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The response of two potato cultivars on combined effects of selenium and drought

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ABSTRACT

The combined effect of selenium (Se) foliar spraying and drought was studied for 3 months in two cultivars of potato; Bard and Adora in Ljubljana, Slovenia. Four combinations of treatments were conducted: well-watered plants with and without Se foliar spraying, and drought exposed plants with and without Se foliar spraying. Net photosynthesis, transpiration rate, quantum yield of photosystem II (PSII), and respiration potential measured by electron transport system activity were monitored throughout the period. After three months of treatment, leaf water potential, the number and size of leaf stomata, and tuber yield were determined. Several impacts of drought and Se application and their combinations were established, and the responses shown to be cultivar-specific. Net photosynthesis, transpiration rate, effective quantum yield of PSII, and respiratory potential were lower in drought exposed plants. Se lowered respiratory potential in the leaves in cv. Bard. The mass of the tubers in cv. Adora, and photosynthesis in cvs. Bard and Adora were lower in Se treated plants. Se treatment did not significantly affect the number and size of leaf stomata in the cultivars.

Key words chlorophyll fluorescence, drought, photosynthesis, respiratory potential, selenium, yield

IZVLEČEK

VPLIV SELENA IN SUŠE NA DVA KULTIVARJA KROMPIRJA

Kombiniran vpliv selena (Se) in suše na dva kultivarja krompirja Bard in Adora, smo preučevali v poskusu, ki je trajal tri mesece. Rastline so bile izpostavljene štirim kombinacijam obravnavanja: zalite rastline z ali brez foliarnega gnojenja s Se in suši izpostavljene rastline z ali brez foliarnega gnojenja s Se. V rastni sezoni smo spremljali neto fotosintezo, transpiracijo, fotokemično učinkovitost fotosistema II (FSII) in respiratorni potencial, merjen s pomočjo meritev aktivnosti terminalnega elektronskega transporta. Po treh mesecih, ko so bile rastline izpostavljene vsem obravnavam, smo izmerili še vodni potencial v listih, število in dimenzije listnih rež in pridelek gomoljev. Preučevana kultivarja sta se na učinke suše in dodanega Se odzvala na različne načine. Neto fotosinteza, transpiracija, fotokemična učinkovitost fotosistema II (FSII) in respiratorni potencial so bili nižji pri rastlinah, ki so bile izpostavljene suši. Rastline, foliarno gnojene s Se so imele nižji respiratorni potencial pri kultivarju Bard.

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Masa gomoljev pri kultivarju Adora in fotosinteza pri obeh kultivarjih sta bili nižji pri rastlinah, kjer smo dodali Se. Dodatek Se ni bistveno vplival na število in dimenzije listnih rež pri preučevanih kultivarjih.

Ključne besede: fotosinteza, klorofilna fluorescenca, pridelek, respiratorni potencial, selen, suša

Abbreviations: cv. - cultivar; cvs. - cultivars; ETS - electron transport system; F - the steady state fluorescence; F_o - minimal chlorophyll *a* fluorescence yield in dark adapted samples; F_m - maximal chlorophyll *a* fluorescence yield in dark adapted samples; F_m' - the maximal fluorescence of an illuminated sample; F_v - variable fluorescence; INT - iodo-nitro-tetrazolium-chloride; PPFD - photosynthetic photon flux density; PSII - photosystem II.

1 INTRODUCTION

In natural environment plants are subjected to many stresses that can have negative effect on growth, metabolism, and yield. Biotic (insects, bacteria, fungi, and viruses) and abiotic (light, temperature, water availability, nutrients, and soil structure) factors affect the growth of higher plants. Among these, drought is a major abiotic factor that limits agricultural crop production (Reddy et al., 2004). Global warming, which causes fluctuations of precipitation distribution, could increase the risk of plants being exposed repeatedly to drought (Miyashita et al., 2005). The frequency of water limitation stress is likely to increase in the future, even outside today's arid/semi-arid regions (Chaves et al., 2002). Stress caused by drought does not occur abruptly, but develops slowly and increases in intensity by the time of duration in contrast to majority of other stress factors (Larcher, 2003). The ability of plants to cope with water stress varies among species and even cultivars. Photosynthesis, which is one of the primary metabolic processes determining crop production, is directly affected by drought (Pieters and El Souki, 2005). Water limitation mainly limits photosynthesis through stomatal closure and through metabolic impairment (Tezara et al., 1999; Lawson et al., 2003). Lower photosynthetic activity includes decreased photochemical efficiency of PSII, as shown by its lower quantum yield (Pieters and El Souki, 2005). Under severe water stress, photodamage of PSII will result with the possible net loss of D1 protein of PSII reaction centres (Baker, 1993; Cornic, 1994). When CO₂ assimilation decreases electron transport to oxygen via photorespiration, Mehler reaction and dark respiration remove excitation energy (Lawlor and Cornic, 2002). Inhibition of ATP synthesis in chloroplasts might be more sensitive to low water content than in mitochondria. Information about respiratory potential, measured by terminal electron transport system (ETS) activity in mitochondria, enables the general metabolic activity of individual organisms to be estimated. Drought stress can also affect the growth of plant organs, resulting in alteration of the morphological features of the plants (French and Turner, 1991). Selenium (Se) is an essential trace element for animals and humans (Tapiero and al., 2003) but its role in plants is still unclear (Hartikainen et al., 2000). It plays a role in the prevention of

