Original Scientific paper
10.7251/AGRENG2202029K
UDC 633.63

THE PHYSIOLOGICAL AND BIOCHEMICAL ESTIMATION OF THE ADAPTIVE ABILITY OF SUGAR BEET (*BETA VULGARIS* L.) TO SHADING AND PLANT DENSITY

Oksana KLIACHENKO[1], Larysa PRYSIAZHNIUK[2*]

[1]National University of Life and Environmental Sciences of Ukraine, Ukraine
[2]Ukrainian Institute for Plant Variety Examination, Ukraine
*Corresponding author: prysiazhniuk_l@ukr.net

ABSTRACT

The study of adaptive resistance to adverse environmental effects, which is connected with mechanisms of ontogenetic adaptation investigation, is an important direction of crop breeding. The adaptive resistance is identified on the phenotype level within the information stored and expressed by the genome. Ukrainian and Swedish lines, hybrids, and hybrid parent components of sugar beet under different shading conditions (30 and 60% of natural light) were investigated. Genotype-specific general physiological and biochemical features of the adaptive changes in leaves and productivity components in the course of metabolism are revealed. A significant decrease in the photosynthesis intensity and photochemical activity of chloroplasts occurred during the sugar beet plant adaptation to shading. The adaptive level of different sugar beet genotypes to low light was also expressed through the significant changes in the water-soluble carbohydrate pool of leaves themselves and leaf petioles. An important physiological parameter of sugar beet adaptive reaction is a response to shading in specific leaf weight (SLW), which is used in plant breeding as the trait of increased photosynthesis intensity. As a result of the study, it was found that the shading impacted significantly on the distribution and ratio of sucrose in the ring zones of vascular bundles and adjacent zones of the root storage parenchyma. The ontogenetic adaptation to photosynthetic active radiation light regime of photosynthetically active radiation (PAR) of sugar beet lines, hybrids, and their parent components of different origins under shading and different plant density in the field was shown. It was found that the stress intensity is a key characteristic of changes in physiological, biochemical, anatomical, and morphological traits of the leaf, which maintain plant homeostasis and ensure maximum efficiency of photosynthesis and productivity of different sugar beet genotypes under these conditions.

Keywords: *ontogenetic adaptation, sugar beet, physiological and biochemical features, adaptation.*

INTRODUCTION

Management of physiological processes, such as photosynthesis at different levels of its organization, optimization of source-sink relations (Kyrizii, 2015), light (Zhu, 2010) and dark (Golovko, 1998) respiration is the modern strategy of plant breeding (Stasik *et al*., 2016). One particularly important environmental cue with economic consequences, that is, early allocation versus later growth trade-offs, is shade. In dense plant canopies such as weedy crop fields, the plant environment is enriched with far-red (FR) light due to reflected FR by green vegetation. For example, the ratio of reflected red (R) to FR was 0.06 when sugar beet was surrounded by common lambsquarters (*Chenopodium album* L.) compared to 0.7 when surrounded by bare soil. With the aid of a family of photoreceptors, particularly cryptochromes and phytochromes, plants can sense and respond to changes in R:FR and blue-violet light in their surroundings. Therefore, a search for informative physiological and biochemical indicators associated with plant productivity in a wide range of growing conditions, which may be used as physiological and biochemical markers to increase the efficiency of the breeding process, is important. The new sugar beet hybrids contain sugar in the amount of 75-76% of dry matter, and a further increase in sugar content is an extremely labor-consuming process. It was found that the anatomical structure of the storage organ is the basis of the pattern of slowing down the rate of sucrose accumulation (Elliot *et al.*, 1996; Fasahat *et al*., 2018). Thus, to improve the existing breeding methodology for obtaining high-sugary breeding genotypes, it is necessary to study the relationship between the anatomical structure and the sugar accumulating capacity of the roots. An important direction in crop breeding is the study of the adaptive resistance of plants to the adverse impact of the environment, which is associated with the study of the mechanisms of ontogenetic adaptation, which is found at the phenotypic level within the information stored and implemented by the genome (Kyrychenko, 2002; Lv *et al.*, 2019; Ghaffari *et al*., 2021). These changes are considered a manifestation of the forms of reliability of biological systems (Grodzinskiy, 1983) from the standpoint of implementing their adaptive potential (Zhuchenko, 2008; Li *et al*., 2019) at the autologous, physiological, biochemical, genetic, and molecular levels. Studies on the influence of seasonal weather variability on sugar beet development recognized that amongst the different environmental variables, the amount of available light for the crop is a predominant factor driving the biomass accumulation after crop canopy closure (Artru *et al.*, 2018).

