

Review

Physiological Responses of Selected Vegetable Crop Species to Water Stress

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Abstract: The frequency of drought periods influences the yield potential of crops under field conditions. The change in morphology and anatomy of plants has been tested during drought stress under controlled conditions but the change in physiological processes has not been adequately studied in separate studies but needs to be reviewed collectively. This review presents the responses of green peas, snap beans, tomatoes and sweet corn to water stress based on their stomatal behaviour, canopy temperature, chlorophyll fluorescence and the chlorophyll content of leaves. These stress markers can be used for screening the drought tolerance of genotypes, the irrigation schedules or prediction of yield.

Keywords: vegetable crops; stomatal conductance; canopy temperature; chlorophyll fluorescence; SPAD; water stress

1. Introduction

As a result of climate change, the increasing atmospheric CO₂ enhances the photosynthesis capacity and improves water use efficiency therefore the amount of yield will increase in most of vegetable crops, however its advantage cannot be shown under limited water and nitrogen deficiency. The high temperature during reproductive growth is harmful for many important vegetable crops, such as tomatoes, peppers, beans and sweet corn, and yield reduction will probably occur [1]. The frequency of drought periods decreases vegetable yield and quality, however soluble solid content of produce may be increased by water deficiency in some crops [2,3]. Nevertheless, the occurrence of excess precipitation causes waterlogging in soils, the symptoms of which are similar to water deficit. Soil waterlogging impedes the oxygen supply and respiration of roots, water uptake and hydraulic conductance which results in stomatal closure [4,5]. Under these conditions the stomatal closure results in a reduction of net photosynthesis which is due to the decrease in stomatal conductance, chlorophyll fluorescence and chlorophyll content of leaves [6]. Excess water causes a decline in grain filling and grain weight of corn leading to decreased yield [7]. However, water stress commonly refers to water deficits not excess water.

The selection of the vegetable crops grown under field conditions for the investigation was based on their production in the world and Europe. During the last twenty years from 1997 to 2017 the growing area of tomatoes increased intensively, that of green peas increased moderately while the growing area of snap beans and sweet corn increased slowly in the world. During this time in Europe the growing area of tomatoes and snap beans decreased from 650.4 to 496.2 thousand ha while that of green peas increased slightly from 208 to 212 thousand ha and sweet corn's increased intensively (from 50.5 to 110.1 thousand ha) (FAOSTAT 2017 [8]). In Hungary, the production of green peas and sweet corn is performed in large field growing areas (19.5 thousand hectares and 34.5 thousand hectares, respectively) while snap beans are grown in smaller ones (1.6 thousand hectares) (FAOSTAT 2017) [8]. The other aspect of the selection was the sensitivity of plant species to water stress.

Corn, soybeans, beans and peas are considered to be moderately water stress sensitive while tomatoes belong to the extremely drought sensitive group [9,10]. The responses of plant species significantly depend on the intensity and duration of stress and their stages of development. The spring-sown green pea utilizes the precipitation well (if there is any) and requires a low temperature during vegetative growth but during the flowering and seed development periods it is sensitive to water deficiency. The crops require a warm temperature, even though they have different ripening times, snap beans have short (60 days), sweet corn has medium (75–90 days) and tomatoes have long ripening times (110–130 days), their generative stages of development coincided with dry June and July, thus they require irrigation. Irrigation scheduling and the amount of irrigation water are determined by the water stress tolerance and water use of the plant varieties. The evaluation of drought tolerance in field conditions is difficult because low soil moisture and high air temperature stress generally occur together, and it is difficult to evaluate the responses separately. Drought under field conditions promotes the evapotranspiration and affects the photosynthesis, which leads to reduced yield [11]. Use of remote-sensing methods makes the measurement of physiological responses of varieties to various strong water stresses easy. These non-destructive methods help the breeder to select drought tolerant genotypes and the growers to measure the water deficit of plants and decide the time of irrigation.

The selection for water stress tolerance in traditional breeding is based on the suitability of performance under a series of environmental conditions using extensive statistical methods. This progress could be improved by the introduction of traits which contribute to the prediction of yield in the drought-prone environments. In this study, the effect of water stress on the plants and those physiological traits which influenced the yield are mainly demonstrated. Information was gathered on the physiological responses of selected vegetable species to drought to analyse their use in breeding for high and stable yield.

2. Water Stress during Growth of Vegetable Crops

Sensitivity of plants to water stress such as snap beans and green peas differs with the stages of development. During the early stages of vegetative growth most crops are less sensitive to water scarcity [2,3,12,13], but during the generative stage the water deficiency results in changes of many physiological traits [2,14–16], causing the disturbance of fertility and reduction of yield. During flowering of legume plants water stress increases the ratio of flower drop [17], decreases the pod numbers and seed abortion in the pods [18,19] and increases the ratio of curved pods [20]. Under water deficiency, bean plants produce shorter shoots and smaller leaves and decrease the length of pods [21]. Semi-leafless pea varieties have reduced leaf area that is presumed to have a low water use and they have higher water use efficiency (WUE) than traditional varieties with normal leaves [22]. In sweet corn, ear differentiation begins at the six- or eight-leaf stage growth when the water deficiency decreases the length of ears and the numbers of ear rows [23], but during tasselling the water deficiency causes significant yield reduction [24,25]. Tomatoes are most sensitive to water deficiency at fruit setting and intensive fruit development periods [3], when the increasing water stress resulted in a 25 to 50% decrease in the yield [10,26–29]. During early flowering of tomatoes, water scarcity causes flower shedding and lack of fertilization [30], and during fruit setting, plants with small sized fruits are produced [10,31].