atherosclerosis, specific cancers, arthritis, and altered immunological functions. Se deficiency in animals and humans can lead to heart disease, hypothyroidism and a weakened immune system (Tinggi, 2002). Slovenia is a country with low amounts of Se in the soil (Kreft et al., 2002). Most cereal crops and fodder plants are relatively weakly able to absorb Se, even when grown on soils with higher Se content (Nowak et al., 2004). Se is chemically similar to sulphur, this may cause a non-specific replacement of S by Se in proteins and other sulphur compounds (Nowak et al., 2004). There are indications that it can also play a positive biological role in higher plants (Hartikainen et al., 2000; Germ et al., 2005). Se can increase the tolerance of plants to UV-radiation induced oxidative stress, delay senescence, and promote the growth of ageing seedlings (Xue and Hartikainen, 2000; Xue et al., 2001). Results of Pennanen et al. (2002) have indicated that plant growth promoted by Se is due to the increased starch accumulation in chloroplasts. The positive effects of Se on the recovery of potato from photooxidative and paraquat-generated oxidative stress point to mechanisms that, although they are not yet known, protect chloroplasts during stress (Seppänen et al., 2003). Recently it has been shown that Se can regulate the water status of plants under conditions of water deficiency and thereby performs its protective effect (Kuznetsov et al., 2003). The goal of this work was to determine the response of two cultivars of potato grown outdoors to combined effect of drought and Se.

2 MATERIALS AND METHODS

Plant Material and Growth Conditions

Potato plants (*Solanum tuberosum* L.) cvs. Bard and Adora (recently among the most cultivated potato cvs. in Slovenia), were planted on April 20, 2005, in plastic pots, inner volume 18x18x18 cm, in a mixture of soil (95%) and crushed peat (5%), one plant per pot, five pots per cv. and per treatment on the experimental field of the Biotechnical Faculty, University of Ljubljana (320 m above sea level, 46°35'N, 14°55'E), Slovenia. Soil, peat and irrigation water contained no detectable Se (i.e. soil and peat less than 0.1 mg Se kg⁻¹, water less than 0.5 µg L⁻¹). Plants were daily (at 19.00 h) watered with an amount of water corresponding to 4 Lm⁻² rainfall (well-watered plants) or 1.5 Lm⁻² (drought exposed plants).

Treatments

Cv. Adora emerged on May 11 and Bard on May 13. On June 20, 2005 plants were sprayed foliarly with a solution of detergent (Triton T-100, Sigma, 0.2 ml L⁻¹) with or without Se (10 mg Se L⁻¹ in the form of sodium selenate). Plants were subjected to one of four treatments: (i) drought exposed without added Se (Se0W0), (ii) well-watered without added Se (Se0W1), (iii) drought exposed with added Se (Se1W0), (iv) well-watered with added Se (Se1W1). Starting values of physiological parameters (net photosynthesis, transpiration rate, quantum yield of PSII, and respiration potential measured by electron transport system activity) were measured just prior to treatment (June 20) and are presented in Table 1. All mentioned parameters were measured two weeks after the start of treatments - a second measurement (II) and four weeks after the start of treatments - a third measurement (III). Leaf water potential, number and dimensions of leaf stomata, and number and mass of the tubers were determined at the end of the growth period on July 30.

Light-saturated Net Photosynthesis and Transpiration Rate

Light-saturated net photosynthesis and transpiration rate were measured with a portable infrared gas analyser (LI-6200, LI-COR, Lincoln, NE, USA) and a porometer (LI-1600, LI-COR, Lincoln, NE, USA) respectively.

