

Review Article

Adaptation to High Temperature and Water Deficit in the Common Bean (*Phaseolus vulgaris* L.) during the Reproductive Period

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This paper reviews the adaptation to heat and drought stresses in *Phaseolus vulgaris*, a grain and vegetable crop widely grown in both the Old and New World. Substantial genotypic differences are found in morphophysiological characteristics such as phenology, partitioning, plant-water relations, photosynthetic parameters, and shoot growth, which are related to reproductive responses. The associations between (a) days to podding and leaf water content and (b) the number of pods per plant and seed yield are consistent across different environments and experiments. Leaf water content is maintained by reductions in leaf water potential and shoot extension in response to heat and drought stress. Heat-tolerant cultivars have higher biomass allocation to pods and higher pod set in branches. These traits can be used as a marker to screen germplasm for heat and drought tolerance. In this paper, we briefly review the results of our studies carried out on heat and drought tolerance in the common bean at the Tropical Agriculture Research Front, Ishigaki, Japan.

1. Introduction

Transitory or constantly high temperatures cause an array of morphoanatomical, physiological, and biochemical changes in plants, which affect plant growth and development and may lead to a drastic reduction in economic yield. The adverse effects of heat stress can be mitigated by developing crop plants with improved thermotolerance using various genetic approaches [1]. However, achieving this requires a thorough understanding of the physiological responses of plants to high temperature, the mechanisms of heat tolerance, and potential strategies for improving crop thermotolerance.

The common bean (*Phaseolus vulgaris* L.) is originally a crop of the New World [2], but it is now grown extensively in all major continental areas [3]. Its production spans from 52°N to 32°S latitude [4] and from near sea level in the continental US and Europe to elevations of more than 3000 m in Andean South America. The common bean has

two major gene pools [5], the Andean and the Mesoamerican, based on their centers of origin in South and Central America, respectively [6]. Within these gene pools are a total of six races, including three Mesoamerican (Mesoamerica, Durango, and Jalisco) and three Andean (Peru, Nueva Granada, and Chile) [7, 8]. An additional Mesoamerican race has been designated Guatemala, which includes certain climbing beans from Central America [9].

After domestication, the common bean spread across Mesoamerica and South America and, after the European discovery of the Americas, to Europe and Africa, where it was cultivated in diverse environments and agricultural conditions [10]. As much as 60% of bean production in the developing world occurs under conditions of significant drought stress [11]. This includes large areas in Mexico and Africa where the growing season is short and the rainfall unreliable; regions of Central America where beans are planted after maize and may be subjected to the abrupt cessation of the rains; areas of Brazil where overall rainfall

may be adequate but the growing period is interrupted by significant periods without precipitation. In the highlands of Mexico, beans are subjected to extended periods of intermittent drought. The only traits that have proven to be valuable in tolerating both terminal (end-of-season) and intermittent drought are earliness and partitioning toward reproductive structures, resulting in a greater harvest index [12, 13]. Bean breeders in Mexico have developed bean cultivars with indeterminate prostrate growth habits similar to pinto bean landraces in the semiarid highlands [14]. Cultivars such as Pinto Villa use phenotypic plasticity to respond to intermittent drought [15]. Interracial and intergene-pool crosses have been made in Mexico to combine different drought tolerance traits [16].

In lowland environments, terminal drought stress can be aggravated by high temperatures [11]. In Central America and the Caribbean, breeders have focused on heat as a constraint to expanding bean production in the lowland tropics [11, 17]. They have made significant progress in developing bean cultivars with improved levels of heat tolerance [18, 19]. In the subtropical island of Okinawa, Japan, vegetable production in the summer season is very difficult due to high temperatures and intense solar radiation, along with associated effects such as drought and infestation by insects and other pests [20]. High temperature in the summer is causing drastic reductions in common bean yield [21–24]. The heat-tolerant cultivar Haibushi was developed by the Okinawa Subtropical Station (now the Tropical Agriculture Research Front), JIRCAS, Okinawa, by screening the germplasm collected from Southeast Asian countries [25].

Development during the reproductive growth stage in the common bean is sensitive to temperature. High temperatures during this stage result in a reduction in pod and seed set due to enhanced abscission of flower buds, flowers, and pods [26–28]. Pollen-stigma interaction, pollen germination, pollen tube growth, and fertilization are all negatively affected by high temperature [29–32], with the lowest pod set observed in plants exposed to high temperature 1–6 days prior to anthesis [11]. Exposure to 35/20°C or 35°C reduced pollen viability (evaluated by pollen staining) [31]. Lower pod and seed set caused by high temperature at anthesis (32/21°C [29] and 35/20°C [28], resp.) were related to pollen injury, as assessed by pollen stainability and reciprocal pollinations. Continued exposure to 35/20°C did not affect embryo sac structure, but fertilization failed and it degenerated after anthesis [33]. Lower pod and seed set after the exposure of common bean plants to high temperature (32/27°C) are the combined result of both lower pollen viability (evaluated by pod and seed set resulting from reciprocal hand pollination) and impaired female performance in a large proportion of the flowers [32]. High temperature (33/25°C) affects the endoplasmic reticulum structure and blocks its function in the tapetum and then induces earlier-than-usual degeneration of the tapetum. Pollen sterility is associated with tapetal degeneration [34]. Weaver et al. [35] reported a close relationship between pollen stainability and tolerance to high-temperature stress among bean selections. Pollen staining by acetocarmine has been used widely for the rapid determination of pollen sterility occurring under

environmental stresses [36, 37]. A highly positive correlation was observed between pod set and pollen stainability in flowers that were affected by high temperature (32/28°C for 24 h) 8 to 11 days before anthesis [23], which corresponds to the early microspore stage in the common bean [38].

