РЕАКЦИЯ НА ФОТОСИНТЕТИЧНИЯ АПАРАТ НА КАРТОФИ (*SOLANUM TUBEROSUM* L.) КЪМ ВИСОКА ТЕМПЕРАТУРА И ЗАСУШАВАНЕ
RESPONSE OF THE PHOTOSYNTHETIC APPARATUS OF POTATO PLANTS (*SOLANUM TUBEROSUM* L.) TO HIGH TEMPERATURE AND DROUGHT

Валентина Петкова*, Емилия Начева, Елена Топалова, Галина Петрова
Valentina Petkova*, Emilia Nacheva, Elena Topalova, Galina Petrova

Институт по зеленчукови култури "Марица" - Пловдив
Maritsa Vegetable Crops Research Institute - Plovdiv

***E-mail: valpetkova@gmail.com**

Резюме

Представени са резултати от сравнителен тест за толерантността на фотосинтетичния апарат (ФСА) на два сорта и 10 селекционни линии картофи към абиотичен стрес (засушаване и висока температура). Влиянието на засушаването и високата температура върху състоянието и функционалната активност на ФСА е проучено чрез анализ на характеристиките на хлорофилната флуоресценция на фотосистема II (ФС II) и съдържанието на пластидни пигменти в листата. Растенията са подложени на стресовите фактори през репродуктивния период (фазите бутонизация – цъфтеж), които са особено критични за картофите.

Установено е, че приложеният стрес повишава началната флуоресценция (F_0) и понижава максималната (F_m) и вариабилната (F_v) флуоресценция в тъмнинно адаптирани листа, както и потенциалния добив (F_v/F_m) на ФС II. Съдържанието на пластидни пигменти е по-ниско в подложените на стрес растения. Установено е, че проучваните образци проявяват различна толерантност към стреса от засушаване и висока температура. Наблюдава се тенденция на по-висока толерантност на ФСА на линиите PC 595, E 102, E 199, следвани от E 68, D 68 и E 136. Сортовете Надежда и Санте проявяват сходна реакция към стресовите фактори. Считаме, че посочените образци са подходящи за включването им в селекционната програма за толерантност към засушаване и висока температура при картофите.

Abstract

Results are presented from a comparative test of the photosynthetic apparatus (PSA) tolerance to abiotic stress (drought and high temperature (HT) in two potato cultivars and 10 breeding lines. The influence of drought and HT on the condition and functional activity of the PSA was studied by analyses of chlorophyll fluorescence characteristics of photosystem II (PS II) and plastid pigments content in the potato leaves. Plants were subjected to stress factors during the reproductive period (bud formation - flowering phases), which is considered particularly critical for potato plants.

It was established that the applied stress increased the initial (F_0) fluorescence in dark adapted leaves and decreased the maximum (F_m) and variable (F_v) fluorescence. The quantum yield (F_v/F_m) of the PS II also decreased in stressed plants. The plastid pigments content was lower in the stressed plants. The conclusion was that the studied accessions possess different tolerance to drought and high temperature stress. The PSA efficiency of lines PC 595, E 102, E 199 revealed a trend to higher tolerance, followed by lines E 68, D 68 and E 136. The varieties *Nadejda* and *Sante* expressed a similar response to stressors. We consider them to be appropriate accessions for the potato breeding programme as far as drought and high temperature stress tolerance are concerned.

Ключови думи: картофи, селекция, абиотичен стрес, фотосинтетичен апарат, хлорофилна флуоресценция.
Key words: potato, breeding, abiotic stress, photosynthetic apparatus, chlorophyll fluorescence.

INTRODUCTION

Productivity of potato plants is very sensitive to drought and heat stress, but the extent of the impact of stressors varies in different genotypes (Vayda,1994; Bohnert et al., 1995; Steyn et al.,1998; Bray et al., 2000). The best way to solve this problem is the creating of germplasm and stress-tolerant varieties (Petkova et al., 2007; Mienie and De Ronde, 2008; Tomlekova, 2010).

