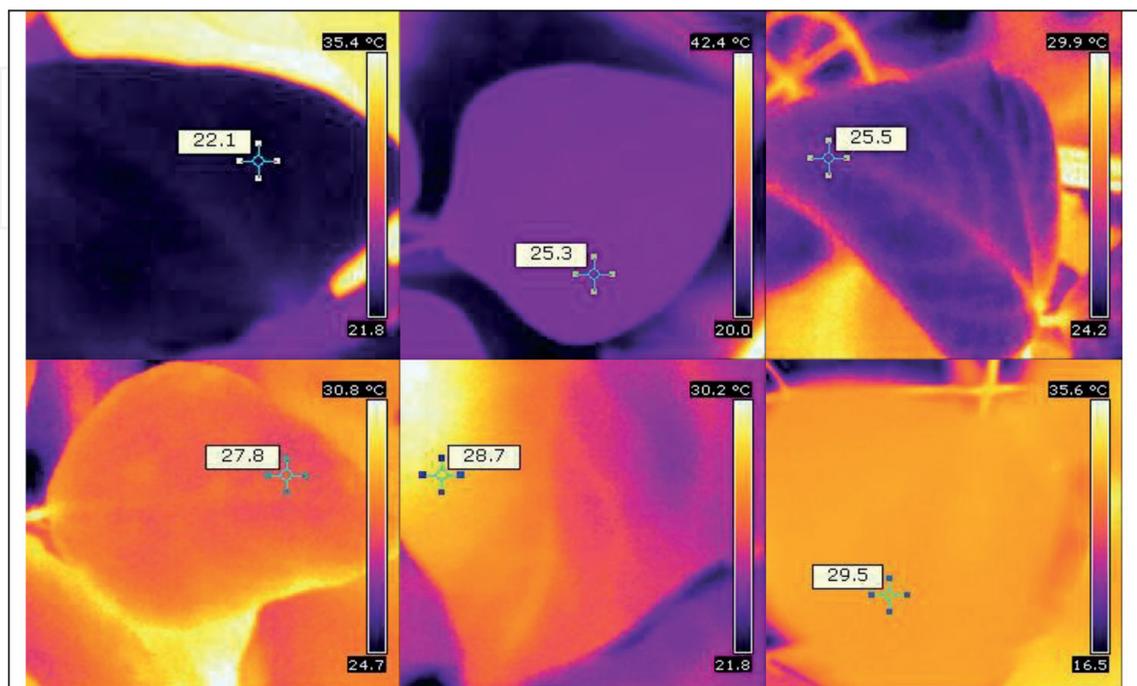


Figure 1.
Infrared camera images of bean leaves (source: P. A. Sofi).

4. CTD as an effective surrogate trait for drought screening

Canopy temperature is one of the many physiological traits that may help to identify drought-tolerant cultivars. Canopy temperature depression is the difference between air temperature and plant canopy temperature [51]. Under drought conditions, stomatal conductance decreases when soil moisture is not adequate to keep up with evaporative demands; and this, in turn, increases canopy temperature [52]. Plant morphological trait such as canopy architecture also influences canopy temperature not only through the angle of leaves to the light source but also through the degree of mutual shading in the canopy. Canopy temperature can provide plant-based information on the water status of the crop [53]. Under both greenhouse and field conditions, genotypes with a cooler canopy temperature (higher CTD) under drought stress use more available soil moisture to cool the canopy by transpiration to avoid excessive dehydration [54, 55]. In a large number of experiments in diverse crops, CTD has been found to have significant correlation with grain yield (**Table 3**).

Canopy temperature is also related directly to the genetic potential of the root's capacity to explore soil moisture [32, 56]. Canopy temperature depression can be used as effective proxy traits for the analysis of root development and biomass partitioning under drought stress [57]. Cool canopy temperatures are reported to be associated with enhanced plant access to water by virtue of deeper roots [49], and the common bean genotypes with cooler canopy temperatures reported 30% more yield associated with an increase of 40% in root dry weight at 60–120 cm. Canopy temperature depression has been shown to be correlated with yield under drought stress ([32, 35, 58, 59]; **Table 3**) and hot irrigated conditions [32, 60]. Canopy temperatures under well-watered conditions also indicate potential yield performance during drought and could effectively be used as a technique to assess genotypic response to drought [61]. Blum et al. [62] used canopy temperatures of drought stress wheat genotypes to characterize yield stability under various moisture conditions. A positive correlation was found between a drought susceptibility index and canopy temperature in stressed environments. Drought-susceptible genotypes which suffered relatively greater yield loss under drought stress tended to have warmer canopies at midday.