This study aimed to identify the most informative physiological and biochemical indicators in the formation of high productivity of sugar beet in connection with their resistance to shading and thickening.

MATERIALS AND METHODS

A diploid hybrid ‘Lgovsko-Verkhniatskyi ChS21’ (‘LV ChS21’) and its parent components, CMS line ‘Hill 13’ (Sweden) and simple interlinear sugar beet hybrids ‘SKF5050’, ‘SKF5084’, and ‘SKF4973’ were used. Plants were grown in soil culture in Wagner's vessels with a capacity of 14 kg of soil at 60% of full soil moisture. A part of 15-day-old plants was shaded with screens of gauze (2-3 layers) and white cloth for the entire growing season (140 days). Biological repetition was 20 plants. The decrease in natural illumination under the screens was 60% (treatment I) and 30% (treatment II). Plants that were grown in natural light served as control. Field two-factor experiments on shading and thickening were carried out at the Yaltushkiv Research Station of the National Academy of Sciences of Ukraine. The intensity of photosynthesis was recorded under controlled conditions using an installation mounted based on an optical-acoustic infrared gas analyzer GIAM-5M, set according to a differential scheme. The contents of chlorophylls *a*, *b,* and carotenoids were determined spectrophotometrically and calculated according to the formula (Musienko *et al.*, 2001). The photochemical activity (PCA) of chloroplasts was assessed spectrophotometrically by the reduction of potassium ferricyanide. The total content of albumins and globulins, protein nitrogen, and water-soluble carbohydrates was determined in accordance with Yermakov (1987), the content of sucrose by the method of cold digestion (Pochynok, 1976), the distribution of sucrose in the zones of the interring parenchyma and vascular bundles on the cross-section of roots in accordance with Okanenko (1968). All experiments were carried out at the experimental plots and laboratories of the National University of Life and Environmental Sciences of Ukraine (Kyiv, Ukraine) in the years 2015-2018. Statistical processing of the obtained experimental data was performed with the Excel Data Analysis package.

RESULTS AND DISCUSSION

As a result of studies of the sugar beet lines, hybrids, and their parent components of Ukrainian and Swedish origin under different shading conditions (30 and 60% of natural light) we found general physiological and biochemical features of adaptive changes in the leaf apparatus and productivity components as well as genotype-specific differences in the metabolic processes of plants. As the data in Tables 1 and 2 show, under shading conditions, there is a clear tendency of increasing the content of chlorophylls *a* and *b* compared to the control per specific leaf weight (SLW) unit by 10-50% in treatment I and 25-60% in treatment II). These parameters reproduce various aspects of the genetic determination of the optical system of a leaf (Lutkov, 1986; Zou *et al*., 2019). At the same time, shading affected the content of chlorophyll *b* more than chlorophyll a, which led to a decrease in the ratio of chlorophyll a/*b,* which is one of the most distinctive characteristics of the adaptation of plant photosynthetic apparatus to the light factor (Mokronosov, 1981). This is a sign of the acquisition of shadow endurance by the photosynthetic apparatus (Dymova, 1998; Holovko, 1998). A similar pattern of adaptation to shading has been described in the literature for sugar beet (Kyriziy, 2004; Artru *et al.*, 2018; Zeng *et al*., 2022) and other crops (Guliyev, 1990).