The photosynthetic apparatus (PSA) has been considered as very sensitive to heat stress (Richardson et al., 2002; Nikolova et al., 2003; Petkova et al., 2003; 2009) and drought (Stoeva et al., 2010; Zlatev et al., 2010). The analysis of the chlorophyll *a* fluorescence parameters is one of the fast contemporary methods for an assessment the physiological status of the plants in different stress conditions (Berry and Björkman, 1980; Strasser et al., 2005; Berova et al., 2007; Zhang and Sharkey, 2009; Vassilev et al., 2010). Synthesis of plastid pigments is an essential factor for the photosynthetic activity of plants. Plastid pigments content in normal and stress environmental conditions has been widely studied and discussed (Mikiciuk et al., 2010; Wrobel et al., 2010; Aienl et al., 2011).

The drought and heat stress tolerance is among the priority directions of the vegetable crops breeding programmes in the "Maritsa" Vegetable Crops Research Institute (MVCRI) in the recent years. Here we present a part of our work at the potato breeding programme for searching and creating tolerant to abiotic stress varieties. The aim of this paper was to make screening for tolerance of PSA in twelve potato accessions from the mid-early group and to determine the promising ones for inclusion in the breeding programme for potatoes to create tolerant to drought and high temperature varieties.

MATERIALS AND METHODS

Experimental set-up

The experiment was carried out with 12 potato accessions from the collection of MVCRI (two varieties and 10 breeding lines) belonging to the mid-early group. The plants were grown in a greenhouse at day temperature of 23-25°C in plastic 5 l pots containing commercial soil-peat substrate with the plant density of two plants per pot.

Plants were subjected to stress influence during the reproductive period (bud formation - flowering phases), which is considered particularly critical for potatoes to environmental factors. Drought was imposed by withholding water for 8-10 days (45% of full soil humidity). The soil moisture was defined by weight-thermostatic method. Whole plants were exposed to HT - 40°C for 2 hours in thermostat. The untreated irrigated plants (70-75% of full soil humidity) were used as controls.

Chlorophyll fluorescence measurements and plastid pigments analysis

The PSA activity was characterized by analysis of the chlorophyll fluorescence parameters, measured by a fluorometer Plant Efficiency Analyser (PEA MK2, Hansatech Ltd, UK). The fluorescence characteristics were registered three times during bud formation-flowering period, minimum in 10 replicas, on the upper surface of intact, fully developed leaves. They were illuminated with actinic light (>650 nm), provided by an array of 6 light-emitting diodes (LED), focused on a leaf area of 4 mm diameter to produce homogeneous illumination with photon flux density (PFD) of 3000 μmol m^{-2} s^{-1}. The initial fluorescence (F_0), maximum (F_m) and variable (F_v) fluorescence were measured in 30-min dark adapted leaves, as well as the ratio F_v/F_m, indicating the potential PSII efficiency in the photochemical reactions.

The content of photosynthetic pigments (chlorophyll *a*, chlorophyll *b* and carotenoids) was defined in three replications in fresh leaf tissue through extraction in 80% acetone. Optical density of the extracts was measured spectrophotometrically, using spectrophotometer PHARO 300.

The data were statistically processed using MS Excel software.

RESULTS AND DISCUSSION

The chlorophyll *a* fluorescence parameters of the studied accessions in normal and stress conditions are presented in Table 1. They are shown also as a percentage of variation compared to the controls (in parentheses). The data show that all parameters were affected by applied stress.

The initial fluorescence (F_0) describes the loss of the excitation energy during its transfer from the pigment bed to reaction centre (RC) of PS II. It is reached immediately after illumination of the dark-adapted leaves. In these conditions most of the RCs of PS II are opened and the first acceptor of the electrons Qa is completely oxidized. The data obtained show that F_0 increased under stress influence in all potato accessions. The extent of the increase varied in broad limits. Smallest change in F_0 was measured in line E 68 and E 199 (107% and 110% compared to the control plants, respectively). The lines E 136 and E 766 showed significant sensitiveness to this paraneter - 172-174% compared to the control. The values of the variable fluorescence (F_v) were significantly decreased in all stressed accessions except line E 102, which did not change. The variety Sante and line PC 595 revealed also slight decrease of this parameter (96% and 90% to the control plants, respectively). In the maximum fluorescence (F_m), as well as in F_0, was established a trend to decrease the values under stress influence excluding plants from line E 102 and variety Sante.