Chlorophyll Fluorescence

Fluorescence measurement as a non-intrusive method, allows the rapid assessment of quantum yield of electron flow through photosystem (PS) II. The method has been widely used for detecting water stress in plants (Reddy et al., 2004). Measurements were carried out with a portable fluorometer (OS-500, Opti-Sciences, Tyngsboro, MA, USA). Potential quantum yield of PSII ($F_v/F_m = F_m - F_o / F_m$) quantifies the maximum efficiency of the primary photochemical events in photosynthesis. It is an important parameter of the physiological state of the photosynthetic apparatus. F_o and F_m are the minimal and maximal chlorophyll *a* fluorescence yields in dark adapted samples, and F_v is the variable fluorescence. Fluorescence was excited with a saturating beam of "white light" (PPFD = 8 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 0.8 s). F_v/F_m ranged from 0.8 to 0.83 for a variety of dark-adapted plants (Björkman and Demmig-Adams, 1995). The effective quantum yield of PSII was measured under saturating irradiance by providing a saturating pulse of "white light" (PPFD = 9 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 0.8 s), using a standard 60° angle clip. The effective quantum yield of PSII ($F_m' - F / F_m'$) = $\Delta F / F_m'$ gives the actual efficiency of energy conversion in PSII (Björkman and Demmig-Adams, 1995). F_m' is the maximum fluorescence signal of an illuminated leaf after a pulse of saturating light (Pieters and El Souki, 2005) and F is the steady state fluorescence (Schreiber et al., 1995).

All gas exchange and fluorescence measurements were made each day between 11.00 h and 15.00 h (local time) (PPFD $\geq 1\ 100 \mu\text{mol m}^{-2} \text{s}^{-1}$) at ambient temperature and CO_2 concentration throughout the drought cycle.

Respiratory Potential

Respiratory potential was measured as electron transport system (ETS) activity of mitochondria, as described by Packard (1971) and modified by Kenner and Ahmed (1975). Leaves of known fresh weight were crushed in a mortar in chilled 0.1 M sodium phosphate buffer (pH = 8.4) containing 0.15% (w/v) polyvinyl pyrrolidone, 75 μM MgSO_4 , and 0.2% (v/v) Triton-X-100, and homogenized by ultrasound (40W, 4710; Cole-Parmer, Vernon Hills, IL, USA). The extract was centrifuged at 8500 x *g* for 4 minutes at 0 °C in a top refrigerated ultracentrifuge (2K15, Sigma, Osterode, Germany). Then 0.5 cm^3 of the supernatant was mixed with the 1.5 cm^3 substrate solution (0.1 M sodium phosphate buffer (pH = 8.4), 1.7 mM NADH, 0.25 mM NADPH, 0.2% (v/v) Triton-X-100), and 0.5 cm^3 INT (20 mg 2-p-iodo-phenyl 3-p-nitrophenyl 5-phenyl tetrazolium chloride in 10 ml of bidistilled water). The mixture was incubated at 20 °C for 40 min. ETS activity was measured as the rate of INT reduction, which was converted to the amount of oxygen utilised per dry matter (DM) of leaves per time, as described by Kenner and Ahmed (1975).

Leaf Water Potential

Leaf water potential was measured using a pressure chamber (PMS Instrument Co., Corvallis, Oregon, USA).

Anatomical and Yield Analyses

The number and dimensions of leaf stomata were counted and measured by Soft Imaging System, GmbH, analySIS 3.0, Münster, Germany. The software used for analysis was Soft Imaging System GmbH analySIS.

Tubers were separated from the plants, counted, washed and weighed. They were then sliced, oven-dried at 90 °C for 72 h and re-weighed.

All measurements and analyses were made on the first, fully developed leaf.

Statistical Analyses

Two-Factor ANOVA was used to test the effect of drought, Se and their interaction on parameters. Differences at the different levels of probability were accepted as significant; n.s. – non significant $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

3 RESULTS

The effects of drought and Se and their interaction were studied on two cvs. of potato. Physiological parameters were measured before drought and Se treatments (starting values) and two (second measurement) and four weeks (third measurement) after treatments. Some anatomical parameters and yield were measured at the end of the experiment. Phenotypically, cv. Bard looked the most vital at the time of the experiment.

Effects of Drought

The ratio of fresh/dry mass and leaf water potential of leaves were lower in drought exposed plants in cv. Bard (Table 2). Photosynthetic activity was the lowest in cultivar Adora in the start and third measurements (Table 1, Fig. 1). The negative effect of drought on photosynthetic activity was significant in the third measurement in both studied cultivars (Fig. 1, Table 3). Values of transpiration rate were lower in the second than the third measurement in both studied cultivars (Fig. 1). Transpiration rate was significantly higher in well-watered plants than drought exposed plants, except in cv. Adora in the second measurement (Fig. 1, Table 3). Values of potential (F_v/F_m) and effective ($\Delta F/F_m'$) quantum yields of PSII were lowest for cv. Adora in all three measurements, except $\Delta F/F_m'$ in the second measurement (Table 1, Fig. 2). F_v/F_m was unaffected by water stress throughout, except in the third measurement in cultivar Bard, where F_v/F_m was lower in drought exposed plants. Values of $\Delta F/F_m'$ were lowest in the drought exposed specimens in the third measurement for both cultivars and for cv. Bard in the second measurement (Fig. 2, Table 3). Plants exposed to drought conditions exhibited statistically significant lower ETS activity than well-watered plants in the third measurement in both cultivars and in cv. Adora in the second measurement (Fig. 3, Table 3). Drought did not affect the number of stomata in cvs. Bard and Adora, or the length of stomata in the latter (Table 4). The number of tubers was lowest in cv. Adora (except in Se0W0 treatment), which corresponded to the lowest efficiency of PSII and photosynthetic rate. Tuber mass was highest in cv. Bard except under Se0W0 treatment (Table 5).