In the process of adapting sugar beet plants to shading, there was a significant decrease in the intensity of photosynthesis and PCA of chloroplasts compared to the control. An important physiological parameter of adaptive reactions of sugar beets to shading is the specific leaf weight (SLW) which is used in breeding as a sign of the increased intensity of photosynthesis (Criswell and Shibles,1971), the value of which naturally decreased in plants of all the studied genotypes along with the increasing stress factor (Tables 1, 2). In the whole plant system, SLW is associated with the level of the pool of assimilates and is an indicator of their utilization for the growth of leaves to form the assimilation surface (Tooming, 1984). From the data given in Tables 1, 2, it can be seen that the decrease in SLW in shading conditions is accompanied by an increase in the leaf area.

Table 1. Physiological and biochemical indices of leaf apparatus of plants of different genotypes of sugar beets in shading.

Hybrid, component	Treatment	Chlorophyll content (mg/g)		Ratio of chlorophylls a/b	PCA (μM [Fe (CN)6]3- /mg chl.·year)	SLW, g/dm^2	Water-soluble carbohydrates (% of dry weight)				Total albumins and globulins (% of dry weight)
							leaf blades		petioles		
		a	b				mono-sugar	total sugars	mono-sugar	total sugars	
75 days											
‘LV ChS21’	C**	0.98	0.34	2.85	53.4	0.56	4.25	9.29	30.90	37.84	11.7
	I	1.11	0.45	2.45	50.3	0.52	3.21	7.54	28.87	35.15	10.85
	II	1.14*	0.49	2.31*	47.5*	0.49	1.99*	5.62*	28.10*	34.40*	9.94*
CMS	C	1.09	0.45	2.62	42.8	0.63	3.84	7.13	33.40	39.74	14.5
	I	1.25	0.54	2.33	40.3	0.58	3.27	5.96	32.17	36.81*	12.1
	II	1.36*	0.60	2.25*	37.9*	0.53	2.89*	4.39*	30.31	33.65*	11.35
Multigerm	C	0.87	0.32	2.69	31.9	0.69	3.49	6.69	24.10	30.79	14.09
	I	1.12	0.43	2.61	29.7	0.63	2.92	5.84	23.09	29.66	12.50
	II	1.16	0.46	2.52	27.6*	0.59*	2.54*	4.65*	21.87	26.59*	11.39*
LSD05		0.09	0.06		1.70	0.02	0.52	0.95	1.01	1.15	0.75
140 days											
‘LV ChS21’	C	1,45	0.46	3.17	64.9	0.63	11.56	16.68	36.10	42.79	10.1
	I	1.71	0.66	2.60	58.7	0.54	9.47	13.18	34.04	37.40	8.7*
	II	1.76*	0.71	2.43*	53.0*	0.51	5.32	9.34*	30 .49*	35.91*	7.6*
CMS	C	1.56	0.49	3.21	52.6	0.67	9.15	13.58	38.89	45.23	13.6
	I	1.87	0.77	2.39	47.5*	0.58	8.06	11.25	36.44	39.36	8.8*
	II	2.10*	0.88	2.31*	42.9*	0.47	7.25	8.11*	32.71*	33.05*	7.3*
Multigerm	C	1.15	0.34	3.43	46.4	0.73	8.61	12.22	33.40	40.34	13.3
	I	1.65	0.53	3.10	41.9*	0.62	7.46	10.53	32.39	38.09	9.3*
	II	1.73*	0.60	2.80*	37.8*	0.53	6.71	8.15*	31.44*	31.75*	7.9*
LSD05		0.10	0.07		2.1	0.04	1.11	1.80	1.51	2.11	1.5

*The difference is significant at $p<0.05$ relative to the control.

**C – Control

Table 2. Physiological and biochemical characteristics of leaf apparatus of sugar beet lines (130 days).

