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ASSESSMENT OF PHYSIOLOGICAL AND MORPHOLOGICAL TRAITS OF PLANTS OF THE GENUS *Fragaria* UNDER CONDITIONS OF WATER DEFICIT – A STUDY REVIEW

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ABSTRACT

The genus *Fragaria* belongs to the *Rosaceae* family. The most popular representatives of this species are the strawberry (*Fragaria* × *ananassa* Duch.) and wild strawberry (*Fragaria vesca* L.), whose taste and health benefits are appreciated by a huge number of consumers. The cultivation of *Fragaria* plants is widespread around the world, with particular emphasis on the temperate climate zone. Increasingly occurring weather anomalies, including drought phenomena, cause immense losses in crop cultivation. The *Fragaria* plant species are very sensitive to drought, due to the shallow root system, large leaf area and the high water content of the fruit. There have been many studies on the influence of water deficit on the morphological, biochemical and physiological features of strawberries and wild strawberries. There is a lack of research summarizing the current state of knowledge regarding of specific species response to water stress. The aim of this study was to combine and compare data from many research carried out and indicate the direction of future research aimed at improving the resistance of *Fragaria* plants species to stress related to drought. These plants show patterns of response to stress caused by drought, such as: osmotic adjustment, reduction of transpiration and photosynthesis, and increased efficiency of water use. Drought also causes significant changes in the composition and palatability of the fruit of the *Fragaria* plant species.

Key words: *Fragaria*, strawberry, drought stress, drought tolerance

Abbreviations: ABA – abscisic acid, AMF – arbuscular mycorrhizal fungi, APX – ascorbate peroxidase, CAT – catalase, DI – deficit irrigation, GPX – glutathione reductase, POD – guaiacol peroxidase, RWC – relative water content in leaves, SOD – superoxide dismutase, WSD – tissue water saturation deficit, WUE – water use efficiency

INTRODUCTION

Water deficit is one of the important issues of climate change. The phenomena of drought and desertification adversely affect the global supply of food and human health, and may even threaten global peace [Ghaderi et al. 2015, Klamkowski et al. 2015b, Hamdan and Shafar 2017]. Cultivation of plants in natural conditions does not allow the elimination of the impact of adverse environmental factors, the most severe of which for crops is drought [Strack et al. 1995]. As much as 30% of the land area on the globe is affected by rainfall deficit and on 12% rainfall covers only 25% of evaporated water [Kacperska 2015].

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Since the drought phenomenon is not a single, evident event (such as a flood) and is often the result of many factors affecting each other, it is difficult to define it unambiguously [Tokarczyk 2008]. The term "drought" is used to describe both meteorological and soil conditions. This is a feature of climate, characterised by a noticeable water deficit, which causes a harmful impact on the environment and the economy and is a threat to people [Hisdal and Tallaksen 2000, Łabędzki 2004, Kędziora et al. 2014]. In terms of physiology, it is the lack of adequate humidity necessary for normal plant growth and ending of their ontogenesis [Zhu 2002]. It should be noted that this term does not refer to the hydration status of plants and its tissues. Physiological drought is caused by water deficiency in the soil or strong evaporation from the surface and water binding by salt ions [Kacperska 2015].

Water stress is a considerable problem in agriculture, and plant resistance to water deficit is of great economic importance [Shao et al. 2008]. In Poland's climate, periodic meteorological droughts occur [Doroszewski et al. 2012, Łabędzki and Bąk 2015], which directly affect the water balance of a specific area, causing soil drought which reduces plant production [Boczoń and Wróbel 2015]. In a moderate climate, drought is one of the most important factors limiting the yield of many crop plants [Treder et al. 2011, Kacperska 2015]. Harasim [2006] reports that crops in Poland are particularly sensitive to water scarcity due to the relatively high share of light soils (about 61%) [for Kędziora et al. 2014].

Strawberry fruits are among the most commonly consumed in the world [Liu et al. 2007]. In Poland, *Fragaria* plant fruits are also of great economic importance and strawberries comprised 34.02% of all Polish berry production in 2016 [Makosz 2007, Treder et al. 2011, GUS 2017]. Strawberries and wild strawberries are plants that are very sensitive to water deficit, even if it is mild [Serrano et al. 1992]. This is mainly related to large leaf area, high water content in the fruit and a shallow root system [Jensen et al. 2009, Li et al. 2010, Yin et al. 2010, Klamkowski and Treder 2011, Caulet et al. 2014, Klamkowski et al. 2015b]. It is also worth noting that *Fragaria* plants suffer from drought more than from excessive irrigation [Blanke and Cook 2002].

MOLECULAR AND PHYSIOLOGICAL SOIL DROUGHT EFFECT ON PLANTS

The effects of drought are not immediate. Due to the fact that this phenomenon accumulates slowly, its consequences are visible for a long time. In the initial stages these are less visible and they extend to larger areas of the environment [Łabędzki 2004].

Plants respond to stress caused by water deficit with changes in almost all processes [Hsiao 1973, Klamkowski et al. 2006, Klamkowski and Treder 2008]. This is manifested mainly by reducing the water potential, cell water activity and turgor pressure, changing the cell volume and thereby changing the relationship between plasmolium, tonoplast, organelle membranes and cell wall, increasing the concentration of compounds contained in the cytoplasm as a result of reducing its volume and changing the structure and the conformation of macromolecules [Jakubowski 2009, Kacperska 2015]. The physiological reactions of plants to water deficit vary depending on the severity, as well as the duration of water stress [Shao et al. 2008]. Mild and moderate stress will already be reflected by the reduction of cell turgor. More severe deficits will affect other phenomena more [Bewley and Krochko 1982].

It should be noted that many plant reactions to stress caused by water deficit in the initial stage of their occurrence are completely reversible [Li et al. 2010]. Destructive processes take place after a long time. The damage caused by the stress of water deficiency, which is disorder of metabolic homeostasis, is very often a signal to change gene expression and reorganise metabolic pathways. This, however, directly contributes to the organism adapting better to the prevailing environmental conditions, which is called the stress reaction syndrome [Kacperska 2015]. Therefore, the conclusion is that long-term moderate water deficiency can cause the plant to adapt to such a condition.