The effect of water stress on morphology and anatomy of plants has been studied by several researchers under controlled conditions [6,32–35], however, the changes in physiological responses have been less investigated under field conditions. The physiological characteristics that have an important role in the defence against drought can be measured by remote sensing techniques using non-destructive methods in open field conditions. The leaf photosynthetic activity of plants can be monitored with measurement of chlorophyll content using a portable chlorophyll meter and chlorophyll fluorescence while the measurement of stomatal conductance indicates the severity of water stress [2,3,14]. Spectral vegetation indices such as the green normalized vegetation index

(GNDVI) and the normalized differential vegetation index (NDVI) were used for monitoring the growth of the plant to detect the water stress and for yield prediction [36–39]. Crop water stress index is determined by an infrared thermometry technique to indicate the change in canopy temperature of plants under water stress conditions. More physiological indices such as leaf water potential, relative water content, turgor potential, osmotic adjustment, difference between canopy and air temperature can also be used as a screening tools for testing the water stress tolerance of genotypes [40]. Studies have focused on the identification of drought tolerance-related traits using Quantitative Trait Locus (QTL)s and Marker Assisted Selection (MAS) techniques [41–44], however, the identification of the most relevant loci controlling drought tolerance and drought-related traits could be achieved by the integration of molecular genetics with physiology [45].

3. Drought Tolerance

Adaptive mechanisms promoting the survival of plants have been grouped into three categories; drought escape, drought avoidance and drought tolerance [46]. Drought escape is the ability of plants to accomplish their life cycle before the development of soil and plant water deficit. The varieties with early flowering and short maturity are able to escape drought [47], however, they are not drought tolerant in every case. The varieties with moderate drought sensitivity developed different defence strategies to avoid short- and long-term water stress which prevents the water loss in their cells and tissues. The essential defence mechanism against drought operating in the plants is the maintenance of the water status and the reduction of tissue water loss (Figure 1).

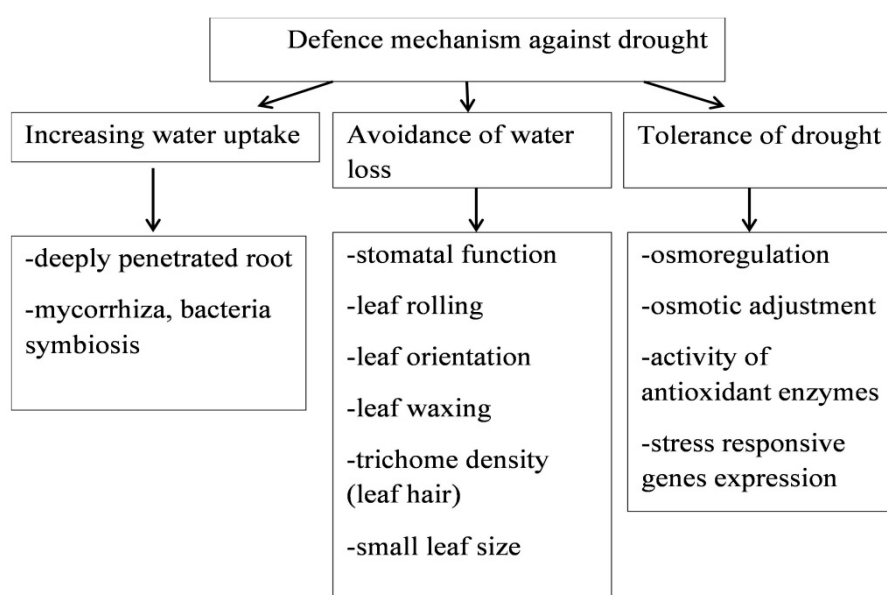


Figure 1. Defence mechanism against drought (Leonardis et al. [46]).

A well-developed deeply penetrating root system provides the water uptake and maintenance of water circulation inside the plant despite the low soil-moisture content. Nevertheless, in dry soil the lives of microorganisms are retarded when the activity of mycorrhiza living symbiotically with root nodules of legumes is low, which results in a decrease in the nitrogen uptake [48,49], therefore the growth of the plant is retarded. Long-term drought of soil accelerates the senescence of root nodules and production of reactive oxygen species (ROS) [50,51], therefore the nodule weight, root and shoot weight are decreased [52]. Water stress results in a change in the proportion of root weight as the ratio of root to shoot increases [53]. Under permanent low moisture content of soil, a 27–42% decrease in leaf weight and 12–27% decrease in specific leaf area of snap bean varieties were found [54]. Tomatoes are able to survive prolonged periods of low soil water content by the development of a deep root system [28,55]. In dry years, tomatoes inoculated with mycorrhiza easily endured the water scarcity,

for example larger weight fruits and higher yield were produced by deficit irrigation than under non-irrigated conditions [56].

4. Reduction of Water Loss

Drought avoidance is the ability of plants to maintain high tissue water potential despite the deficiency of soil moisture. The mechanisms developed for the reduction of water loss are related to the duration of water stress.