Line	Treatment	Chlorophyll (mg/g)			Carotenoids (mg/g)	Carotenoids (mg/dm^2)	Intensity of photosynthesis (mg CO_2·dm^{-2}·h	PCA (μM $[Fe(CN)_6]^{3-}$ /mg chl.·year)	SLW (mg/dm^2)	Albumins + globulins (% of dry matter)	Leaf area (dm^2)
		a	b	a/b							
'SKF 5084'	c**	0.382	0.260*	1.46	0.228	0.68	15.4	34.68	668.2	14.71	25.43
	s***	0.621	0.573	1.08	0.682*	0.69	6.95*	15.61*	476.3*	13.85	53.88*
'SKF 5050'	c	0.340	0.211	1.61	0.215	0.61	16.1	29.40	696.5	15.91	33.39
	s	0.789	0.561*	1.40	0.283*	0.67	7.24*	12.94*	479.6*	14.83	60.42*
'SKF 4973'	c	0.456	0.348	1.31	0.170	0.52	11.85	37.68	691.2	11.54	41.77
	s	0.683*	0.537*	1.27	0.200	0.56	5.45*	16.96*	527.5	12.18	48.92*
'Hill 13'	c	0.736	0.463	1.58	0.456	1.36	11.08	30.60	747.9	13.60	37.97
	s	1.076	0.879*	1.22	0.335*	0.87	4.76*	12.85*	508.8*	7.6*	50.16*
LSD_{05}		0.120	0.040	0.23	0.01	0.12	0.70	0.80	14.10	1.40	1.12

*The difference is significant at p<0.05 relative to the control.

**C - Control

***S - shading

Shading was also accompanied by a decrease in the total content of albumins and globulins in the leaves depending on the genotype, especially at the end of the growing season. The decrease ranged from 13.9 to 35% in treatment I and from 24.8 to 46.4% in treatment II (Table 1, 2). The degree of adaptability of various sugar beet genotypes to reduced illumination was also manifested due to significant changes in the pool of water-soluble carbohydrates in leaf blades and petioles, the content of which decreased in the studied genotypes by 11.9-25% (treatment I) and by 20.5-54% (treatment II) compared to the control (Table 3, 1).

Table 3. Water-soluble carbohydrate content in leaves and sugar content of roots in sugar beet lines.

Line	Treatment	Leaf blades		Petioles		Root
		monosaccharides	disaccharides	monosaccharides	disaccharides	sucrose content (%)
		(% of dry matter)				
'SKF 5084'	control	14.18	18.29	30.81	46.54	15.95
	shading	12.8	16.75	27.2	40.9	14.75
'SKF 5050'	control	10.91	16.15	34.69	47.15	15.17
	shading	6.07*	8.77*	30.5	44.65	13.55
'SKF 4973'	control	19.15	22.88	41.87	51.44	16.83
	shading	7.5*	12.81*	34.6*	46.71	14.55
CMS line	control	9.1	13.58	32.71	45.23	18.84
	shading	8.06	12.52	26.44*	33.0*	15.9
LSD_{05}		1.20	1.22	1.30	1.25	0.90