The ratio variable/maximum fluorescence (F_v/F_m) is a parameter characterizing the potential PS II efficiency in the photochemical reactions. It is established that in healthy leaves the values of this ratio varied in the range of 0.75-0.85 (Bolhar-Nordenkampf and Oquist, 1993). Our data show that among the studied genotypes, the ratio F_v/F_m was very slightly reduced under applied stress in line E 102 (3%). Lines E 199, E 68, PC 595, as well as varieties Sante and Nadejda also showed a slight reduction of the PS II efficiency (<10% to the controls). In contrast, in line E 766 the value of the ratio F_v/F_m was below the physiological norm (0,610, or only just 74% compared with the control).

Significant decrease in the F_v/F_m ratio (20-21%) was registrated also in the stressed plants of lines E 28, E 136 and E 147. The values of F_v/F_m in these accessions (below 0,700) were indicative of serious disturbances in PS II (Table 1). Ogren (1990) has pointed out that a reduction in photosynthetic efficiency may play a role in yield loss during water stress as it influences carbon assimilation. The research work carried out by Havaux (1993) established that critical value of temperature at which irreversible damage of photosystem II in potato occurs at about 38°C. The acclimated at 30 to 35°C plants, however, retained high level of the activity of photosystem II even at 40°C.

Among the cell organelles, chloroplasts are the most sensitive to stress conditions. The concentration of photosynthetic pigments is one of the indicators of stress in various stress influences. Chlorophyll *a* serves a dual role in oxygenic photosynthesis: in light harvesting as well as in converting energy of absorbed photons to chemical energy (Björn et al., 2009). The obtained data about chlorophyll *a* content showed that due to the applied stress it decreased in all studied accessions, but there were differences between the genotypes in the rate of the reduction (Table 2). The concentration of chlorophyll *a* content varied between 1,663 mg g^{-1} fw in line E 199 and 1,075 mg g^{-1} fw in line E 28. The reduction was less pronounced in E 102, E 68, E 199 and PC 595. The chlorophyll *a* content in these accessions declined under stress influence and was lower with 8 to 13% in comparison with the control plants. The decrease was most pronounced in line E 28 (25 % below the control), which is indicative for disorders in photosynthetic apparatus. A trend to conformity between the changes in the chlorophyll *a* content and the efficiency of PS II of the stressed plants was observed.

In our experiment, chlorophyll *b* concentration decreased in all accessions subjected to drought and high temperature influence (Table 2). Chlorophyll *b* significantly decreased by stress environments in variety Sante and lines E 147, E 154 and E 102 (about 20% below controls) while in D 68 and E 28 the effect of applied stress was smaller. Reduction rate of the chlorophyll *b* content was highest in lines E 68 and PC 595 (72% and 76% to the controls, respectively).

The changes in the total chlorophyll content *(a+b)* are in conformity with these in the chlorophyll *a* content (Table 2). Data show that as a result of the applied stressors the chlorophylls *(a+b)* decreased in all accessions. Among the studied genotypes, magnitude of the reduction varied between 90 and 78,6% compared with the unstressed plants. The rate of reduction of total chlorophyll content was similar in lines E 102, E 199 and D 68, which retained 88-90% of the content in control plants. The lowest value of chlorophyll *(a+b)* and the most pronounced decrease in comparison with control was measured in E 68. According to Herbinger et al. (2002) a decrease of total chlorophyll with drought stress implies a lowered capacity for light harvesting. Since the production of reactive oxygen species is mainly driven by excess energy absorption in the photosynthetic reactions, this might be avoided by degrading the absorbing pigments.

Effect of applied stress on carotenoids content was observed in all accessions but there were significant genotypic differences (Table 2). In our experiment, carotenoids concentration under stress conditions decreased slightly in E 147, E 154, E 68, D 68 and PC 595 (< 5%), while in E 136 the reduction was biggest (23% below control).

The chlorophyll *a/b* ratio is wide used as indicator for early senescence. Our results show divergent changes in the chlorophyll *a/b* ratio. In the majority of the samples it was lower compared to the control but in five genotypes it was higher. According to Mafakheri et al. (2010) the lack of effects on the chlorophyll *a/b* ratio in drought-stressed plants indicates that chlorophyll *b* is not more sensitive to drought than chlorophyll *a*. The ratio between chlorophylls and carotenoids is sensitive indicator for distinguishing the timely natural aging from aging caused by environmental stress factors. In our experiment it decreased in stressed plants in all accessions except lines E 136, E 766 and variety Nadejda.