A slight decrease in turgor pressure is a factor directly contributing to the inhibition of cell growth [Olszewska 2009]: it is enough that it is 0.1–0.2 MPa lower than the pressure level below which the cell wall does not undergo plastic deformation [Jaleel et al. 2007, Karthikeyan et al. 2007, Blum 2011, Kacperska 2015]. This reduced plasticity is biochemically related to the reduction of cell wall acidity and increased crosslinking by phenolic substances, such as lignin and diferulide bridges [Blum 2011]. Loss of turgor can cause wilting of leaves, resulting in reduced light photon capture and, thus, a reduction in the intensity of photosynthesis. However, under these conditions the pressure potential (Ψp) has a greater impact on the rate of photosynthesis than wilting [Sarker et al. 2005].

Drought stimulates the synthesis and accumulation of abscisic acid (ABA) [Giannina et al. 1997] originating from carotenoides in the roots. The ABA limits the growth of shoots and the opening of stomata in the leaves. This contributes to reducing the consumption of carbon and energy by these organs [Blum 2011]. Consequently, the transport of assimilates to those roots located in the more irrigated part of the soil is intensified. Thus, the roots grow faster allowing the plant to supply water – the ratio of the mass of shoots to roots changes in favour of the latter [Morgan 1984, Rane and Maheshwari 2001, Shao et al. 2008, Caulet et al. 2014]. This phenomenon is a method for plants to defend against drought. When there are fruits on the shoots, which are a strong acceptor of metabolites, root growth occurs less intensively [Kacperska 2015]. Therefore, the plants are more sensitive to water deficit at the time of fruiting [Chmura et al. 2009]. Moderate water stress can lead to faster germination of seeds and to disturbances in the plant reproduction phase. However, longer exposure of plants to drought can lead to xeromorphism. The ABA additionally causes morphological changes, such as increasing the density of hairs on the epidermis and production of thicker cork layers [Kacperska 2015].

Long-term water stress causes the predominance of catabolic processes over anabolic ones [Klamkowski et al. 2015a] which causes the plant to shed leaves and thus reduce the transpiration area [Shao et al. 2008]. It is worth noting that, at first, only older leaves are dropped to reduce transpiration and water consumption [Blum 2011]. This phenomenon occurs under the influence of ethylene, which is extensively synthesised in cells exposed to severe stress [Lynch and Brown 1997].

Lowering the water potential (Ψw) in the tissue reduces the intensity of photosynthesis (faster than cell growth), which is also contributes to the closing of stomata [Kaiser et al. 1981, Sarker et al. 2005, Olszewska 2009, Suchocka 2011].

The processes of protein metabolism and amino acid synthesis are very sensitive to water deficit [Olszewska 2003, Suchocka 2011]. A short-term drought may contribute to a significant inhibition of nitrate reductase activity, which results in the accumulation of nitrates in plant tissues [Huffaker et al. 1970, Koszański et al. 2006, Boguszewska 2007, Kacperska 2015]. Intensified synthesis of the amino acids (mainly proline) that are involved in the osmotic alignment of cells is also observed [Sarker et al. 2005, Bertamini et al. 2006, Shao et al. 2008, Kacperska 2015, Sun et al. 2015]. These phenomena may also contribute to the significant inhibition of the synthesis of many proteins [Klamkowski et al. 2015a] and an increase in the activity of hydrolytic enzymes, e.g. proteases [Kacperska 2015].

Water deficit directly contributes to the reduction of cell turgor [Olszewska 2009]. Plants more resistant to this type of stress activate the mechanisms of osmoregulation, allowing for regulation of the osmotic potential, which is called osmotic adjustment [Shao et al. 2008, Jakubowski 2009]. It consists of intensified synthesis and accumulation of osmolytes (osmotically active substances) in vacuoles. The purpose of the osmolytes is to regain turgor and the ability to grow [Zhang and Archbold 1993a, b, Jakubowski 2009]. This mechanism allows plants to adapt to drought as well as increased salinity conditions [Kacperska 2015]. However, it has been shown that the physiological age of the leaves limits the ability of osmotic adjustment in the case of very young and very old leaves, which is associated with the closure of stomata and the production of ABA [O'Neil 1983].

The effects of strong water stress are structural changes. The damage occurs as a result of cell contraction causing a change in the interaction between the wall and the plasmolema [Wyka 2010], including the opening of tension-dependent ion channels. Strong dehydration of the cells may cause the lyotropic change of the phase of the membrane (transition of sol into gel) – changes in the positioning and conformation of membrane proteins [Blum 2011]. It can also cause the oxidation of polyunsaturated fatty acids in the cell membranes, resulting in the loss of their semipermeable properties. In addition, cell dehydration may lead to changes in the tertiary structures of proteins and further irreversible denaturation of their aggregates [Kacperska 2015]. This, in turn, may result in plant death [Shao et al. 2008].

CONSEQUENCES OF WATER DEFICIT OF *Fragaria* PLANTS IN THE CONTEXT OF THE RESEARCH CARRIED OUT

A lot of research on irrigation of plants has been carried out, analysing the reaction of various species and cultivars to drought [Bota 2001, Reymond et al. 2003, Pereyra-Irujo et al. 2008]. There are many reports on differences in the tolerance to drought of various species of the genus *Fragaria* [Zhang and Archbold 1993a, Vun Der Zunden and Cameron 1996, Pirker et al. 2002, Koszański et al. 2006, Klamkowski and Treder 2008, Giné-Bordonaba and Terry 2010, Grant et al. 2010, Ghaderi and Siosemardeh 2011, Klamkowski and Treder 2011, Grant et al. 2012a, b, Klamkowski et al. 2013, 2015b, Martínez-Ferri et al. 2016]. There have also been studies looking for the genes determining tolerance to drought in plants of the genus *Fragaria* [Razavi et al. 2011].

It is reported that *Fragaria chiloensis* (L.) Mill. is the most drought-tolerant *Fragaria* species [Zhang and Archbold 1993a, b, Vun Der Zunden and Cameron 1996, McDonald and Archbold 1998, Grant et al. 2012b]. The studies by Zhang and Archbold [1993a] provided evidence for greater osmotic regulation in response to the stress of water deficiency in *F. chiloensis* (L.) Mill. than in *F. virginiana* Duch., which is a potential source of plant material for breeding programmes to increase the tolerance of these plants to drought.

A number of studies have also been carried out to assess the sensitivity to drought variation within the species *Fragaria × ananassa* Duch. [Serrano et al. 1992, Savé et al. 1993, Klamkowski and Treder 2008, Ghaderi and Siosemardeh 2011, Caulet et al. 2014, Klamkowski et al. 2015b, Sun et al. 2015]. According to Savé et al. [1993], the ‘Chandler’ cultivar is one of those more resistant to drought. Other findings by Serrano et al. [1992] pointed out that the ‘Chandler’ cultivar is very sensitive to water deficit. More recent studies suggest that the ‘Elsanta’ cultivar is the most resistant to stress caused by water deficit [Klamkowski and Treder 2008, Klamkowski et al. 2015b].