*The difference is significant at p<0.05 relative to the control

Studies have shown that the adaptation of sugar beet to shading also occurred as a result of a change in source-sink relations, the original program of which is embedded in the plant genome (Mokronosov, 1981). In the conditions of shading, photoassimilates were mainly directed to the growth of the leaf apparatus of plants, the leaf area of which in all studied genotypes increased 1.5 to 2 times compared to the control plants (Table 1, 4), which was also noted by other authors (Kiriziy, 2002). The rate of aging and withering of leaves, which lifespan is under the influence of phytohormonal status (Sytnik *et al*., 1978), was significantly slowed down, especially in CMS lines (Table 5), hybrid, and its components (Table 4).
Under the conditions of shading, the weight of raw and dry matter of roots in the hybrid and its components decreased from 21.3 to 35.4% (treatment I) and from 40.1 to 53.2% (treatment II), which was accompanied by an increase in the ratio of the tops/root, a decrease in the ratio of the weight of root to the weight of the whole plant, and an increase in the ratio of the dry matter of petioles to the dry matter of tops (Table 4). In the studied sugar beet lines, the decrease in the accumulation of dry matter of roots compared to the control was 30% in multigerm sugar beet lines and 16% in CMS lines (Table 3). Shading negatively affected the process of sugar accumulation due to the primary biosynthesis of sucrose in the leaf and its entry into the storage compartment of the root (Kuznecov *et al*., 1990; Khozaei *et al*., 2020). Among the studied sugar beet genotypes, the greatest decrease in the sugar content of roots was 1.8-4.6% in treatments I and II in ‘LV ChS21’, and the least decrease, from 0.9 to 1.2% was observed in the ‘Hill 13 (Table 4). In the sugar beet lines, sugar content decreased in the range from 1.24 to 2.8% (Table 3).
The revealed peculiarities of the formation of sucrose content in various sugar beet genotypes are generally consistent with the peculiarities of the growth and development of the leaf apparatus and the functional photosynthetic characteristics of leaves in the donor-acceptor system. In shaded plants in the second half of vegetation, the period of leaf apparatus formation was prolonged, and the competitive relations between young growing leaves and roots in the aspect of photoassimilation were aggravated. These circumstances limit the inflow of sucrose from the above-ground part into the roots and lead to inhibition of the growth processes and accumulation of sucrose in the roots (Pavlinova, 1981). In addition, in shaded sugar beet plants, the intensity of photosynthesis decreases, which in turn leads to a decrease in the pool of newly formed plastic substances.
Studies have shown that shading significantly influenced the distribution and ratio of sucrose in the zones of vascular bund rings and adjacent zones of the stocking root parenchyma. At harvest, these adaptive changes are more clearly expressed in the inner part of roots (1st to 3rd rings), which is supplied with the assimilates by phloem vascular bundles of mature leaves (Kliachenko and Shevchenko, 2007; Kliachenko, 2007), than in the middle (4th to 5th ring) and peripheral part (Table 6). At the same time, the greatest stability of the concentration of sucrose in the transporting and storing root tissues was demonstrated by the hybrid component ‘Hill 13’. The results of field experiments on the influence of different plant densities on the production process of sugar beet showed that the studied CMS

hybrids and their parent components demonstrated different adaptive resistance to the thickening of sowings. At the plant densities of 100 and 120 plants/ha, the most resistant appeared the component of ‘Hill 13’ and CMS component of ‘LV ChS21’, which yield increased by 4.6-4.4 and 4.2-4.1 t/ha, sugar yield by 1.1-0.4 and 1.09-0.5 t/ha, respectively (Table 7). Thus, as a result of the studies of ontogenetic adaptation of sugar beet lines, hybrids, and their parent components to the light regime of PAR under shading and different plant density, it was found that the stress factor intensity is a key characteristic of changes in the physiological, biochemical, anatomical, and morphological parameters of the leaf apparatus, which provide plant homeostasis and ensure the maximum efficiency of photosynthesis and productivity of different sugar beet genotypes under these conditions.

Table 4. Indicators of plant productivity of sugar beet genotypes under shading.

Hybrid, component	Treatment	Dry matter (g)					Leaf area (dm^2)	Root weight (g)	Sucrose (% of wet weight)
		leaf blades	petioles	root	whole plant	dead leaf			
75 days									
‘LV ChS21’	Control	39.3	16.9	71.9	128.1	7.5	60.5	323	12.64
	I	40.5	20.1	51.0*	111.6*	1.3*	63,6	288	12.19
	II	43.9*	22.8*	39.9*	106.6*	1.2*	67.1*	275*	11.72
CMS	Control	45.6	21.3	58.9	125.8	6.8	76.5	283	13.04
	I	46.9	25,2	45.3*	117.7*	1.2*	79.6	258	12.61
	II	48.4*	27.5*	34.7*	110.6*	.07*	83.7*	235*	12.58
Multigerm	Control	31.5	14.1	53,9	99,5	5.1	59.9	291	12.98
	I	32.9	15.8	35.6*	84.3*	0.7*	61.5	248*	12.56
	II	34.1*	17.2*	30.7*	82.0*	0.5*	62.9*	223*	12.43
LSD_{05}		1.2	1.7	5.6		0.04	1.21	6.58	0.11
140 days									
‘LV ChS21’	Control	43.1	22,7	273.8	339.6	65.4	45.9	1126	17.55
	I	45.7	29.2	194.6*	269.5*	12.3*	52.1	885*	15.75*
	II	52.4*	40.4*	156.7*	249.5*	10.8*	59.2*	793*	12.95*
CMS	Control	54.3	22.3	260.7	337.3	66.1	31.4	1031	18.20
	I	56.3	30.1	202.6*	289.0*	11.8*	51.7	850*	16.50*
	II	59.8*	34.5*	153.7*	248.0*	6 7*	60.5*	675*	15.90*
Multigerm	Control	42.8	23.6	269.1	335.5	80.5	46.2	1097	17.90
	I	45.5	27.1	177.5*	250.1*	10.7*	49.3	770*	16.22
	II	47.9*	30.1*	128.2*	206.2*	9.5*	51.4*	600*	15.15*
LSD_{05}		1.9	1.1	10.3		1.92	1.5	15.4	0.35