The obtained data are in agreement with the publications of many researchers that stress factors cause disturbances in the biosynthesis of photosynthetic pigments with subsequent reduction of their content. The reduction however varied broadly, depending on many factors, such as plant species and phenological phase of the plants, type, strength and impact of the stressors, etc. (Kpyoarissis et al., 1995). A reduce in chlorophyll content, chlorophyll *a/b* ratio and chlorophyll/carotenoid ratio in various Solanum species subjected to heat stress has been reported by Reynolds et al. (1990). Drought and heat stress has been reported to reduce chlorophyll content, chlorophyll *a/b* ratio and chlorophyll/carotenoids ratio in various plant species (Langjun et al., 2006; Stoeva et al., 2010). Alienl et al. (2011) has reported that total chlorophyll and carotenoids decreased but chlorophyll *a/b* ratio increased in potato plants subjected to high temperature environments.

CONCLUSION

Alterations in chlorophyll fluorescence parameters and photosynthetic pigments content in drought and HT stress conditions are appropriate indicators for screening for thermotolerance in potato genotypes.

Drought and HT stress imposed during reproductive period (phases bud formation - flowering) decreased the photosynthetic activity of the potato plants, expressed by changes in the chlorophyll fluorescence parameters and plastid pigments content. Genotypic differences in response to the stress factors was revealed. The PSA efficiency of lines PC 595, E 102, E 199 showed a trend to higher tolerance, followed by lines E 68, D 68 and E 136. Both varieties (Nadejda and Sante) expressed

Таблица 1. Параметри на хлорофилната флуоресценция в тъмнинно адаптирани листа от картофи на контролни и подложени на абиотичен стрес (засушаване и висока температура) селекционни образци. Данните са осреднени от 15 измервания ± стандартно отклонение. В скобите - процент спрямо контролата
Table 1. Chlorophyll fluorescence parameters of dark adapted potato leaves in control and imposed to abiotic stress (drought ant high temperature) breeding accessions. Values represent the means of 15 measurements ± standard deviation. In parentheses - per cent to control

Accessions/ Variants Образци/Варианти	Fluorescence parameters ($\bar{x}$ ± sd)			
	F_0	Fm	Fv	Fv/Fm
Variety Sante				
Control	334±5,00	1709±34,7	1375±37,0	0,804±0,016
Drought+HT	457±12,82 (137)	1781±139,7 (104)	1324±118,3 (96)	0,742±0,021 (92)
Variety Nadejda				
Control	312±25,01	1694±61,53	1382±53,4	0,815±0,013
Drought+HT	445±91,31 (142)	1669±148,28 (98)	1224±166,4 (89)	0,732±0,026 (90)
Line D 68				
Control	310±22,8	1855±170,94	1544±123,4	0,831±0,029
Drought+HT	380±63,2 (122)	1489±156,06 (80)	1109±121,7 (72)	0,744±0,020 (90)
Line E 28				
Control	327±20,8	1974±95,1	1647±104,3	0,835±0,001
Drought+HT	558±71,7 (171)	1658±86,4 (84)	1101±106,3 (67)	0,664±0,031 (80)
Line E 68				
Control	331±13,4	1625±55,37	1295±62,6	0,796±0,013
Drought+HT	354 ±77,4 (107)	1462±74,2 (90)	1108±122,5 (85)	0,758±0,028 (95)
Line E 102				
Control	329±27,5	1599±78,2	1270±56,1	0,794±0,010
Drought+HT	375±28,4 (114)	1650±106,4 (103)	1275±120,5 (100)	0,770±0,027 (97)
Line E 136				
Control	307±9,8	1777±20,5	1470±28,58	0,827±0,007
Drought+HT	534±30,3 (174)	1631±60,3 (92)	1096±72,3 (75)	0,672±0,025 (81)
Line E 147				
Control	335±23,3	1801±101,38	1466±98,2	0,814±0,001
Drought+HT	522±92,7 (156)	1558±65,9 (86)	1036±113,4 (71)	0,663±0,025 (81)
Line E 154				
Control	305±7,09	2015±78,8	1709±123,0	0,847±0,014
Drought+HT	443±36,7 (145)	1633±105,4 (81)	1190±115,3 (70)	0,729±0,011 (86)
Line E 199				
Control	363±37,4	1870±96,5	1507±107,9	0,806±0,009
Drought+HT	401±9,2 (110)	1687±56,4 (90)	1286±51,3 (85)	0,762±0,017 (95)
Line E 766				
Control	323±13,3	1813±57,2	1490±43,9	0,822±0,002
Drought+HT	556±3,9 (172)	1422±43,3 (78)	866±94,3 (58)	0,610±0,045 (74)
Line PC 595				
Control	336±4,36	1888±48,9	1552±45,4	0,822±0,003
Drought+HT	400±61,21 (119)	1798±137,7 (95)	1398±113,31 (90)	0,772±0,046 (94)