The water potential in the leaf

To assess the physiological status of plants under drought stress, water potential (Ψw) and osmotic potential (ΨO) are used [Kacperska 2015]. In a situation where the water content in the substrate is insufficient to ensure an adequate supply for the plants, the loss of water by transpiration reduces the water potential in tissues [Klamkowski et al. 2015b]. Hasiao [1973] reports that a water potential above –1 MPa indicates mild dehydration of the tissue. The decrease in the potential by –1.2 to –1.5 MPa indicates moderate water stress, and less than –1.5 MPa indicates severe water stress. According to Sruamsiri and Lenz [1986], strawberries begin to wither at a water potential in the leaf equal to –1.7 MPa, while at the potential value of –2.5 MPa irreversible changes are already observed. A value of water potential at –1.0 MPa is considered by the authors as a threshold in the case of stress in strawberries. They also note that the physiological parameters of plants, such as the intensity of photosynthesis and transpiration, do not decrease until the leaf water potential reaches a value of –1.0 MPa. According to Sun et al. [2015], the strawberry has some ability to adapt to drought conditions by reducing the cell water potential and increasing water absorption efficiency.

According to Klamkowski and Treder [2011], in conditions of optimal hydration, there was no difference in the water potential in the strawberry leaves of the ‘Elsanta’ and ‘Sonata’ cultivars. However, a significant decrease in the Ψw parameter was observed in these plants under water deficit conditions, but no differences were found between the cultivars (Tab. 1). Similarly, Grant et al. [2012b], who studied cultivars of strawberry and *Fragaria chiloensis* (L.) Mill. of the ‘Manzanar Alto’ cultivar growing in drought conditions, showed lower values of water potential in leaves than plants irrigated optimally. Also, in the studies of Van Der Zunden and Cameron [1996], a significant reduction in leaf water potential was found in 11 genotypes of *F. chilioensis* (L.) Mill., *F. virginiana* Duch. and *Fragaria × ananassa* Duch. Similarly, in Blanke and Cook’s [2002] study, drought stress caused a reduction in average water potential in the leaves from –1.12 MPa to –2.02 MPa. This is also confirmed by the studies of Klamkowski et al. [2006] (Tab. 1).

In the studies of Klamkowski and Treder [2011], in strawberries of the ‘Elsanta’ and ‘Sonata’ cultivars,

Table 1. Percent reduction (–) or increase (+) of the physiological characteristics of plants from the *Fragaria* genus growing under water stress conditions, in comparison with plants growing under optimal irrigation conditions (according to different authors)

Species	Cultivar	RWC	Water potential in leaf	WUE	Intensity of photosynthesis	Intensity of transpiration	Authors
Fragaria × *ananassa* Duch.	‘Magic’	–63	n.d.	–35	–49	–35	Caulet et al. 2014
	‘Real’	–65		–35	–51	–36	
	‘Honeoye’	n.d.		+28 (f.m.) +50 (d.m.)	n.d.	n.d.	Liu et al. 2007
				–70	–92	–79	Klamkowski et. al 2015b
	‘Elsanta’		–91	–26	–54	–37	Klamkowski and Treder 2011
			n.d.	n.d.	–16	–27	Klamkowski et al. 2013
				–45	–79	–54	Klamkowski et al. 2015b
				–1	n.d.	n.d.	Grant et al. 2010
			–112	+42	–75	–82	Klamkowski and Treder 2008
	‘Sonata’		–91	+13	–31	–39	Klamkowski and Treder 2011
	‘Elkat’		n.d.	n.d.	–66	–69	Klamkowski et al. 2013
			–131	+49	–44	–68	Klamkowski et al. 2006
			–116	n.i.	–72	–72	Klamkowski and Treder 2008
	‘Grandarosa’		n.d.	n.d.	–47	–53	Klamkowski et al. 2013
				–46	–81	–63	Klamkowski et al. 2015b
	‘Kurdistan’	–6 (m) –25 (s)		+233 (m) 0 (s)	–14 (m) –10 (s)	–74 (m) –90 (s)	Ghaderi and Siosemardeh 2011
		–8		n.d.	n.d.	–69	Ghaderi et al. 2015
	‘Selva’	–7 (m) –38 (s)		+133 (m) +17 (s)	–32 (m) –83 (s)	–71 (m) –92 (s)	Ghaderi and Siosemardeh 2011
	‘Salut’	n.d.		+85	–35	–61	Klamkowski and Treder 2006
			–171	–18	–67	–60	Klamkowski and Treder 2008
	‘Cambridge’ ‘Favourite’		n.d.	–1	n.d.	n.d.	Grant et al. 2010
	‘Delia’			+11			
	‘Elvira’			+9			
	‘Emily’			+92			
	‘Florence’			+21			
	‘Hapil’			+23			
	‘Idea’			+70			
	‘Symphony’			+8			
	‘Totem’			+14			
	‘Tonoyoka’		–38 (m) –96 (mt) –132 (s)	n.d.			Sun et al. 2015
	‘Queen Elisa’	–4				–68	Ghaderi et al. 2015
	‘Florika’	n.d.	–80		–20	–75	Blanke and Cook 2002
Fragaria chilioensis (L.) Mill.	‘BSP14’	–23	n.d.		n.d.	n.d.	Zhang and Archbold 1993b
Fragaria virginiana Duch.	‘NCC85–13V’	–10					

m – mild stress, mt – moderate stress, s – severe stress, n.d. – no data, n.i. – statistically insignificant differences, f.m. – fresh mass, d.m. – dry mass and Srumsiri and Lenz [1986], in strawberries of the 'Bogota' cultivar, wilting were not observed. Similarly, with the cultivars 'Elkat', 'Elsanta', 'Salut' and 'Grandarosa' [Klamkowski and Treder 2008, Klamkowski et al. 2013], wilting did not occur even at the lowest registered water potentials (–1.87 MPa). Klamkowski et al. [2006] stated that strawberries of the 'Elkat' cultivar began to wilt when the water potential decreased below –1.5 MPa, which may indicate a lower tolerance of this cultivar to drought.

By the presented research results, it could be stated that the reaction of different plant cultivars within the *Fragaria* genus to water deficit can be significantly different. Therefore, there are grounds to believe that the desirable traits associated with resistance to water deficit, in this case reducing wilting at very low water potentials should be sought at the varietal level.