It is recognized that high temperature affects many physiological processes, including photosynthesis and the translocation of photosynthetic production, across a wide range of crops [39–41]. For example, in studies on birch trees, river birch was found to maintain the high net photosynthetic rates (P_n) at high temperature, ranging from 25 to 40°C, while the P_n of paper birch was reduced the most. Inhibition of P_n at higher temperatures was due largely to nonstomatal limitations in both taxa [41]. At high temperature (40°C), Norchip, the most heat-tolerant cultivar of potato, synthesized small heat shock proteins for a longer time period than the other cultivars. The levels of an 18 kDa small heat shock protein increased up to 24 h in Norchip and Desiree, which are heat-tolerant cultivars, whereas the levels started to decrease after 4 h in Russet Burbank and after 12 h in Atlantic, which are heat-sensitive cultivars [39]. Suzuki et al. [42] examined the effect of succinic acid 2,2-dimethylhydrazide (SADH) on the drought tolerance of bean plants. In SADH-applied plants, leaf water potential below which photosynthetic rate decreased was lower than that in control plants. Phenological adjustment and shoot biomass distribution on seed yield of drought-stressed common bean were assessed in two locations in Mexico [43]. Days to flowering and days to physiological maturity showed a negative and significant relationship with seed yield. Under drought stress, a significant reduction in the harvest index was observed in susceptible cultivars. Genotypic variation was detected in all partitioning indices, chiefly harvest index and relative sink strength by drought stress [44]. The crop faces water deficit due to excessive transpiration caused by high temperature (31/27°C) [45]. Even short diurnal fluctuations in the plant's water status [46] at the time of anthesis could adversely affect the development and function of its reproductive organs [24].

Phenological adjustment, plant-water relations, photosynthetic parameters, and shoot growth are all related to reproductive responses and thus may play an important role in heat and drought tolerance in the common bean. In this paper, we reviewed the results of our own studies on the above factors, but focused on photosynthesis in relation to leaf water status, genotypic differences in water status in relation to reproductive responses, genotypic differences in drought tolerance in relation to vegetative growth, and the seasonal performance of cultivars to elucidate the way in which heat tolerance and water deficit are related to reproductive responses in the common bean.

2. Photosynthesis and Leaf Water Status

Under field conditions in a hot summer season, the heat-tolerant cultivars differ markedly in leaf water status, leaf conductance, and intercellular CO₂ concentration, while there are no consistent differences in photosynthesis and

transpiration rates, which vary within a narrow range [47]. This indicates that the effect of high temperature on the biochemical factors controlling intercellular CO₂ assimilation is similar in all the cultivars. The midday leaf water potential decreases with increasing air temperature, but the decline is greater in heat-tolerant cultivar Haibushi and strain Ishigaki-2 than in the remaining cultivars/strains. A steeper water potential gradient from soil to plant may enhance the ability of plants to absorb water at a faster rate [48]. This would reduce the development of severe internal water deficit in the reproductive organs and increase their survival and growth. Sinclair and Ludlow [49] support our assumption that photosynthesis, protein synthesis, NO₃ reduction, and leaf senescence are better correlated with changes in tissue water content than with leaf water potential. It is worth noting that the heat-tolerant cultivar Haibushi and strain Ishigaki-2 display an association between (a) photosynthesis and leaf conductance and (b) leaf water potential, while this is absent in the heat-sensitive cultivars [47]. This indicates that the heat-tolerant cultivars possess better stomatal control over CO₂ and H₂O exchange in leaves in response to high temperature. This is evidenced by the fact that the sensitive cultivar Kentucky Wonder and strain 92783 show greater water loss [50].

3. Genotypic Differences in Water Status in relation to Reproductive Responses

Haibushi, a heat-tolerant cultivar, displays better leaf water status than Kentucky Wonder, a heat-sensitive cultivar, which exhausted soil water quickly, resulting in a greater deterioration in water status [51]. The reduction in leaf water content with water potential occurred faster with the increase in high temperature and is larger in the heat-sensitive than in the heat-tolerant cultivar [52]. Under field conditions, strains 86884 and 92783, collected from Southeast Asia countries [25] and cultivar Kentucky Wonder failed to show any relationship between leaf water potential and water content and produced very few pods despite the higher pollen fertility. In contrast, in strains 45817, Ishigaki-2, and 3028520 and cultivars Kurodane Kinugasa and Haibushi, relatively higher leaf water content was maintained with declining water potential and a larger number of pods were set [50]. Osmotic adjustment and cell wall elasticity enable the plants to maintain higher water content, turgor, and other turgor-related processes during water deficit [53, 54]. This allows plant organs to survive longer in tolerant than in sensitive types. The cultivars with a smaller midday drop in leaf water content showed a higher pod-setting ratio and consequently had higher yield than the plants with a larger midday drop in leaf water content [55].