Crop	Trait relationship with yield	References
Wheat	Positive association ($r^2 = 0.45\text{--}0.89$; $P \leq 0.001$)	Amani et al. [60]; Fischer et al. [37]; Balota et al. [33]
Chickpea	Positive association ($r^2 = 0.40$; $P \leq 0.001$)	Purushothaman et al. [59]
Common bean	Positive association ($r^2 = 0.11\text{--}0.32$; $P \leq 0.001$)	Asfaw et al. [25] and Polania et al. [28]
Groundnut	Positive association ($r^2 = 0.44$; $P \leq 0.001$)	Singh et al. [67]
Sorghum	Positive association ($r^2 = 0.19$; $P \leq 0.001$)	Mutawa [58]
Triticale and barley	Positive association ($r^2 = 0.76$; $P \leq 0.001$)	Roohi et al. [68]

Table 3.
Correlation of CTD with grain yield in various crops.

CTD can be affected by biological and environmental factors like water status of soil, wind, evapotranspiration, cloudiness, conduction systems, plant metabolism, air temperature, relative humidity, and continuous radiation [63] and has preferably been measured in high air temperature and low relative humidity because of high vapor pressure deficit conditions [60]. At the end of the 1980s, CIMMYT began CTD measurements on different irrigated experiments in Northwest Mexico. Phenotypic correlations of CTD with grain yield were occasionally positive [37]. CTD has been used as selection criteria for tolerance to drought and high temperature stress in wheat breeding, and the used breeding method is generally mass selection in early generations like F3. According to this method, firstly, bulks which show high CTD value (have cool canopy) are selected in F3 generation. Later, single plants which show high stomata conductance (g) among bulks also show cool canopy at the same selection generation; thus, both of these traits are used at the same breeding program [63].

CTD can be a reliable indicator of crop performance under both irrigated and drought stress conditions. Under irrigated conditions there was a linear trend of higher yield with CTD; however, under drought stress, both negative CTD and positive CTD could be identified, and in both classes, high-yielding genotypes were identified. The water savers probably could sense drought stress in early phases of growth and could trigger conservative water use that could be used in later stages of growth [30]. However, the reduction in water use is generally achieved by plant traits and environmental responses that could also reduce yield potential [64]. Under optimum experimental conditions provided that data are collected when the canopy is sufficiently expanded to cover the soil, CTD can be a good predictor of crop yield ($r = 0.6-0.85$; [65]). In wheat, yield progress was found to be associated with cooler canopies [37], and significant genetic gains in yield have been reported in response to direct selection for CTD [55, 65]. Reynolds et al. have made a comparative analysis of aerial and handheld IR thermometers and found that correlation of CTD with grain yield was comparable ($r = 0.68^{**}$ and 0.73^{**} , respectively).

5. Toward a crop ideotype based on canopy temperature depression

Blum has proposed ideotypes of crop plants based on canopy temperature depression for use in plant breeding as per the drought types such as the isohydric (“water saving”) model and the anisohydric (“water spending”) model. The water saving model has a distinct advantage in the harsher environments, whereas the water spending model is expected to perform relatively better under more moderate/mild drought situations. Polania et al. [28] have proposed that the water spender genotypes can be used for cultivation in areas exposed to intermittent drought stress with soils that can store greater amount of available water deep in the soil profile. However, water savers can be more suitable in semiarid to dry environments dominated by the terminal drought stress. The water savers or isohydric genotypes are characterized by a shallow root system with intermediate root growth and penetration ability and thin roots. Such genotypes are early and have high water use efficiency, reduced transpiration and limited leaf area and canopy biomass development, reduced sink strength, and superior photosynthate remobilization to pod and grain formation. Contrary to this, water spenders or anisohydric genotypes have a vigorous and deep rooting system with rapid root growth rate and penetration ability and a thicker root system. Such genotypes are early and have highly effective water use, moderate transpiration and fast leaf area and canopy biomass development, moderate sink strength, and superior photosynthate remobilization to pod and grain formation.