The relative water content in leaves (RWC)

Indicators of relative water content in leaves (RWC) and tissue water saturation deficit (WSD) are some of the most important parameters commonly used to assess plant water management. The RWC is considered a measure of water status in a plant that reflects metabolic activity in tissues [Sinclair and Ludlow 1986]. Plants characterised by low RWC are usually characterised by low photosynthetic activity [Tezara et al. 2002]. According to Hsiao [1973], the RWC, with values ranging from 8 to 10%, indicates mild dewatering of the leaf, 10–20% is moderate, and over 20% is acute dehydration of the leaf. A loss of over 50% of the relative water content leads directly to the plant's desiccation [Kacperska 2015].

In a Caulet et al. [2014] study, the RWC decreased in the leaves of strawberry plants of the 'Real' and 'Magic' cultivars subjected to a water deficit. The decrease was similar in both cultivars and reached 65% in 'Real' and 63% in 'Magic'. Similar results were obtained by Ghaderi and Siosemardeh [2011] in the strawberries of the 'Kurdistan' and 'Selva' cultivars, which, subjected to a water deficit, had significantly lower RWC values than controls (Tab. 1). Also, in the 'Antilla', 'Benicia', 'Sabrina', 'Fortuna' and 'Camarosa' cultivars, the water content in the leaves under the influence of drought decreased significantly. This was not observed in the 'Santaclara' and 'Splendor' cultivars [Martínez-Ferri et al. 2016]. Zhang and Archbold [1993a] found that the plants *Fragaria virginiana* Duch. wilted at 82% RWC and were more sensitive to water stress than *Fragaria chiloensis* (L.) Mill. plants, which wilted at 60% RWC. According to Jensen et al. [2009], RWC of FI plants (full irrigation), DI (irrigation deficit) and PRD (partial root zone drying) in the whole experiment was 95%, where NI (nonirrigation) plants wilted within 6 days at 82% RWC.

The above results indicate that there are significant differences in the response of *Fragaria* plants to water deficit, as evidenced by the fact that they wither at different RWC values – from 82% (plants most sensitive to water scarcity) to 60% (relatively resistant plants).

The water use efficiency (WUE)

The size that integrates changes in the intensity of gas exchange parameters of plants is the ratio of photosynthesis to transpiration (in physiological terms) or the ratio of yield to water consumption (in agronomic terms) [Blum 2005]. It is one of the parameters of expressing the effectiveness of water use by plants (WUE – water use efficiency) and describes the relationship between carbon assimilation and stomatal conductivity [Klamkowski and Treder 2008]. It can also be expressed as the ratio of dry matter accumulation to water consumption during the period considered [Shao et al. 2008]. High WUE values indicate the ability of plants to maintain high photosynthetic activity under stress and higher resistance to water scarcity [Bota et al. 2001]. According to Chaves et al. [2003], most plants tend to increase WUE in mild to moderate water deficit conditions. This increase is the result of the relationship between stomatal conductivity and carbon assimilation, which means that water loss is limited earlier and more intensely than the inhibition of photosynthesis [Klamkowski and Treder 2008]. This coefficient was used in many works on the influence of water deficiency on the physiological state of plants [Tezara et al. 2002, Liu and Stützel 2004, Blum 2005, Shao 2008, Battipaglia et al. 2014], including plants from the genus *Fragaria* [Klamkowski et al. 2006, Klamkowski and Treder 2008, Grant et al. 2010, Klamkowski and Treder 2011, Grant et al. 2012a, Klamkowski et al. 2015b]. The results obtained, however, are very divergent (Tab. 1), mainly due to the use of various calculation methods.

Chandler and Ferree [1990] and Bota et al. [2001] argue that cultivars with a higher WUE value usually produce less yield under optimal conditions. Different results were obtained by Grant et al. [2010], who found that the high WUE value shown in the ten strawberry cultivars tested was correlated with their high yield potential. The cited research results indicate a diversified relationship between the value of the WUE index and the yield in plants of the *Fragaria* genus.

In Klamkowski and Treder's [2008, 2011] studies, the WUE index for strawberries of 'Elsanta' and 'Sonata' cultivars, growing under water scarcity, was higher than the control. The high WUE values observed are a consequence of the large values of the net photosynthesis rate with low transpiration intensity. These results indicate an increased ability to save water by 'Elsanta' in comparison with two other cultivars ('Elkat' and 'Salut') [Klamkowski and Treder 2008] (Tab. 1).

Based on the data contained in Table 1, it could be noticed that not all tested cultivars showed an increase in the WUE indicator in water deficit conditions. Reducing this indicator may suggest a lower ability to adapt to stressful conditions by saving water and reducing photosynthetic activity, as demonstrated for the 'Grandarosa' cultivar [Klamkowski et al. 2015b]. WUE, therefore, also indicates the existence of significant differences in resistance to water scarcity among individual plant cultivars of the *Fragaria* genus.

Gas exchange and the condition of the photosynthetic apparatus of plants

In conditions of mild or moderate water deficiency and with high light intensity, photoinhibition may occur in plants [Wyka 2010]. The plant's defence path is the scattering of absorbed light energy through chlorophyll fluorescence and a change of chlorophyll redox homeostasis [Starck et al. 1995, Olszewska 2003, Kacperska 2015]. Therefore, some fluorescence parameters can be used to assess a plant's response to water deficit or other stress factors [Olszewska 2009, Klamkowski et al. 2013, Kacperska 2015, Klamkowski et al 2015a]. To describe the effects of drought on plants, many authors also used such traits as parameters related to the intensity of photosynthesis and transpiration [Tourneux and Peltier 1995, Koszański and Rumasz-Rudnicka 2008, Olszewski et al. 2008, Rumasz-Rudnicka 2010, Klamkowski et al. 2015a], the content of photosynthetic pigments [Olszewska 2003, Bertamini et al. 2006, Olszewska et al. 2010, Cui et al. 2015], the free proline content [Zhang et al. 2011, Sun et al. 2015, Qayyum et al. 2017] and the leaf greening index SPAD [Podleśny and Podleśna 2003, Olszewska 2004].