*The difference is significant at $p<0.05$ relative to the control.

Table 5. Accumulation of dry matter in plants of sugar beet lines.

Line	Root (g)		Leaf blades (g)		Petioles (g)		Whole plant weight (g)		Weight of withered leaves (g)		Above-ground mass root	
	c**	s***	c	s	c	s	c	s	c	s	c	s
'SKF 5084'	116.15	47.04*	37.04	39.48	16.73	36.58*	169.92	123.11*	21.92	6.72*	0.46	1.61*
'SKF 5050'	84.11*	40.*65	53.42 *	57.89*	20.34	43.64*	157.87	142.18*	22.11	13:30	0,87	2.49*
'SKF 4973'	142.87	53.85*	52.81	40.38*	40.19	47.88*	235.87	182.49*	15:57	7.17*	0.65	1.63*
CMS line	260.20	152.68*	56.16	66.39*	22.65	34.57*	339.01	253.58*	65.55	6.74*	0.30	0.66*
LSD_{05}	10.11	1.15	1.10	1.21	1.13	1.07	11.12	10.12	1.09	0.07		

*The difference is significant at p<0.05 relative to the control
**C - Control
***S - shading

Table. 6. Distribution of sucrose (% to wet weight) in roots of different sugar beet genotypes under shading (140 days).

Hybrid, component	Treatment	1st ring		2nd ring		3rd ring		4th ring		5th ring		Periphery
		vascular bundles	parenchyma	vascular bundles	parenchyma	vascular bundles	parenchyma	vascular bundles	parenchyma	vascular bundles	parenchyma	
'LV ChS21'	C** I II	17.1 15.3 13.8*	16.4 14.7 13.3*	17.5 15.6 15.3*	16.6 15.4 13.6*	17.7 16.8 15.6	16.9 16.3 14.8*	18.1 17.8 16.9	18.0 17.6 16.8	18.4 18.0 17.6	18.6 18.2 18.0	18.3 18.1 17.8
CMS	C I II	15.7 15.1 14.8	15.0 13/6. 13.3	16.0 15.9 15.6	15.6 15.0 14.7	16.4 15.9 15.7	15.9 15.1 15.0	17.0 15.7 15.4	16.8 15.6 15.4	17.4 16.0 15.8	17.8 16.8 16.6	17.6 16.9 16.7
Multigerm	C I II	19.8 17.8 16.2*	15.8 15.2 1.7*	20.2 17.8 16.7*	15.6 15.2 14.9	20,6 18.8 17.3	17.4 16.4* 15.7*	21.0 19.3 18.0	18.6 18.0 17.8*	21.2 20,6 19.0	22.6 21.0 20.2*	20.8 20.4 19.8
LSD_{05}		0.30	0.25	0.35	0.20	0.35	0.25	0.35	0.35	0.35	0.30	0.20

*The difference is significant at p<0.05 relative to the control
**C - Control

Table 7. Yield performance of sugar beet under different plant densities.