During short-term water deficiency the leaf movement, deep penetrating roots with strong suction force and partial or total stomatal closure provide a decrease in the water loss. Leaf movement of plants not only protects from the photodamage caused by high irradiation but reduces the effective leaf area for transpiration [57]. Paraheliotropic movement of leaves occurs mainly in beans while leaf rolling is typical for maize. Fernandez and Castrillo [58] found that the extent of leaf rolling is linearly correlated with the water potential. During leaf rolling of maize the transpiration, stomatal conductance, intracellular CO₂ concentration and net photosynthetic rate decreased [59]. Pastenes et al. [60] found that the degree of paraheliotropic leaf movement was larger in the water stressed plants because of lower water potential, however, it also occurred in the water supplied crops. Deep, thick and dense roots intensively promote the use of available water and the optimal development of aboveground parts. During short-term water stress (<7 nap), abscisic acid (ABA) is produced in the roots then it is transported into the leaves where ABA induces the stomatal closure and thus decreases the water loss [61,62]. Partial or total stomatal closure restricts the transpiration therefore the water and nutrient uptake is decreased, which results in a decrease in photosynthesis and growth of plants [63]. Stomatal responses of legume species are different; under water deficiency, beans have a rapid and complete stomatal closure generating the stomatal conductivity and photosynthesis decreases significantly, whereas in cowpeas (*Vigna unguiculata*), the stomata remain partially open and have a lower decrease in their net photosynthetic rate under the same conditions [64]. Under moderate water deficit conditions, the growth of snap beans was already retarded, and their leaf area decreased while the leaf area index (LAI) of sweet corn did not change [3,15]. Nevertheless, water scarcity did not influence the leaf area of tomatoes [65] but heat and water stress up to 6 days already significantly decreased the weight of shoots and roots of tomato seedlings under a controlled environment [66].

During long-term water deficiency, plants try to prevent the dehydration of cells of vegetative and generative organs with some morphological and physiological changes. Trichome density (leaf hairs) on the leaf protects the tissues from sunlight injury, decreases the water loss by evaporation and enhances the transpiration resistance [67]. Under water stress conditions, a lower number of trichomes was found only on the basal zone of leaves on both surfaces in comparison with irrigated plants [68]. However, according to Nobel [69], the length of trichomes can be more important than their frequency. The epicuticular wax layer of the leaf controls the water flow across the cuticle and protects from high radiation and prevents damage caused by UV light. Water stress induced the increase in the wax layer on the leaf surface of peas and the wax-rich varieties had significantly lower canopy temperature [70].

Drought tolerance is the ability of the plants to endure the long-term moisture deficit and survive the water loss. When the morphological changes seem to be insufficient to avoid the water deficiency, biochemical processes of plants are activated to maintain the osmotic adjustment and the structure of cell membranes in order to avoid cell dehydration. Decreasing the water potential of leaves induces the accumulation of different osmotic compounds such as sugars, amino acids and quaternary ammonium compounds. The osmotic pressure of cells is increased by the accumulation of osmotic compounds because water movement into the cells and tissues provides the maintenance of turgor [71]. It was found that peas and castor beans exposed to water deficit accumulate a significant amount of soluble sugars and proline [72,73], and the raffinose and sucrose level of leaves are significantly increased by water stress during flowering of snap beans [74]. Action of enzymatic and non-enzymatic antioxidants is intensified to alleviate the oxidative damages in the tissues. Concerted operation of numerous water soluble antioxidant compounds (ACW) contributes to the adaptation of plants to environmental

stresses. The level of ACW in the leaves is influenced by stomatal closure because it is related to ascorbic acid redox potential of guard cells [75]. In snap bean genotypes that have a high ACW level in leaves during the flowering and pod development periods, this provides a defence against water deficiency [74].

4.1. Regulation of Water Circulation in Plants under Drought

Many physiological processes are activated to mitigate the water loss of plants (Table 1). Transpiration is restrained as a result of stomatal closure and by decreasing leaf area. Stomata play an important role in the regulation of transpiration and CO₂ uptake. Use of light energy gathered by photosynthesis determines the growth and biomass production of plants. In these processes, the stomatal characteristics such as stomatal size, number and ratio of stomata on abaxial and adaxial surfaces significantly affect the C assimilation and water use efficiency (WUE) [76,77]. The higher stomatal density on the abaxial surface of the leaf is related to a higher water use efficiency [78], while those existing on upper epidermis (adaxial surface) of the leaf influenced the water use of plants [15]. Nevertheless, the number of stomata on both epidermis of leaves changes significantly depending on the variety and water supply.

Table 1. Physiological traits relevant for response to drought.

Physiological Traits	Effect Relevant for Yield	Alteration under Stress	References
Size and density of stomata	relation to leaf water potential and water consumption	increase/decrease depending on species	Hardy et al. [79], Nemeskéri et al. [14,15]
Leaf temperature	relation to transpiration	increase	Helyes et al. [31], DeJonge et al. [80]
Stomatal conductance	correlation with water consumption, decrease in individual yield	decrease in diffusion of CO ₂ , stomatal resistance increases	Jones [81], Nemeskéri et al. [14,15]
Photosynthetic capacity	modulation of activity enzymes of Calvin cycle	reduction under stress	Lawlor and Cornic [82]
Change in chlorophyll fluorescence	alteration of quantum yield of PSII photosystem	decrease in Fv/Fm under severe drought	Flagella et al. [83], Pol et al. [84], Yordanov et al. [85]
Chlorophyll content of leaf	decrease in photosynthesis	decrease under stress, relative chlorophyll content (SPAD value) can increase	Nankishore and Farrell [32], Nemeskéri et al. [16]
Reduced growth rate		leaf area reduces, biomass decreases	Ghanbari et al. [86], Guida et al. [87]