Our studies in beans and cowpea have also revealed that CTD measurements can be used to build a crop ideotype for water stress response. In our studies with beans and cowpea, we found that CTD values across stages decreased progressively on account of rapid depletion of moisture (**Figure 2**). The genotypes could be grouped into water savers and water spenders using the sign of CTD values (**Figures 3 and 4**). The water spenders have higher stomatal conductance and lose water through transpiration, whereas water savers have conservative water use on account of lower stomatal conductance or early closure of stomata and as such have hotter canopies. Under irrigated conditions also, we found a linear relationship with genotypes having higher CTD values showing better yields, whereas under water-stressed conditions, high-yielding genotypes could be found in both groups.

Canopy temperature can be related to the genetic potential of the root's capacity to explore soil moisture [32, 56] and as such can be used as effective surrogate trait for the analysis of root development and biomass partitioning under drought stress [57]. Cool canopies (+CTD) are reported to be associated with enhanced plant access to water by virtue of deeper roots (Lopes and Reynolds 2010), and the genotypes with cooler canopies have been reported to yield 30% more, with a concomitant increase of 40% in root dry weight. CTD has been reported to be correlated with yield under both drought stress [32, 35, 59] and hot irrigated conditions [32]. Drought-susceptible genotypes which suffered relatively greater yield loss under drought stress tended to have warmer canopies at midday. Our studies have revealed that CTD can be a reliable indicator of crop performance under both irrigated and drought stress conditions. Under irrigated conditions, there was a linear trend of higher yield with CTD; however, under drought stress, both negative CTD and positive CTD could be identified, and in both classes, high-yielding genotypes were identified. The water savers probably could sense drought stress in early phases of growth and could trigger conservative water use that could be used in later stages of growth [30]. However, the reduction in water use is generally achieved by plant traits and environmental responses that could also reduce yield potential [64].

In recent years, with the availability of high-throughput phenotyping platforms, canopy temperature depression has been widely used to study genotypic response to drought. Blum et al. [62] used canopy temperatures of drought stress wheat genotypes to characterize yield stability under various moisture conditions. In most of the studies using CTD, a positive correlation has been found between

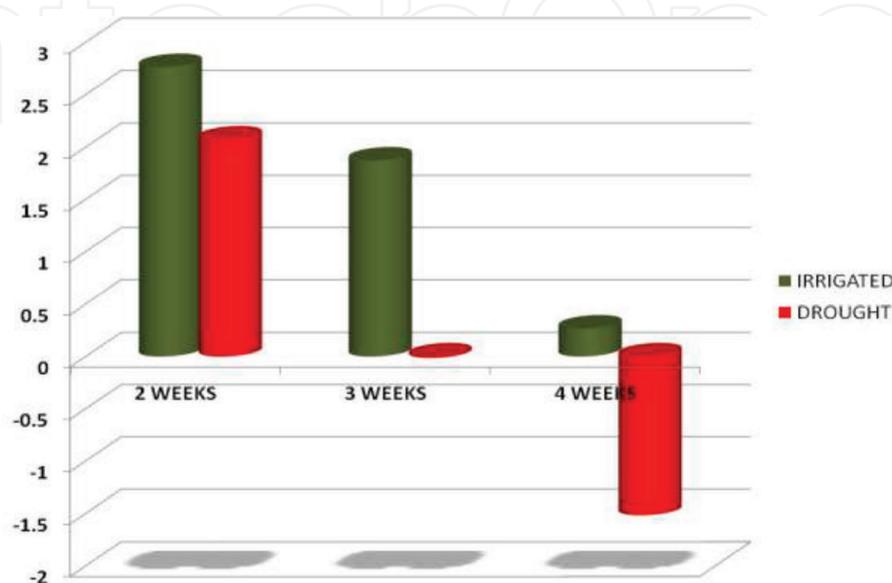


Figure 2. Mean CTD across genotypes at the second, third, and fourth week of stress imposition.