Hybrid, component	Plant density (1000 plants/ha)	Yield (t/ha)	Root weight (g)	Sucrose content (% of wet weight)	Sugar yield (t/ha)
'LV ChS21'	80	40.0	501.0	17.1	6.8
	100	43.4	434.4	17.4	7.4
	120	42.9	357.8	15.9	6.9
CMS	80	38.8	485.5	17.6	6.8
	100	43.0	437	17.9	7.7
	120	42.9	357.5	16.9	7.3
Multigerm	80	39.9	498.5	17.3	6.9
	100	42.9	429.0	17.8	7.6
	12	42.5	354.1	16.9	7.2
LSD_{05}		2.1	19	0.40	0.60

CONCLUSIONS

Since a certain type of reaction or the norm of reaction to environmental conditions (i.e. the ability to optimally change the organization in response to changes in internal and external factors) is inherited, in the process of obtaining thickening-resistant breeding genotypes of sugar beet, their comprehensive assessment and selection should be carried out by the integral physiological and biochemical parameters, with selecting progeny of plants that are less responsive to a decrease in illumination.

REFERENCES

Adjesiwor, A. T., Ballenger, J. G., Weinig, C., Ewers, B. E., & Kniss, A. R. (2021). Plastic response to early shade avoidance cues has season-long effect on Beta vulgaris growth and development. *Plant, Cell & Environment*, *44*(11), 3538-3551. https://doi.org/10.1111/pce.14171

Artru, S., Lassois, L., Vancutsem, F., Reubens, B., & Garré, S. (2018). Sugar beet development under dynamic shade environments in temperate conditions. European Journal of Agronomy, 97, 38-47. https://doi.org/10.1016/j.eja.2018.04.011

Criswell, J. G., Shibles, R. M. (1971). Physiological basis for genotypic variation in net photosynthesis of oat leaves. Crop Sci., 11(1), 550-553.

Dymova, O. V., Dymov, O. V., Golovko, T. K. (1998). Adaptation of the photosynthetic apparatus of shade-tolerant plants to the light. Plant Physiology, 45(4), 521-528. [in Russian]

Elliot, M. C., Slater, A., Garland, F. S. et al. (1993). New approaches to sugar beet improvement. Opportunities for Molecular Biology in Crop Production, 55, 20-214.

Ermakov, A. I. (1987). Methods of biochemical research of plants. Leningrad, Agropromizdat. Leningradskoe otdelenie. [in Russian]

Fasahat, P., Aghaeezadeh, M., Jabbari, L., Sadeghzadeh Hemayati, S., & Townson, P. (2018). Sucrose accumulation in sugar beet: From fodder beet selection to genomic selection. Sugar Tech, 20(6), 635-644. https://doi.org/10.1007/s12355-018-0617-z

Ghaffari, H., Tadayon, M. R., Bahador, M., & Razmjoo, J. (2021). Investigation of the proline role in controlling traits related to sugar and root yield of sugar beet under water deficit conditions. Agricultural Water Management, 243, 106448. https://doi.org/10.1016/j.agwat.2020.106448

Golovko, T. K. (1998). Breathing in the donor-acceptor system of plants. Plant Physiology, 45(4), 632-640. [in Russian]

Grodzinskiy, D. M. (1983). Reliability of plant systems. Kyiv, Naukova Dumka. [in Russian]

Guliev, N. I. (1990). Study of the physiological characteristics of corn hybrids in connection with resistance to thickening and shading: Dissertation abstract. Kyiv. [in Russian]

Khozaei, M., Haghighi, A. A. K., Parsa, S. Z., Sepaskhah, A. R., Razzaghi, F., Yousefabadi, V. A., & Emam, Y. (2020). Evaluation of direct seeding and transplanting in sugar beet for water productivity, yield and quality under different irrigation regimes and planting densities. Agricultural Water Management, 238, 106230. https://doi.org/10.1016/j.agwat.2020.106230

Kirichenko, V. V. (2002). Methodological problems of adaptive breeding. Proceedings of International Conf. Adaptive Plant Breeding: Theory and Practice, Kharkov, 3-5. [in Russian]

Kiriziy, D. A. (2002). Photosynthesis and distribution of assimilates in the change of donor-acceptor relations in plants with the non-deterministic type of growth: Dissertation abstract. Kyiv. [in Ukrainian]