4.1.1. Stomatal Characteristics

More stomata (134–195 stomata mm^{−2}) were observed on the abaxial surface of tomato leaves but it was significantly less (40–62 mm^{−2}) on the adaxial surface of leaves [76]. A significant difference can be demonstrated in stomatal density of leaves between snap beans, green peas and sweet corn grown under non-irrigated and deficit irrigated (50% water deficiency) conditions (Table 2). On the basis of 3 year experiments, on the lower epidermis of leaves the stomata density was significantly higher for snap beans under moderate and severe water stress and it was similarly high for sweet corn only in severe water deficiency, but no difference could be shown for green peas in comparison with the optimal water supplied plants [14,15,88]. On the upper epidermis of leaves more and larger sized stomata can be found for snap beans exposed to drought while there were fewer similar sized stomata for the green peas compared to the irrigated plants (Table 2). However, under water scarcity,

significant differences in stomata number and size can be detected between the varieties. Under non-irrigated conditions, the size of stomata on the upper (adaxial) surface of leaves of green-podded bean varieties was smaller by 5–12%, but more of them were found than on optimal water supplied plants. Nevertheless, yellow-podded snap bean varieties had 13–18% larger sized stomata on the adaxial surface of leaves of plants exposed to water deficiency in comparison with the irrigated plants [15]. A larger stomatal density was observed for late ripening green pea varieties [14] and late ripening sweet corn hybrids under water scarcity [88] than for the short duration ones. Nevertheless, the distribution and size of stomata can be different on both areas and surfaces of the same leaf. Various number and sized stomata were detected on different areas of leaves of tomatoes; on the abaxial surface of leaves and their apical and middle areas, larger sized (32–34 μm) and more stomata were found than that on the adaxial surface. The stomata on the apical areas of leaves responded sensitively to water deficiency in that they showed fewer and larger sized stomata on the adaxial surface of leaves than for well-watered plants [68]. A significant correlation between the stomatal density and stomatal conductance ($r^2 = 0.958$) was established in tomatoes. According to this correlation, 130 stomata mm^{-2} was associated with high stomatal conductance ($0.1 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) [76]. Others [89] found that the relationship between stomatal density and WUE was positive and the size of stomata correlated negatively with the WUE for grass peas.

Table 2. Size and density of stomata measured during generative stages of vegetable crops under different water supplies Source: modified from Nemeskéri et al. [14,15,88].

Species	Water Supply	Lower Epidermis		Upper Epidermis	
		Stomata mm^{-2} *	Size of Stomata μ	Stomata mm^{-2}	Size of Stomata μ
Snap bean	I0	387.79	23.72	104.81	30.51
	DI	374.17	-	93.41	-
	WI	331.22	24.90	78.61	29.64
	average	364.39	24.31	92.28	30.08
Green pea	I0	214.29	25.82	165.70	25.79
	DI	214.65	25.48	170.86	24.68
	WI	214.74	24.35	194.72	25.21
	average	214.56	25.22	177.10	25.23
Sweet corn	I0	145.61	-	95.23	-
	DI	140.79	-	94.98	-
	WI	136.13	-	93.73	-
	average	140.84	50.04	94.65	53.22

* Based on average of years [14,15,88], μ = micron, I0 = non-irrigation, DI = deficit irrigation, WI = optimal water supply.

4.1.2. Canopy Temperature-Transpiration

Under high photosynthetically active radiation (PAR) water deficit combined with high temperature results in an increase in leaf temperature and air temperature oscillation ($\pm 3\text{--}4^\circ\text{C}$) due to the opening and closing of stomata [53]. Stomata closure triggers the decrease in the transpiration which contributes to the increase in canopy temperature of plants. One of the tasks of transpiration is to keep the temperature of plants at a favourable level for life processes. Decreasing transpiration causes the temperature of plants to increase. If soil water content is sufficient for the plant stand, the difference between canopy temperature and air temperature is zero or negative, but if the plants suffer from water stress this value is positive. An increase of 1°C in canopy temperature related to a 10% decrease in the transpiration [31]. Size and stomatal density of genotypes are different thereby the transpiration varies in intensity which correlates with the difference of the canopy temperature of plants. Changes in canopy temperature have often been used to signal water stress [90] to evaluate the

drought tolerance of bean genotypes and the difference in canopy temperature and air temperature was used for the real time irrigation [91–94]. During the daytime the canopy temperature rises along with the daily air temperature and radiation as the available soil water changes. The lowest value of crop water stress index (CWSI) of maize was measured at 10:00 and 11:00 and it was the largest between 12:00 and 13:00 [95]. Under water deficiency, the canopy temperature of both snap beans and tomatoes was higher than the air temperature from 09:00 to 15:00 however, that of tomatoes was higher than the air temperature only at 12:00 and 13:00 [96]. Under water stress conditions, between 09:00 and 15:00, the canopy temperature of snap beans was higher by 3.8 °C than the air temperature while it was lower by 1.6 °C in well-watered plants [93]. When the amount of available moisture in the soil for the plants decreases, then the transpiration is limited depending on the air temperature, which results in an increasing canopy temperature. Under moderate water deficiency, at 25–50% available soil water the canopy temperature of snap beans almost coincided with the air temperature (Figure 2a) that denoted the need for irrigation [93]. Nevertheless, the available soil water below 25% was not able to satisfy the water demands of plants. In this case the cooling of the canopy was not shown by transpiration and the temperature on the foliage surface was higher than the air temperature by 2.5 °C on average, indicating the plants suffered from water stress (Figure 2b) [93].