4. Genotypic Differences in Drought Tolerance in relation to Vegetative Growth

The common bean cultivars display distinct responses to prolonged drought stress under field conditions. The

responses of photosynthetic parameters and shoot extension to leaf water status are related to soil water content. A decrease in soil water causes a decline in leaf water status. The high-yielding cultivars display a smaller reduction in leaf water content but a larger reduction in leaf water potential than the poor yielders. Such differences in leaf water content and leaf water potential may arise due to differences in osmotic adjustment [48, 56, 57] and cell wall elasticity [53]. Coyne et al. [58] argue that a steeper leaf water potential gradient from soil to plant may enhance the ability of the plants to extract soil water at low soil water content. The reduction in leaf water potential due to water stress is linearly correlated with reductions in shoot extension rate and leaf water content.

A discriminant analysis revealed that the five cultivars display two distinct types of responses [59]. One group includes cultivars Haibushi, Kurodane-Kinugasa, and strain Ishigaki-2, which showed a large reduction of about 16–20% in both shoot extension and water potential, and they also produced a higher number of pods per plant and seed yield than cultivar Kentucky Wonder and strain 92783. Kentucky Wonder and 92783, which form a separate group, displayed a comparatively smaller reduction (4–8%) in both water potential and shoot growth. In contrast, the former group displayed a smaller reduction in leaf water content, while the latter group showed a larger reduction in leaf water content. This suggests that tissue water content is kept high by restricting excessive vegetative growth and a large reduction in water potential. The reduction in shoot growth due to stress contributes to a build-up of water-economizing traits, such as specific leaf weight and succulence index.

5. Seasonal Performance of Cultivars

The performance of common bean cultivars Haibushi, Kentucky Wonder, and Kurodane Kinugasa and the strains Ishigaki-2, 45817, 92783, 86884, and 3028520 was evaluated between 2003 and 2005 in many field and controlled-environment experiments during the winter and summer seasons. Across the seasons, days to pod formation was positively associated with the number of pods per plant, seeds per pod, seed weight, and yield ($r > 0.97$). On the contrary, among the cultivars/strains, shorter duration to podding or flowering resulted in a higher number of pods per plant ($r = 0.93$) and number of seeds per pod ($r = 0.82$). Haibushi and Ishigaki-2 consistently produced a higher number of pods per plant and seed yield across the seasons and environments than the remaining cultivars. The number of pods per plant is the most important yield attribute and is precisely determined by thermal units and the duration between emergence and flowering. Porfirio and James [44] report that a high partitioning index (chiefly harvest index) shows high heritability, contributing to drought stress in the common bean. Thus, we can evaluate this character as genetic variation for adaptation to high temperature and drought.

6. Morphological Characters and Partitioning for Adaptation to High Temperature

The partitioning of dry matter (the ratio of dry weight of individual parts to that of total dry matter) was analyzed in the common bean at four temperature regimes (24/20, 27/23, 30/26, and 33/29°C) [60, 61]. Haibushi, a heat-tolerant cultivar, has a higher pod weight per plant, number of pods per plant, average pod weight, pod set ratio, number of branches, and rate of biomass allocation to pods, but lower rates of biomass allocation to leaves, stems, and roots, than Kentucky Wonder, a heat-sensitive cultivar, across all temperature regimes [61]. A sharp decline in dry matter partitioning to pods is observed at 33/29°C [60]. In the temperature range of 24/20 to 30/26°C, Haibushi showed higher partitioning to pods than Kentucky Wonder, independent of temperature. On the contrary, Kentucky Wonder showed higher partitioning to pods at 27/23°C than at 24/20°C. These results show that higher biomass allocation to pods and higher pod set in branches, which vary with the cultivar and temperature, play an important role in achieving a higher harvest index in the heat-tolerant compared to the heat-sensitive cultivars. Konsens et al. [27] recognize that high night temperature promotes branching in the common bean. Drought stresses induce genotypic variation of shoot biomass accumulation, pod and seed number, and biomass partitioning index [43, 44].

7. Concluding Remarks

Our results reveal that leaf water content is involved in heat and drought tolerance in the common bean, but the supporting system for maintaining high water content is unclear. Leaf water content is better correlated with leaf vapor pressure deficit, internal CO₂ concentration, and leaf conductance than with water potential. Therefore, plant water status can be explained better in terms of leaf water content in the common bean. Evaluation of the association between (a) number of pods per plant and seed yield and (b) midday drop of leaf water content provides clear evidence that leaf water content is responsible for the genotypic variations in heat and drought tolerance. A small reduction in leaf water content is displayed by the tolerant cultivars, which show larger reductions in shoot extension and leaf water potential than the sensitive cultivars. Therefore, we can conclude that leaf water content is an important physiological trait for improved productivity and that it can be used as a screening tool for heat and drought tolerance in the common bean.

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