One of the indicators of photosynthetic efficiency of plants is the Fv/Fm parameter (maximum potential photochemical activity) [Klamkowski et al. 2013]. It should be noted that many authors suggest that changes in the value of this parameter in water scarcity only occur in the case of severe stress [Ögren 1990, Reynolds et al. 2012, Klamkowski et al. 2013]. Razavi et al. [2008] state that the parameters of fluorescence qP (photochemical quenching) and qN (non-chemical quenching) are better than the Fv/Fm parameters used to assess the strawberry reaction to drought stress. Photochemical quenching determines the level of the conversion efficiency of light energy to chemical energy necessary for the transformation in the dark photosynthesis phase (Calvin cycle). The parameters of the actual (temporary) performance of the photosynthetic apparatus under specific environmental conditions are also useful, e.g. the Yield (Y) parameter describing the actual activity of the photosystem II [Klamkowski et al. 2013].

In the studies of Klamkowski et al. [2013], it was shown that the stress of moderate water deficit did not destructively affect the photosynthetic apparatus of the 'Elsanta', 'Elkat' and 'Grandarosa' cultivars, as evidenced by small decreases in the Fv/Fm parameter. The reduction of the Fv/Fm parameter value in plants growing under drought stress conditions was also observed in strawberries of the 'Real' and 'Magic' cultivars [Caulet et al. 2014]. Klamkowski et al. [2013] found that the strawberries of the 'Elkat' and 'Grandarosa' cultivars responded to the stress of water deficit by reducing the value of the Y parameter (by 51% and 49% respectively). In the 'Elsanta' cultivar, this parameter decreased by 31%, which may indicate, compared to the other studied cultivars, a more efficient functioning of its photosynthetic apparatus, and, thus, higher tolerance to drought stress. For the 'Elsanta' cultivar, it has also been shown that the photochemical quenching parameter (qP) was 7% smaller, compared to the other tested cultivars [Klamkowski et al. 2013].

Different research results were obtained by Roiloa and Retuerto [2007], who showed that the values of maximum potential photochemical activity (Fv/Fm), photochemical reflection (PRI index) and chlorophyll content in the leaves of *Fragaria vesca* L. plants subjected to stressful drought were higher than in plants growing in conditions of optimal soil moisture. The reduction of these values was observed only in conditions of simultaneous impact of water and light scarcity on the studied plants.

In the experiment of Razavi et al. [2008], on strawberries of the 'Elsanta' cultivar maintained under mild drought stress [according to Hsiao 1973], it was shown that the distribution of absorbed photons between photochemical and non-chemical quenching changed with increasing drought levels, as evidenced by the decrease in the qP index and a qN index increase. In the studies of these authors, no effect of the drought conditions on the value of the Fv/Fm parameter was found.

Grant et al. [2010] showed that the intensity of transpiration in ten studied strawberry cultivars growing under water deficit conditions was lower than in plants irrigated optimally. According to these authors, the reaction of individual cultivars to drought, determined on the basis of transpiration intensity, was dependent on the place of cultivation of the plants (polyurethane tunnel, greenhouse). Similar results regarding the effect of drought on the intensity of transpiration were obtained by Grant et al [2012b] in the four strawberry cultivars and four genotypes of *Fragaria chilioensis* (L.) Mill. and by Ghaderi and Siosemardeh [2011] in two cultivars of strawberry. These authors also demonstrated the negative impact of water scarcity on the intensity of CO_2 assimilation, transpiration and stomatal conductivity for water. Pirker et al. [2002] showed a decrease in stomatal conductivity for the water in strawberries of the 'Elsanta' and 'Semperflorens' cultivars growing in drought conditions.

By the presented research results, it can be stated that the water deficit has reduced the intensity of photosynthesis and transpiration in all tested plants. In the case of photosynthesis, this reduction ranged from 10% in the 'Selva' cultivar [Ghaderi and Siosemardeh 2011] to as much as 92% in the 'Honeoye' cultivar [Klamkowski et al. 2015b]. The lowest intensity of transpiration, in the light of the presented research, was recorded in the 'Elsanta' cultivar – it amounted to 27% [Klamkowski et al. 2013] and the highest in the case of 'Selva' (92%) [Ghaderi and Siosemardeh 2011] (Tab. 1). It can, therefore, be concluded that water scarcity significantly limits the intensity of gas exchange of plants from the genus *Fragaria*, to varying degrees, depending on the species and cultivar.

Many authors, for numerous cultivars of strawberries, state that, in conditions of water deficiency, the content of photosynthetic pigments such as chlorophyll a, chlorophyll b, total chlorophyll and carotenoids in leaves decreases [Blanke and Cook 2002, Klamkowski and Treder 2006, 2008, Grant et al. 2010, Ghaderi and Siosemardeh 2011, Caulet et al. 2014, Klamkowski et al. 2015b].

The results presented indicate that various species and cultivars of plants from the *Fragaria* genus react to drought by developing a mechanism of avoidance, based on the closure of stomata and reducing transpiration, which is one of the first plant reactions to drought [Klamkowski et al. 2006]. The main function of stomata is to control and regulate gas exchange between the interior of the leaf and the atmosphere. Because of this mechanism, it is possible to regulate water relations and carbon assimilations in plants [Hetherington and Woodward 2003]. Closure of the stomata protects plants from excessive water loss, but also limits the diffusion of CO_2 into the leaves [Chaves et al. 2003]. The decrease in the rate of photosynthesis in plants growing under water deficit conditions may be the result of both stomatal (stomata closure) and non-stomatal (disorders of metabolic processes) processes. The closure of stomata and the resulting CO_2 deficiency is the main cause of decreased photosynthesis with mild and moderate deficits, while changes in photosynthetic reactions occur in the state of severe stress [Klamkowski and Treder 2008].

The activity of antioxidant enzymes

Exposure of plants to abiotic stress often leads to the generation of reactive oxygen species (ROS) [Ashraf and Akram 2009]. Increasing levels of ROS causes oxidative damage to cellular components such as lipids, proteins and nucleic acids [Ghaderi et al. 2015, Sun et al. 2015]. This in turn activates antioxidant enzyme systems (POD, CAT and APX) [Hayat et al. 2010, Zhang et al. 2011] (Tab. 2). These enzymes react with ROS to keep them in low concentration and then regenerate cellular antioxidants, including

Table 2. Percent reduction (–) or increase (+) of the activity of antioxidant enzymes of plants from the *Fragaria* genus growing under water stress conditions, in comparison with plants growing under optimal irrigation conditions (according to different authors)

Species	Cultivar	SOD	POD	CAT	APX	Authors
Fragaria × *ananassa* Duch.	'Kurdistan'	n.d.	+12	+22	+19	Ghaderi et al. 2015
	'Queen Elisa'		+33	+70	+51	
	'Tudla'	–41	–28	–27	–47	Yin et al. 2010
F. vesca L.	'EMb'	–34	+290	–25	n.d.	Wang 1999