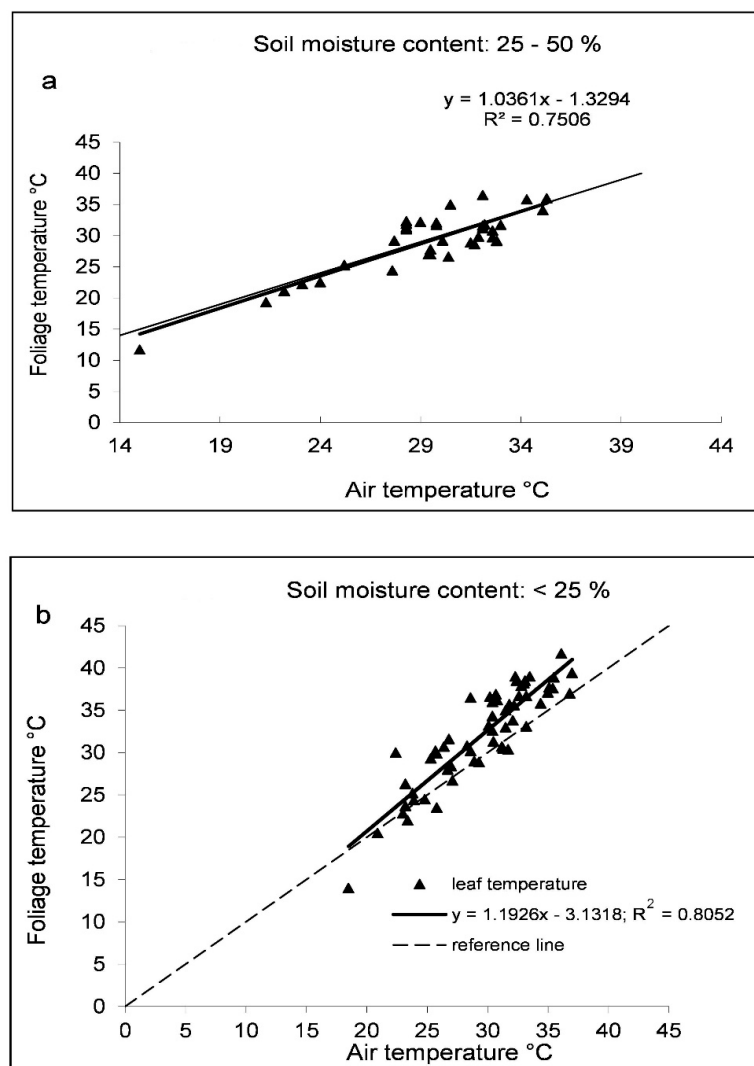


Figure 2. Relationship between air and canopy temperature for snap beans under water deficit (a) and severe water stress (b). The thick line shows the increase in leaf temperature compared to air temperature (broken line) Source: Helyes et al. [93].

Tomatoes seemed to better use deep soil moisture with deep, strong suction force roots than the shallow rooted snap beans. Under water stress conditions, the canopy temperature of tomatoes was only higher than the air temperature by 1.8 °C, while it was significantly lower (0.6 °C) under optimal water supply conditions [92]. Air temperature had a small impact on the canopy temperature of tomatoes grown under regular irrigation and cut-off stand (i.e., irrigation was stopped 30 days before harvest) ($r^2 = 0.60$; $r^2 = 0.55$), however, the canopy temperature of water stressed plants increased with rising air temperature ($r^2 = 0.59$) (Figure 3) [31]. A close correlation between canopy temperature and leaf water potential of maize was established [80] and the lowest CWSI values were measured between 10:00 and 11:00 and the highest ones between 12:00 and 13:00 [95].

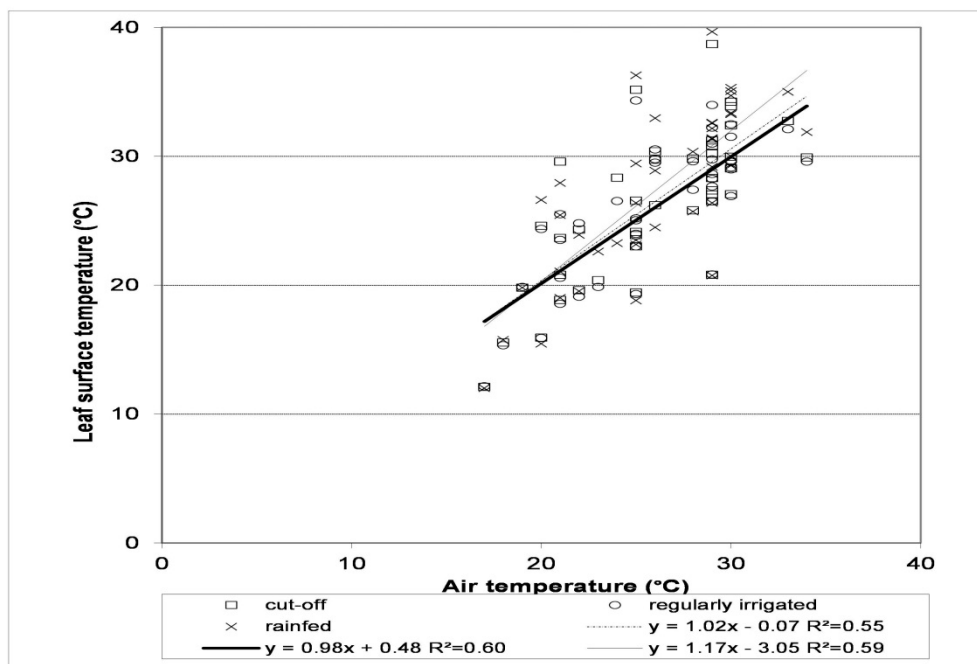


Figure 3. Relationship between the air and canopy temperature for the Kecskeméti jubileum tomato variety under rain-fed (thin line), cut-off (broken line) and regularly irrigated (thick line) conditions Source: Helyes et al. [31].

4.1.3. Stomatal Conductance

Stomatal conductance indicates the speed of water vapour evaporation that depends on more plant-specific characteristics such as stomatal density, leaf age and size, guard cell and cell turgor [97]. Stomatal conductance is related to the photosynthetic assimilation rates ensuring an appropriate balance between CO₂ uptake for photosynthesis and water loss through transpiration [98]. Variability in photosynthesis capacity can be explained by the CO₂ diffusion through stomata and leaf mesophyll which was influenced by the mesophyll thickness and porosity and size of stomata. In drought-acclimated tomato plants the decrease in mesophyll CO₂ conductance was due to an increased cell wall thickness [76]. Water stress significantly decreased the transpiration rate (37%) and stomatal conductance (26%) of maize [99]. Nevertheless, the extent of decrease in stomatal conductance depends on the growing period when the water deficiency occurred; at 7 days after anthesis of maize cultivars stomatal conductance decreased by 35% on average but at 21 days after anthesis this decrease was significantly larger (74%) under water deficiency than in well-watered cultivars [100]. In the case of tomatoes grown under non-irrigated conditions, stomatal conductance decreases from 14 to 73% depending on the weather and variety in comparison with the well-watered plants [3,32,87,101] (Table 3).