Таблица 2. Съдържание на пластидни пигменти (mg g^{-1} свежо тегло) в листа от картофи при контролни и засушени селекционни образци. В скобите - процент спрямо контролата

Table 2. Plastid pigments content (mg g^{-1} fresh weight) in potato leaves of control and stressed breeding accessions. In parentheses - per cent to control

Accessions/ Variants Образци/Варианти	Chl *a*	Chl *b*	Chl *a*+ Chl *b*	Carotenoids	Chl *a* / Chl *b*	Chl (*a*+*b*) /Carotenoids
Variety Sante						
Control	1,78	0,47	2,25	0,54	3,79	4,16
Drought+HT	1,49 (84)	0,38 (81)	1,87 (83)	0,48 (88,8)	3,92	3,89
Variety Nadejda						
Control	1,81	0,45	2,26	0,58	4,02	3,90
Drought+HT	1,52 (84)	0,38 (84)	1,90(84)	0,47 (82)	4,00	4,04
Line D 68						
Control	1,91	0,40	2,31	0,52	4,77	4,44
Drought+HT	1,66 (87)	0,37(92.5)	2,03 (88)	0,50 (96)	4,48	4.06
Line E 28						
Control	1,43	0,35	1,78	0,44	4,08	4,04
Drought+HT	1,08 (75)	0,32 (91)	1,40(78.6)	0,42 (95)	3,37	3,33
Line E 68						
Control	1,65	0,42	2,07	0,47	3,93	4,40
Drought+HT	1,43 (87)	0,32 (76)	1,75 (85)	0,45 (96)	4,46	3,89
Line E 102						
Control	1,91	0,49	2,40	0,58	3,89	4,14
Drought+HT	1,76 (92)	0,40 (82)	2,16 (90)	0,53 (91,4)	4,40	4,07
Line E 136						
Control	1,52	0,36	1,88	0,49	4,22	3,84
Drought+HT	1,23 (81)	0,32 (89)	1,55 (82)	0,38 (77)	3,84	4,08
Line E 147						
Control	1,63	0,43	2,06	0,46	3,79	4,47
Drought+HT	1,40 (86)	0,33 (77)	1,73 (84)	0,45 (98)	4.24	3,84
Line E 154						
Control	1,86	0,45	2,31	0,52	4,18	4,45
Drought+HT	1,49 (80)	0,36 (80)	1,85 (80)	0,51 (98)	3,75	3,27
Line E 199						
Control	1,51	0,34	1,85	0,47	4,44	3,93
Drought+HT	1,32 (**87**)	0,30 (89)	1,62 (88)	0,38 (81)	4,40	4,26
Line E 766						
Control	1,67	0,40	2,07	0,52	4,18	3.98
Drought+HT	1,41 (84)	0,34 (85)	1,75 (84)	0,42 (81)	4.14	4.17
Line PC 595						
Control	1,87	0,51	2,38	0,52	3,67	4,57
Drought stressed	1,62 (87)	0,37 (72)	1.99 (84)	0,50 (96)	4.37	3,98

a similar response to stressors. We consider that the pointed accessions are appropriate for the potato breeding programme to drought and high temperature stress tolerance.

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Рецензент – доц. д-р Малгожата Берова
E-mail: maberova@abv.bg