Explanations as in Tab. 1

glutathione reductase (GPX) and ascorbate peroxidase (APX) [Sun et al. 2015]. In studies by Sun et al. [2015], the activity of SOD (superoxide dismutase), CAT (catalase) and POD (peroxidase) increased on average to the 6th day of maintaining the strawberry 'Tonoyoka' cultivar under conditions of mild, moderate and severe water deficiency and then decreased. These results suggest that, in strawberries, SOD, POD and CAT can alleviate oxidative stress induced by drought. These enzymes can play a key role in adapting plants to drought conditions. However, the activity of SOD, POD and CAT began to decrease six days after drought stress, which indicates that the ability of strawberries to adapt in drought-related stress was limited [Ghaderi et al. 2015]. In the studies of Yin et al. [2010], the activity of enzymes such as SOD, POD, CAT, APX in the leaves of the strawberry of the 'Tudla' cultivar growing in drought was significantly lower than in plants optimally provided with water.

The results contained in Table 2, concerning changes in the activity of antioxidant enzymes in plants of the *Fragaria* genus, growing under water deficit conditions, may be crucial in biotechnological work, when selecting plants with features indicating high resistance to drought. Unfortunately, there are still few studies discussing this issue, in particular in the case of plants from the *Fragaria* genus.

Growth, development and yielding of plants

Due to the fact that disturbances in physiological processes caused by water scarcity directly affect the yield of plants [Olszewska and Grzegorczyk 2013], many authors also assess the physiological state of plants under water stress conditions with determining their yield [Grzebisz and Musolf 1999, Koszański and Rumasz-Rudnicka 2008, Chmura et al. 2009].

According to Yuan et al. [2004], the reduction in irrigation resulted in a decrease in a number of leaves, flowers and fruits, fresh weight of aboveground parts, fruit yields (including commercial yield) and the size of the strawberry fruit of the 'Sachinoka' cultivar.

Growth inhibition under the influence of water deficit was found in *Fragaria vesca* L. [Roiloa and Retuerto 2007], strawberries of 'Elkat', 'Elsanta' and 'Grandarosa' [Klamkowski et al. 2006, Razavi et al. 2008, Klamkowski et al. 2013], 'Antilla', 'Benicia', 'Sabrina', 'Fortuna', 'Santaclara', 'Splendor', 'Camarosa' [Martínez-Ferri et al. 2016] and many other cultivars (Tab. 3).

The drought reduced the leaf area and the size of the root system of the 'Sonata' cultivar. However, it limited the growth of the aboveground part more than the roots, which may indicate the plant's defensive strategy – the maximum use of water resources [Klamkowski and Treder 2011]. The increased investment in roots enlarges root depth. This allows plants to increase water abstraction and survival during drought [Klamkowski et al. 2006]. In the Caulet et al. [2014] study, strawberries of the 'Magic' and 'Real' cultivar, under the influence of drought, did not develop more roots, however, the roots were significantly longer.

Studies by Borowicz [2010] show that *Fragaria virginiana* Duch. responded to water deficit by reducing the mass of aboveground parts and roots, but, in the case of roots, this interaction was largely dependent on the genotype of the plant. In addition, plants growing under water stress conditions produced shorter runners. This is also confirmed by Grant et al.

[2012b], who showed that the number of leaves produced by strawberries and wild strawberries growing under water deficit conditions was lower than in control plants, but also significantly differed between genotypes, where 'ZB4' (*F. chiloensis* (L.) Mill.) produced the largest number of leaves, and 'Totem' and 'Elsanta' (*Fragaria* × *ananassa* Duch.) the least. Reduction of the total leaf area reduces transpiration and, thus, can be an element of plant resistance to water scarcity [Grant et al. 2010].

The weight of a single strawberry fruit is closely related to the amount of water supplied to plants during flowering and fruit development [Serrano et al. 1992, Terry et al. 2007, Giné Bordonaba and Terry 2010]. It has been reported that deficit irrigation (DI) of strawberries results in a decrease in yield (Tab. 3). This was also confirmed by the studies of Terry et al. [2007], which showed that DI reduced the fresh and dry weight of the strawberry fruit of the 'Elsanta' cultivar. Also, Yuan et al. [2004] found that reducing the amount of water supplied could reduce the yield of strawberries. In the studies of Giné Bordonaba and Terry [2010], the strawberry fruit mass was significantly reduced (approx. 1/3) by DI in the cultivars of 'Symfonia', 'Elsanta' and 'Sonata'.

It can be clearly stated that the yielding of plants from the *Fragaria* genus is limited by the water deficit, mainly due to the fact the fruits are characterized by significant water content, while the root system is relatively shallow and not very extensive. However, in this case, also variation in the reaction is observed, depending on the cultivar. The yield may be reduced by 7% in the 'Flamenco' cultivar [Weber et al. 2016] to 63% in the 'Elkat' cultivar [Klamkowski et al. 2013] (Tab. 3).

The fruit colour

The supply of water may affect the colour of the fruit of plants of the genus *Fragaria* [Terry et al. 2007]. According to these authors, the fruits of the strawberry of the 'Elsanta' cultivar irrigated with the least amount of water (50 cm^{-3} day^{-1}) were characterised by a less red colour compared to the others (irrigated 100 and 200 cm^{-3} day^{-1}). Also, in the studies of Giné Bordonaba and Terry [2010], the effect of drought on the colour of the strawberry fruit was found. It has been shown that water deficit significantly reduced the chroma of the fruit colour in all tested strawberry cultivars ('Christine', 'Sonata', 'Elsanta', 'Symphony', 'Florence'). Changes in factors such as lightness and the hue angle depended on the cultivar. On this basis, however, one could not infer the drought resistance, but there are grounds to believe that the colour of the fruit may be related to their chemical composition. However, there is not enough research on this subject.

The chemical composition of fruits and plants

The deficiency of water leads to changes in the chemical composition of the fruit of plants of the genus *Fragaria* [Koszański et al. 2006, Weber et al. 2017]. Koszański et al.'s [2006] studies showed that the fruits of optimally irrigated 'Elsanta', 'Senga Sengana' and 'Elkat' cultivars were characterised by a higher content of phosphorus and potassium in comparison to plants kept under water deficiency, which may be the result of the increased flow of these components with water and lower content of nitrogen and nitrates (III). This may be related to the inhibition of nitrate reductase activity. Pirker et al. [2002] showed that drought caused a decrease in the general level of antioxidants in the strawberry fruit of the 'Elsanta' and 'Semperflorens' cultivars.