Table 3. Physiological traits related to water use and photosynthesis for vegetable crops under optimal water supply (OW) and water stress (WS) conditions.

Traits	Crops	Units	OW	WS	Difference %	References
Stomatal resistance	green pea	s cm^{-1}	2.87	3.22	12.2	Nemeskéri et al. [14]
	snap bean	s cm^{-1}	1.33	2.54	90.9	Nemeskéri et al. [15]
	sweet corn	s cm^{-1}	2.13	2.85	33.8	Nemeskéri et al. [88]
Stomatal conductance	green pea	$\text{mmol m}^{-2} \text{s}^{-1}$	0.57	0.32	−43.9	Gurumurthy et al. [35]
	tomato	$\text{mmol m}^{-2} \text{s}^{-1}$	1200	125	−89.6	Nankishore and Farrell [32]
		$\mu\text{mol m}^{-2} \text{s}^{-1}$	457.26	394.95	−13.6	Nemeskéri et al. [3]
		$\text{mol m}^{-2} \text{s}^{-1}$	20.2–37.9	6.3–10.2	−68.8 −73.1	Helyes et al. [101]
Chlorophyll fluorescence	snap bean	Fv/Fm	0.80	0.78	−2.5	Tari et al. [102]
	maize	Fv/Fm	0.810	0.695	−14.2	Yan et al. [103]
	tomato	Fv/Fm	0.785	0.745	−5.1	Nankishore and Farrell [32]
		Fv/Fm	0.748	0.696	−7.0	Nemeskéri et al. [3]
		Fq'/Fm'	0.4	0.25	−37.5	Zhou et al. [66]
Chlorophyll content	green pea	SPAD *	48.16	49.02	1.8	Nemeskéri et al. [14]
	snap bean	SPAD	34.57	38.94	12.6	Nemeskéri et al. [16]
	sweet corn	SPAD	47.48	44.67	−5.9	Nemeskéri et al. [2]
	tomato	SPAD	50.97	52.63	3.3	Nemeskéri et al. [3]
Vegetation index	green pea	NDVI	0.679	0.693	2.3	Nemeskéri et al. [14]
	snap bean	NDVI	0.778	0.681	−12.5	Nemeskéri et al. [16]
	sweet corn	NDVI	0.743	0.711	−4.3	Nemeskéri et al. [2]

* SPAD = relative chlorophyll content of leaves; NDVI = normalized differential vegetation index.

Under water scarcity, stomatal conductance for both water and CO_2 flow decreased by closing the stomata [104], thus it can be said that stomatal resistance increased. The extent of stomatal resistance mainly gives information about the speed of water vapour. Under severe water deficit conditions, stomatal resistance increased by 91% for snap beans, 34% for sweet corn and 12% for green peas in comparison with the well-watered plants (Table 3). The studies shown in Table 3 proved that snap beans responded more intensively to severe water stress than sweet corn and green peas. Flowering and pod development periods of legume crops are the most sensitive to water stress when stomatal resistance changes depending on the varieties and the degree of water stress. Under moderate water deficiency, the late ripening green pea varieties had high stomatal resistance ($>3.0 \text{ s cm}^{-1}$), while that of green-podded snap bean varieties was relatively low ($0.8\text{--}1.2 \text{ s cm}^{-1}$) and yellow-podded snap beans showed different values depending on the varieties ($1.0\text{--}1.43 \text{ s cm}^{-1}$) [14,15]. During tasselling, the late ripening sweet corn hybrids responded with higher stomatal resistance (3 s cm^{-1}) to medium water deficiency than during the silking period [88].

4.2. Photosynthesis in Drought

The aspects of photosynthesis of selected vegetable crops which can be measured by remote sensing methods and used for the evaluation for drought tolerance of genotypes have to be taken into consideration. In the photosynthesis process the light capture and conversion of light energy to chemical energy is made by photosynthetic pigments in the photochemistry photosystems (PSI, PSII) of leaves. The light energy in the leaf that is not used for photosynthesis is either emitted as fluorescence or released as heat [105]. The efficiency of photosynthesis can be measured by the efficiency of PSII photochemistry or by the amount of photosynthetic pigments [106].

4.2.1. Chlorophyll Fluorescence

Intense dry conditions of soil cause stomatal closure, reduced CO₂ mesophyll conductance [107] and decreasing activity of PSII [108], which contributes to the decrease in photosynthesis. Photosystem II (PSII) is highly sensitive to light and drought [60] and the maximum quantum yield of PSII photochemistry (Fv/Fm) indicates an undisturbed or deficient operation of photosynthesis. Chlorophyll *a* fluorescence is considered to be suitable for the measurement of activity of photosynthesis because environmental stresses significantly affect the emission of chlorophyll fluorescence [109]. For example, UV-B radiation decreased the chlorophyll fluorescence of green peas [110] and ozone stress decreases the Fv/Fm and chlorophyll *a* concentration of leaves [111]. In higher plants, Fv/Fm fluorescence ranged from 0.78 to 0.84 [112], however this change depended on the variety and intensity of water stress.

In snap beans, the Fv/Fm ratio was relatively high (0.82–0.83) under optimal water supply conditions and it only decreased to 0.80 in the drought sensitive genotype under water stress conditions [102], which proved that chlorophyll fluorescence was not highly sensitive to water deficit.