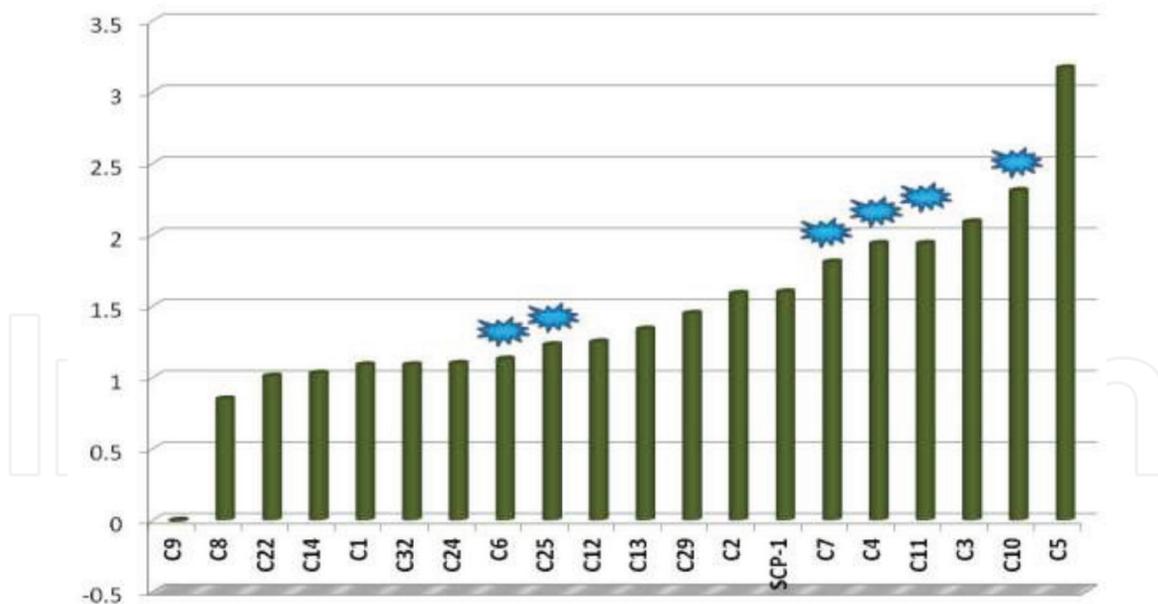


Figure 3.
 Variation for CTD averaged over 3 stages in 20 genotypes of cowpea under irrigated conditions.

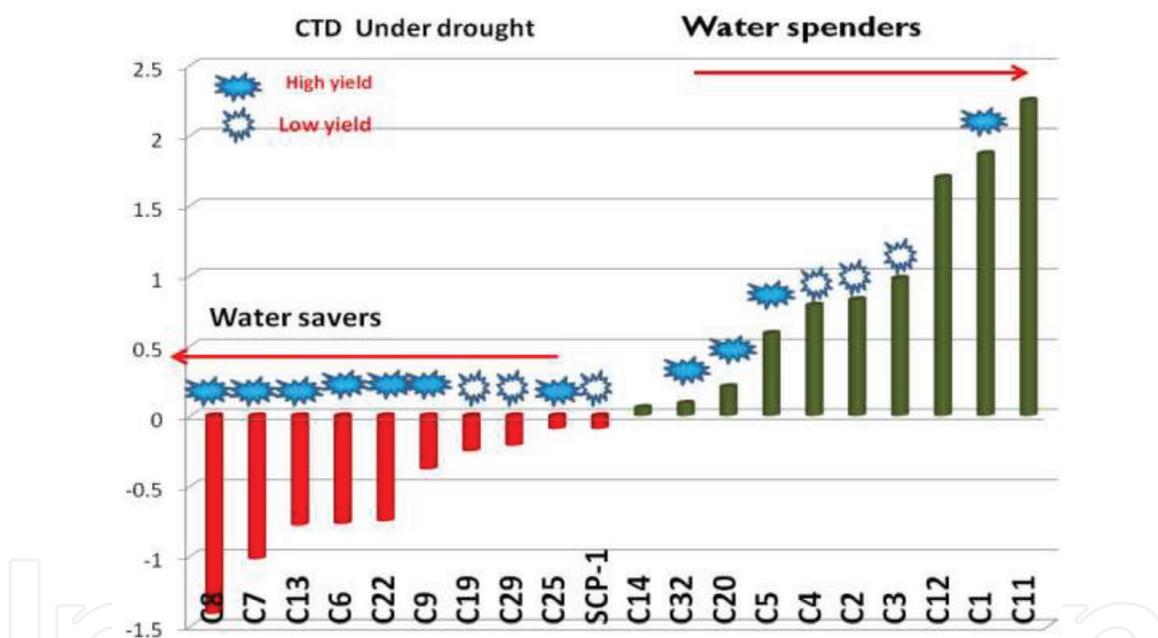


Figure 4.
 Variation for CTD averaged over 3 stages in 20 genotypes of cowpea under drought stress.