According to Koszański et al. [2006], optimal irrigation increased the vitamin C content and reduced the sugar content in the strawberry fruit of the 'Elsanta', 'Elkat' and 'Senga Sengana' cultivars. Weber et al. [2017] showed that the deficit irrigation increased the content of sugars and organic acids in the fruits of the 'Flamenco' cultivar (by 18% and 29% respectively), while in the 'Eva's Delight' cultivar, this content decreased by 20% and 42%, respectively. Sun et al. [2015] found that the content of soluble sugar in the leaves of the 'Toyonoka' cultivar of strawberry, growing in drought conditions, increased with increasing severity and duration of drought stress. Control plants, irrigated as needed, did not show changes in the content of sugars in the leaves over time. At the end of the experiment, the soluble sugar content in leaves treated with mild, moderate and severe drought stress were, respectively, 1.6-, 2.2- and 2.5-times higher than in the leaves of control plants. These results suggest that soluble sugars are important, osmotically active compounds that mediate osmoregulation and reduce damage caused by a water deficit in plants. It is also

Table 3. Percent reduction (–) or increase (+) of the morphological characteristics of plants from the *Fragaria* genus growing under water stress conditions, in comparison with plants growing under optimal irrigation conditions (according to different authors)

Species	Cultivar	Leaf fresh mass	Leaf area	Root fresh mass	Yield	Authors
Fragaria × *ananassa* Duch.	'Magic'	n.d.	–94	n.d.	n.d.	Caulet et al. 2014
	'Real'		–23			
	'Honeoyne'		–28		–23	Liu et al. 2007
		–35	–20	–40	–47	Klamkowski et al. 2015b
	'Elsanta'	n.i.	–37	–43	–45	Klamkowski and Treder 2011
		–57	–48	–52	–26	Klamkowski et al. 2013
		–7	–6	–22	–26	Klamkowski et al. 2015b
		–47	–42	–24	n.d.	Grant et al. 2010
		–34	–33	n.d.		Razavi et al. 2008
		n.d.	–58			Grant et al. 2012b
			n.d.		–26	Klamkowski and Treder 2008
	'Sonata'	–17	–29	–21	–37	Klamkowski and Treder 2011
	'Elkat'	–72	–72	–54	–63	Klamkowski et al. 2013
		–61	–67	n.i.		Klamkowski et al. 2006
			–34		–38	Klamkowski and Treder 2008
	'Grandarosa'	–45	–34	–29	–42	Klamkowski et al. 2013
		–27	–36	–30	–59	Klamkowski et al. 2015b
	'Flamenco'	n.d.	n.d.	n.d.	–7	Weber et al. 2016
	'Eva's Delight'				–33	
	'Salut'	–50	–42	n.i.		Klamkowski and Treder 2006
		n.d.	–19	n.d.	–29	Klamkowski and Treder 2008
	'Cambridge' 'Favourite'	–37	–25	–12	n.d.	Grant et al. 2010
	'Delia'	–44	–41	–15		
	'Elvira'	–59	–50	–12		
		n.d.	–55	n.d.		Grant et al. 2012b
	'Emily'	–39	–33	–26		Grant et al. 2010
	'Florence'	–43	–40	–14		
		n.d.	–59	n.d.		Grant et al. 2012b
	'Hapil'	–47	–47	–15		Grant et al. 2010
	'Idea'	–47	–45	–22		
	'Symphony'	–37	–44	–12		
	'Totem'	–45	–40	–17		
		n.d.	–60	n.d.		Grant et al. 2012b
	'Kurdistan'		–21		–23	Ghaderi et al. 2015
	'Queen Elisa'		–24		–18	
F. chilioensis (L.) Mill.	'Manzanar Alto'		–50		n.d.	Grant et al. 2012b
	'TR4'		–57			
	'ZB4'		–23			
	'BSP14'		–23			

Explanations as in Tab. 1

worth noting that according to Giné Bordonaba and Terry [2010], irrespective of the amount of water used for irrigation, sugars were from 6 to 8% of the total fresh weight of the strawberry fruit. Taking into account the fact that fructose is 1.8 times sweeter than sucrose, and the sweetness of glucose is 60% of the sucrose sweetness, in the studies of Giné Bordonaba and Terry [2010] the fruits of strawberry plants growing under water scarcity conditions were sweeter. In the case of the 'Elsanta' cultivar, the fruits of plants kept under drought conditions were characterised by up to one third higher sweetness than the control plants. The results obtained by Giné Bordonaba and Terry [2010] also indicate that the deficit irrigation (DI) 'Christine' and 'Florence' strawberry cultivars did not adversely affect the overall quality of their fruits (dry fruit mass, sugar content in fruit, sweetness).

In studies by Terry et al. [2007], water deficit affected the reduction of anthocyanin content, increase of total phenolics, abscisic acid (ABA), non-structural and non-volatile organic carbohydrates content and antioxidant capacity (FRAP) in the leaves.

In studies by Sun et al. [2015] on the impact of three levels of water deficit on the strawberry of the 'Toyonoka' cultivar, it was shown that, at each of these levels, the plants accumulated larger amounts of proline in the leaves than control plants growing under optimal water supply conditions, which may be an adaptive reaction of plants to drought conditions.

The presented results allow presuming that there is a relationship between the level of irrigation of plants and the content of important for health-related fruit ingredients. Also, the presented research results show that by applying a varied level of soil moisture, it is possible to some extent affect the content of chemical compounds of fruits such as sugars or antioxidants.

Progenies and ramets

One of the features of vegetative reproduction of plants (via runners) is the ability to exchange compounds such as water, assimilates, nutrients, defence compounds, signalling molecules or pathogens between interconnected ramets [Zhang et al. 2008, Zhang et al. 2011]. Some studies have reported that, under stress, this connection may result in the poorer condition of plants, and parental plants may stop supporting dependent ramets [Zhang et al. 2008, 2009, 2011]. In such plants, physiological integration enables the transport of water from ramets which are well-supplied with water to ramets under drought conditions, and this is a way of reducing their stress levels [Alpert and Mooney 1986, Alpert 1999, Savini et al. 2008, Zhang et al. 2008, 2009, 2011].