In dry years, tomatoes grown under non-irrigated conditions had low photosynthetic activity (Fv/Fm = 0.662) and under moderate and optimal water supply conditions the Fv/Fm value ranged between 0.753 and 0.758 [3]. Likewise, the above-mentioned results from Nankishore and Farrell [32] showed a small decrease in Fv/Fm (5.1%) in tomatoes under drought (Table 3).

The maximum efficiency of PSII (Fv/Fm) of well-watered maize plants stayed constant while that of drought stressed plants stayed at control level during the first 2 days then decreased sharply as the soil became drier [103].

Use of Fv/Fm to evaluate the drought tolerance of crops is contradictory. Under controlled conditions, Fv/Fm for pot-grown grapevines decreased when water potential dropped but it seemed to be a good indicator to distinguish the moderate and severe drought stress in the field [113]. Drought stress affected the Fv/Fm parameter of the asparagus bean (*Vigna unguiculata* L.) [114]. Contrary to these results, no change was detected in the Fv/Fm for strawberries [115] and soybeans [116] grown under drought. Others [117,118] stated that PSII activity expressed by the Fv/Fm of drought tolerant tomato genotypes was less decreased under intensive water stress than sensitive ones. Likewise, Li et al. [119] found that Fv/Fm in drought tolerant barley varieties was higher than those of the drought sensitive group under drought stress. Under 4 day waterlogging conditions, the chlorophyll fluorescence (Fv/Fm) of flooding stress tolerant wax maize hybrids did not change significantly, while the photosynthesis efficiency of sensitive hybrids was relatively low and the Fv/Fm value decreased by 5.2% in comparison with the control [6]. The measurement of chlorophyll fluorescence as a rapid non-destructive method can be easily carried out in the field, thus it can be recommended for screening for drought tolerance [120].

4.2.2. Photosynthetic Pigments

Environmental stresses change not only the activity of the photochemistry apparatus but the chlorophyll concentration in the leaf due to metabolic disturbance [121], whereupon the light absorption decreases. Water also absorbs the radiation in the infrared wavelength of the spectrum and as the water content of leaf decreases, the light absorption decreases and reflectance increases due to the radiative attributes of water [122,123]. Therefore, the water content of leaves and the amount of photosynthetic pigments in leaves both influence the light absorption by leaves. The light absorption of the leaf can be indirectly measured by portable chlorophyll meter. In this way the calculated SPAD values correlated with the chlorophyll content of leaves [124] expresses the efficiency of photosynthesis by the intercepted photosynthetic active radiation. The high SPAD value indicates the low water and chlorophyll concentration simultaneously in the leaf, resulting in a decrease in light absorption and increase in reflectance that is larger in extent in snap beans and smaller in green peas and tomatoes (Table 3). Iturbe-Ormaetxe et al. [125] stated that the decrease in chlorophyll *a* concentration of leaves was larger (−30%) than that of chlorophyll *b* (−20.8%) for green peas exposed to water stress than in well-watered plants.

5. Relationship between Drought Stress Markers and Yield

During reproductive periods of plants that are most sensitive to water deficiency, the changes in physiological responses can be used to screen the water stress tolerance of genotypes. During this time the water supply determines the yield production. Stomatal resistance and the relative chlorophyll content of leaves (SPAD) of the individual plants indicate the disturbance of water circulation and photosynthesis. Spectral vegetation indices indicate the absorption of solar energy of the canopy in the visible light spectrum. Health status and water deficit of vegetation can be monitored by different vegetation indices and it can also determine the need for irrigation [126–129]. The normalized differential vegetation index (NDVI) expresses the ratio of spectral reflectance on the canopy in the infrared and red region and it is used to monitor the effect of water stress on plant growth and forecast biomass [130,131].

The question is how closely the physiological traits are related to water circulation and photosynthesis and can be used to predict the expected yield. Nevertheless, the physiological traits measured during the generative stages of plant species are different (Table 4). On the basis of long-term experiments, stomatal resistance measured during flowering of snap beans and tomatoes correlated with the pod yield of individual plants and weight of tomato fruits under severe drought. A close correlation between the relative chlorophyll content of leaves (SPAD) and weight of tomato fruits and final yield was detected under both mild and severe water deficiency which can be used for selection of genotypes with water stress tolerance. During tasselling of sweet corn, the expected yield of plants can be less predicted by stomatal resistance (47%) and to a higher extent by spectral traits (58–68%) under moderate water deficiency. During flowering of green peas, stomatal resistance and chlorophyll content of leaves showed a close correlation with the expected yield only under severe drought (Table 4).

Table 4. Correlation coefficients between physiological traits measured during flowering and yield under drought.

Crops	Water Supply	NI	DI		
	Traits	Yield g plant ^{−1}	Yield t ha ^{−1}	Yield g plant ^{−1}	Yield t ha ^{−1}
Green peas	SR	0.3885	0.7648	0.3541	0.4371
	SPAD	0.4685	0.7027	0.6378	0.5301
	NDVI	0.5550	0.7192	0.6200	0.2891
Snap beans	SR	0.6075	0.4687	0.5249	0.7163
	SPAD	0.4326	0.4671	0.6567	0.4385
	NDVI	0.4251	0.7300	0.3356	0.7665
Sweet corns *	SR	0.6184	0.5756	0.6866	0.6214
	SPAD	0.5346	0.4614	0.8221	0.6250
	NDVI	0.6804	0.4619	0.7648	0.4907
Tomato	gs	0.6851 ^y	0.7153	0.3026 ^y	0.3018
	SPAD	0.8655 ^y	0.8405	0.9256 ^y	0.8482
	Fv/Fm	0.4505 ^y	0.3669	0.1103 ^y	0.0961

* during tasselling ^y = fruit weight (g), gs = stomatal conductance, SR = stomatal resistance, NI = non-irrigation, DI = deficit irrigation Source: [2,3,14–16].