Kiriziy, D. A. (2004). Photosynthesis and growth of plants in the aspect of donor-acceptor relations. Kyiv, Logos. [in Russian]

Kiriziy, D. A. (2015). Photosynthesis and donor-acceptor relations between organs as components of the production process of wheat. Plant Physiology and Genetics. (47)5, 393-419. [in Russian]

Kliachenko, O. L, Shevchenko, I. L., (2007). Structure and sugar accumulation capacity of sugar beet roots at different planting densities. Physiology and Biochemistry of Cultural Plants, 4, 144-151. [in Russian]

Kliachenko, O. L. (2007). Structure of roots of modern sugar beet hybrids as an indicator of their sugar accumulation capacity. Bulletin of Agrarian Science, 4, 12-18. [in Ukrainian]

Kuznecov, V. V., Hydyrov, B. G., Racupkin, B.V. Borisova, N. N. (1990). General Systems of Cotton Tolerance to Salinity and High Temperature. Plant Physiology. 5, 987-991. [in Russian]

Li, Y., Liu, N., Fan, H., Su, J., Fei, C., Wang, K., ... & Kisekka, I. (2019). Effects of deficit irrigation on photosynthesis, photosynthate allocation, and water use efficiency of sugar beet. Agricultural Water Management, 223, 105701. https://doi.org/10.1016/j.agwat.2019.105701

Lutkov, A. A. (1986). Genetics of photosynthetic signs of sugar beet: Dissertation Abstract. Minsk. [in Russian]

Lv, X., Chen, S., & Wang, Y. (2019). Advances in understanding the physiological and molecular responses of sugar beet to salt stress. Frontiers in Plant Science, 10, 1431. https://doi.org/10.3389/fpls.2019.01431

Mokronosov, A. T. (1981). The ontogenetic aspect of photosynthesis. Moscow, Nauka. [in Russian]

Musienko, M. M. Parshykova, T. V., Slavnyi, P. S. (2001). Spectrophotometric methods in the practice of physiology, biochemistry and plant ecology. Kyiv, Fitosotsiotsentr. [in Ukrainian]

Okanenko, A. S. (1968). Sugar in beets. Biology and breeding of sugar beet. 327-415. [in Russian]

Pavlinova, O. A. (1981). The role of sucrose synthase in the transformation and accumulation of sucrose in sugar beet root. Modern problems of physiology and biochemistry of sugar beet. Kyiv, Naukova Dumka. [in Russian]

Pochinok, H. N. (1976). Methods for biochemical analysis of plants. Kyiv, Naukova Dumka. [in Russian]

Stasik, O. O., Kiriziy, D. A., Pryadkina, G. A. (2016). Photosynthesis and crop productivity of agricultural plants. Plant Physiology and Genetics. 48(3), 232−251. [in Russian]

Sytnik, K. M., Musatenko, L. I., Bogdanova, T. I. (1978). Physiology of leaf. Kyiv, Naukova Dumka. [in Russian]

Tooming, H. G. (1984). Ecological principles of maximum crop productivity. Leningrad, Gidrometeoizdat. [in Russian]

Zeng, Y., Chen, M., Hao, D., Damm, A., Badgley, G., Rascher, U., ... & Berry, J. A. (2022). Combining near-infrared radiance of vegetation and fluorescence spectroscopy to detect effects of abiotic changes and stresses. Remote Sensing of Environment, 270, 112856. https://doi.org/10.1016/j.rse.2021.112856

Zhu, X.-G. (2010). Improving photosynthetic efficiency for greater yield. Annu. Rev. Plant Biol. 61, 236–261.

Zhuchenko, A. A. (2008). Adaptive crop production (ecological-genetic bases): theory and practice. Moscow, Agrorus. [in Russian]

Zou, C. L., Wang, Y. B., Liu, L., Liu, D., Wu, P. R., Yang, F. F., ... & Li, C. F. (2019). Photosynthetic capacity, osmotic adjustment and antioxidant system in sugar beet (*Beta vulgaris* L.) in response to alkaline stress. Photosynthetica, 57(1), 350-360. https://doi.org/10.32615/ps.2019.010