Research by Zhang et al. [2011] suggests that the connection of the ramets with *Fragaria orientalis* L. can suppress the negative effects of drought stress when the difference in access to water in the ramets is high. The connection of plants through runners can therefore be understood as part of a stress tolerance strategy that increases the survival and growth of clonal plants growing in heterogeneous environments [Zhang et al. 2008, Zhang et al. 2011]. This is also confirmed by the studies of Roiloa and Retuerto [2007] on *Fragaria vesca* L., in which the effect of water deficiency on parental and progeny plants connected with runners was observed, manifested by the increased photosynthetic efficiency of parents connected to offspring growing in water scarcity conditions.

In a study by Blanke and Cook [2002], it was shown that the intensity of transpiration in runners was about ten times smaller than in the leaves of the mother strawberry plant. These results suggest that strawberry runners seem to be more sensitive to drought than their leaves. Hence the conclusion that strawberry plants which produce a greater number of runners, may be less able to withstand water deficit [Blanke and Cook 2002].

The studies presented above indicate a significant relationship between the occurrence and amount of ramets and plant resistance to water deficit. These studies may suggest that the cultivation of plants in conditions of water deficit, in places of irregular irrigation, may be more effective when using species and cultivars that produce runners. It is also possible to reduce water consumption by optimizing the cultivation of growing plants. However, the results of previous studies are not ambiguous and the above statements are only suggestions of the author.

The impact of factors limiting the negative effects of drought

In the studies of Caulet et al. [2014], the effect of the foliar furostanol glycosides, extracted from *Lycopersicon* sp. and *Digitalis* sp. leaves, on the tolerance of drought on two strawberry cultivars, 'Magic' and 'Real', was evaluated. Plants growing in drought conditions treated with the glycosides developed a greater number of longer roots compared to plants growing without the addition of glycosides, wherein the number and area of leaves was similar. The addition of glycosides also mitigated the effects of stress related to the water content in the leaves – the RWC index values were higher. In drought conditions, the beneficial effects of the studied glycosides on several strawberry fluorescence parameters were also demonstrated, such as: photochemical quenching factor (qP) and maximum potential photochemical reaction in PS II determined after dark adaptation (Fv/Fm) and the content of carotenoids in leaves. It can, therefore, be concluded that the use of furostanol glycosides leads to the stimulation of the development of the root system, which allows the plants to adapt to water scarcity conditions.

It is reported that the addition of jasmonic acid can mitigate the effects of water scarcity, e.g. in soy [Wang 1999, Hassanein et al. 2009]. In the studies of Giné Bordonaba and Terry [2016], it was found that the addition of a methyl ester of jasmonic acid (MeJa) administered by foliar feeding does not minimise the effects of water deficiency in sensitive strawberry cultivars. Nevertheless, the addition of MeJa caused an increase in fructose content in the leaves of plants growing in drought conditions. Wang [1999] found, however, that the plants of the species *Fragaria vesca* cv. 'EMb' maintained under water stress, showed higher activity of superoxide dismutase (SOD) and chloramphenicol acetyltransferase (CAT) after the addition of MeJa, and higher content of ascorbic acid in the leaves. MeJa did not affect peroxidase activity. However, it had a significant impact on the change in the content and ratios of fatty acids in strawberry leaves. In particular, water stress reduced the content of linolenic acid, increased the ratio of linolenic and oleic acids and decreased the ratio of unsaturated to saturated fatty acids in the leaves.

Salicylic acid is a naturally occurring signal molecule that plays an important role in the formation and signalling of plants' defence response against various biotic and abiotic stresses (including drought) through their physiological processes, growth, development and productivity [Arfan et al. 2007, Karlidag et al. 2009, Wang et al. 2010, Ghaderi et al. 2015]. In studies by Ghaderi et al. [2015], the influence of salicylic acid on strawberries growing under water stress conditions was evaluated. It was shown that the addition of 0.1 $mmol \cdot dm^{-3}$ of salicylic acid positively influenced the number of leaves, dry weight of the leaf, total dry matter, RWC, free proline content and peroxidase activity (POD).

It is reported that mycorrhiza formation may increase the root absorption surface, reduce leaf water potential and permanent wilt point, increase stomata, improve the transpiration rate and relative leaf water content and reduce chlorophyll degradation under drought stress [Yin et al. 2010]. Borowicz [2010] showed, however, that the symbiosis of arbuscular mycorrhizal fungi (AMF) and *F. virginiana* Duch. gives various effects that do not allow stating clearly whether these treatments are beneficial for plants subjected to stress drought. Yin et al. [2010] found that the inoculation by fungi from the species *Glomus mosesseae* on strawberry of the 'Tudla' cultivar can significantly slow down the decline in protective enzymatic activity (SOD, POD, CAT, APX) caused by drought stress.

Robinson Boyer et al. [2015] investigated the effect of the inoculation of fungi from the *Funneliformis mosseae* and *Funneliformis geosporus* species and their combination for drought tolerance in the 'Everest' strawberry cultivar. They found that the addition of the AMF inoculum to plants subjected to reduced irrigation restored the growth of plants to the same or higher values as non-mycorrhized, fully watered plants. The effectiveness of the use of water by plants was greater in plants vaccinated with AMF, but there were no significant differences between plants vaccinated with a single or composite inoculum.

The above results indicate that both jasmonic acid and salicylic acid and the use of mycorrhizalisation can effectively reduce the negative effects of water stress, especially in the case of non-covered crops in areas affected by precipitation deficits.

CONCLUSIONS

Based on the results of research carried out by various authors, it can be pointed out that the most drought-tolerant *Fragaria* species is *F. chiloensis*.

The 'Chandler' and 'Elsanta' cultivar are mentioned among the most tolerant cultivar for water deficit. These plants are a source of plant material for breeding programmes, the aim of which is to increase tolerance to drought of *Fragaria* plants.

In plants from the *Fragaria* genus, drought causes a significant reduction in fruit yield, while increasing the content of sugars. Strawberries adapting to drought conditions reduce the potential of cell water, close stomata and reduce the transpiration intensity, and use antioxidative enzymes and osmotically active substances. In addition, the vegetative reproduction of plants and connections through runners between the parent and offspring plants may eliminate the adverse effects of water deficit in a specific manner. The effects of drought can also be removed by other compounds added to the substrate, for example, furostanol glycosides, salicylic acid and by inoculation with arbuscular mycorrhizal fungi (AMF). Therefore, the mentioned mechanisms that build drought resistance in strawberries would be the basis for future biotechnological work to improve the resistance of strawberries to drought stress.

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