drought susceptibility index and canopy temperature in stressed environments. Drought-susceptible genotypes which suffered relatively greater yield loss under stress tended to have warmer canopies at midday. Under well-watered conditions also, CTD provides a fair indication of potential yield performance during drought and could effectively be used as a technique to assess genotypic response to drought. Rashid et al. [35] reported that significant correlation between canopy temperature and yield under moisture-stress conditions and stress susceptibility index values indicated the potential for screening wheat genotypes for drought response. Canopy temperature depression is positive when the canopy is cooler than the air ($CTD = T_a - T_c$). It has been used in various practical applications including evaluation of plant response to environmental stress [66] and irrigation scheduling [69], to evaluate cultivars for water use [70], tolerance to heat [71], and drought [35, 62]. In general, CTD has been used to assess plant water status because it represents an overall, integrated

physiological response to drought and high temperature [60]. Overall, the existing literature suggests that dominant mechanisms that increase CTD vary with environment and crop species.

Canopy temperature is a useful indicator of crop water status [43] and has the potential as a tool for indirect selection of genotypes tolerant to drought and heat-stressed environments [55]. For field experiments in wheat, CT data is most commonly measured on a whole-plot basis using a handheld infrared thermometer [71], although more rapid assessment using thermal imaging [72] is growing in popularity. CT is influenced by a number of environmental factors including the amount of solar radiation hitting the canopy, soil moisture, wind speed, temperature, and relative humidity [73]. Genetic differences in CT result from variation in the plant's ability to move water through the vascular system, differences in stomata aperture driving transpiration, root biomass and depth, metabolism, and source sink balance [74]. As such, CT has been shown to correlate with these physiological traits under field conditions and integrates them into a single low-cost diagnostic measurement that has a potential for selection of tolerant parental genotypes or early generation breeding lines [55]. CT has moderate heritability across environments in both diverse sets of germplasm [49] and in related material such as recombinant inbred populations [73]. Lopes and Reynolds [49] found similar broad-sense heritability for a diverse set of 294 spring wheat lines ($H^2 = 0.38$) and a set of 169 sister lines ($H^2 = 0.34$) across well-watered, drought-stressed, and heat-stressed environments in Northwest Mexico. Genetically, CT is a quantitative trait. Pierre et al. [74] determined the gene action for CT to be mainly additive by additive in five wheat populations with some dominant effects. Genetic mapping shows CT to be controlled mostly by small effect loci that are pleiotropic with variation in other traits, such as days to heading and plant height [20]. The correlation between CT and yield is consistently negative in the literature in both drought and heat environments such that a cooler canopy provides a yield benefit under stress [73]. Exceptions have been shown in both bread wheat [75], where CT measurements taken in Mexico were positively correlated with yield at international sites, and in durum wheat [76], where CT was found to increase with date of cultivar release and increasing yield. Experiments investigating CT are often conducted with sets of lines preselected for variation in canopy temperature or other tolerance traits [49], international trials of elite drought and heat tolerant lines [45], or using historical germplasm [9, 19, 21] and may not be representative of variation present in the early stages of yield testing in a breeding program. Reynolds et al. [55] demonstrated that advanced lines derived from "physiological crosses" targeted at one or more adaptive traits had a definite yield advantage over "conventional crosses" where physiological traits including CTD were not considered in parental selection. However, there is a need to investigate the ability of CT to select high-yielding lines within the germplasm flow of a breeding program where very little preselection for stress tolerance per se has been done.

6. Conclusion

Both empirical breeding and analytical approaches are used for improving crop performance under changing climate (drought, high temperature, etc.). However, there is a strong argument evolving in support of the analytical approaches based on indirect selection approaches using efficient surrogate traits to enhance the scale and reliability of phenotyping. Infrared thermometry can detect small differences in leaf temperature in both field and greenhouse conditions, measurements are fast and nondestructive, and the trait has a moderate to high heritability and

shows positive correlation with yield [44]. Measurements should however be made well before the crop maturity and due consideration should be given to biological and environmental factors such as water status of soil, wind, evapotranspiration, cloudiness, conduction systems, plant metabolism, air temperature, relative humidity, and continuous radiation [55]. In light of substantial experimental evidence that a fairly positive relationship exists between yield and CTD under both stressed and nonstressed conditions, it is essential to incorporate CTD as effective complementary trait in selection programs aimed at developing climate resilient varieties.

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