Other researchers used the normalized differential vegetation index (NDVI) for yield prediction; it was successful for castor beans [132], soybeans [133] and beans [134]. According to Spitkó et al. [38], a medium correlation ($r = 0.5–0.6$) was detected between NDVI and final yield at 15 days after flowering of maize but not during the flowering period. Different stress indices such as stress degree days (SDD) or crop water stress index (CWSI) can be used to evaluate the water stress tolerance of genotypes [25] for scheduling of irrigation [93] and maybe for prediction of yield. In the case of sweet corn, significant

negative correlation was detected between the CWSI and chlorophyll content of leaves ($r = 0.802$) but for the CWSI, a significant positive ($r = 0.478$) correlation was observed with the yield [25].

Helyes et al. [31] found a close correlation between the stress degree days (SDD) and yield of tomatoes. If the canopy temperature exceeded the air temperature (at noon), transpiration was reduced, which indicated water stress and resulted in yield reduction and quantity. Figure 4 shows the interrelation between the canopy and air temperature difference values and the yield. In our experiments the correlation was significant at $p = 0.01$ level with $r^2 = 0.57$ correlation coefficient. High yield per hectare can be achieved if the difference between the cumulative canopy and the air temperature is negative during the growing season.

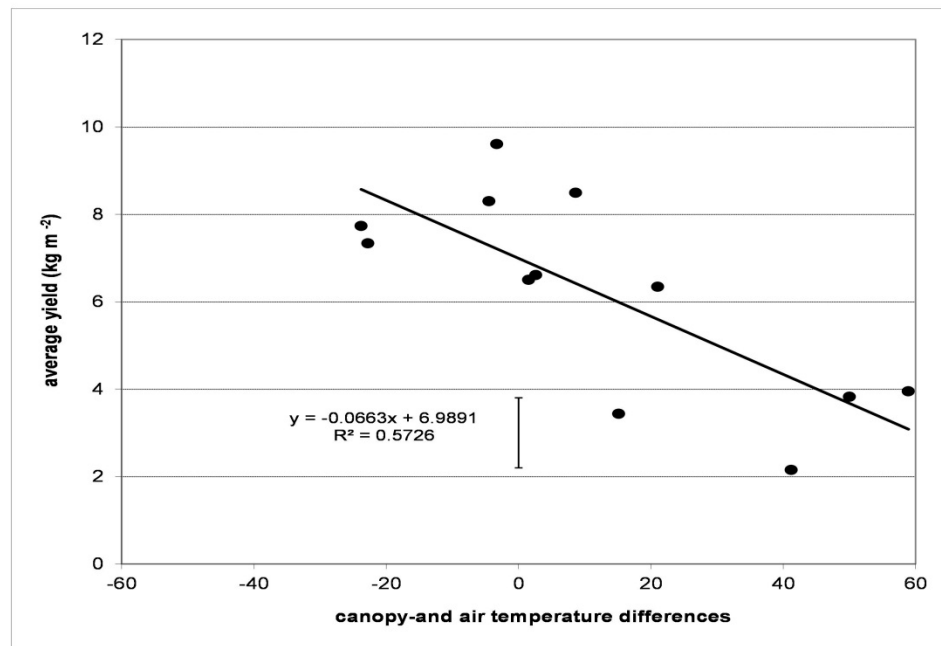


Figure 4. Correlation between canopy and air temperature differences and yield Source: [31].

6. Use of Physiological Characteristics

The use of physiological traits in a breeding program, either directly by selection or stress markers, depends on their genetic correlation with the yield, heritability and genotype $\times$ environment interaction [11,135]. Under water stress, high heritability of stomatal resistance, photosynthesis rate and transpiration rate ($h^2 = 0.91\text{--}0.99$) was found for *Vigna mungo* that gives a possibility for successful selection of genotypes [35]. Under severe drought, stomatal conductance and relative chlorophyll content of leaves (SPAD) measured during flowering correlated with the expected yield therefore they are suitable for the selection of individual genotypes for green peas and tomatoes, while the use of these traits for the selection of sweet corn can be efficient only under moderate water stress (Table 4). In the case of snap beans, because the water deficiency has a significant effect on leaf area, the normalized differential vegetation index (NDVI) measured during flowering can predict the expected yield more efficiently than the SPAD value of the leaves of individual plants.

Application of remote sensing techniques makes monitoring the water status of plants and real time irrigation easy [39,136]. The trend in the canopy temperature and the difference between the leaf temperature and air temperature (SDD) can be considered to be the water stress markers of plants [92]. The relationships between the canopy temperature, air temperature and transpiration involving the atmospheric and soil conditions and plant characteristics [40], was used to develop the crop water stress index (CWSI), indicating the need for irrigation. During drought, the decrease in NDVI occurred to a larger extent in snap beans, while it was less in sweet corn and hardly changed in green peas in

comparison with optimal water supply conditions (Table 3). This explained why the NDVI was used as spectral indicator for irrigation scheduling mainly in snap beans [136].

In summary, some of the physiological traits influencing the decrease of water loss and biomass production of plants can be used to evaluate the water status of vegetable crops and the water stress tolerance of genotypes. During the generative period, under water deficit conditions, the changes in the stomatal conductance and chlorophyll content of leaves for individual plants is suitable for the estimation the productivity of genotypes. Nevertheless, leaf area of crops should be taken into consideration as they determine the transpiration and their chlorophyll density influences the intensity of photosynthesis and finally the yield. Water stress indices and spectral vegetation indices seemed to be more appropriate in the detection of perceived water deficiency than for the prediction of final yield.

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