Effects of Se

The ratio of fresh/dry mass of the leaves in cv. Bard was higher in Se treated plants (Table 2). Leaf water potential in cvs. Bard and Adora was higher in the presence of Se (Table 2). Se lowered transpiration rate in the third measurement in cv. Adora. In contrast, cv. Bard had a higher transpiration rate in Se sprayed plants in the third measurement (Fig. 1, Table 3). Se lowered ETS activity in cv. Bard in the third measurement (Fig. 3, Table 3). Se did not affect the number of stomata in cvs.

Bard and Adora, or the length of stomata in the latter (Table 4). The presence of Se resulted in a decrease in the mass of tubers in well-watered and drought exposed cv. Adora (Table 5).

Effects of Drought in Combination with Se

Se lowered photosynthetic activity in drought exposed plants and had no effect on well-watered plants in the third measurement in cv. Bard, while it did not affect photosynthetic activity in drought exposed plants and lowered it in well-watered plants in the third measurement in cv. Adora (Fig. 1, Table 3). Drought caused lower transpiration rate in the presence of Se in cv. Bard in the third measurement, but not in its absence (Fig. 1, Table 3). $\Delta F/F_m'$ was lower in drought exposed plants in cv. Adora in the third measurement in the presence of Se only. Differences between well-watered and drought exposed plants was small in the absence of Se (Fig. 2, Table 3). The differences in ETS activity between drought exposed and well watered plants were greater in the absence of Se in cv. Bard in the third measurement (Fig. 3, Table 3). The length of the stomata was greater in drought exposed plants in the absence of Se, while the stomata were of similar lengths in the presence of Se in drought exposed and well-watered plants in cv. Bard (Table 4). Se led to an increase in mass of the tubers in plants exposed to water deprivation in cv. Bard and a reduction in mass of tubers in well-watered plants (Table 5).

4 DISCUSSION

The exposure of plants to progressive drought caused disruption of physiological function. The growth of plants of cv. Bard during the vegetative season under water deficiency was accompanied by a significant decrease of ~10% in the water content of leaf tissue, and also by lower leaf water potential of the leaves (Table 2). Interestingly, the ratio of fresh/dry mass and leaf water potential of the leaves in cv. Bard were higher in Se treated plants (Table 2). Under conditions of drought, Se causes enhanced water retention in wheat tissue (Kuznetsov et al., 2003). The latter was achieved by increasing the water uptake capacity of the root system. These results indicate an important role for Se in plants exposed to deprivation of water. Photosynthetic rate was lowest in plants exposed to a limited supply of water in the third measurement (Fig. 1, Table 3). The foliar photosynthesis rate of higher plants is known to decrease as the leaf water potential decreases (Lawlor and Cornic, 2002). However, in drought exposed kidney bean, photosynthesis decreased because stomata were closed before leaf water potential dropped (Miyashita et al., 2005). The addition of high doses of Se to soil (1 mg kg^{-1}) had a harmful effect on photosynthetic processes in strawberry, through changes in activity and/or biosynthesis of enzymes, rather than changes in PSII (Valkama et al., 2003). Lower photosynthetic activity caused by Se in cvs. Bard and Adora in the third measurement are in agreement with these findings (Fig. 1, Table 3). However, the lowering of photosynthetic activity caused by Se in drought exposed plants of cv. Bard, and the similar effect, but on watered plants, in cv. Adora, indicate that the responses to drought and to Se are cultivar-specific. It is expected that under stress conditions photosynthetic processes in different genotypes may be affected differently (Cai et al., 2005; Sharma et al., 2005). Drought caused strong stomatal

limitation in both studied cultivars in the third and in cv. Bard also in the second measurement (Fig. 1, Table 3). It has been shown to cause loss of transpiration in *Allium schoenoprasum* (Egert and Tevini, 2002) and lowered stomatal conductance in potato plants (Kawakami et al., 2005). With the continuation of drought stress, the stomata gradually lose their ability to close and finally remain permanently open (McKersie and Leshem, 1994). Rigidity of the stomata could therefore be the reason for the highest transpiration rate in the third measurement in cvs. Bard and Adora in the present experiment (Fig. 1). Lower transpiration rate and leaf water potential in cv. Bard accompanied the decrease in photosynthesis, indicating that stomatal closure as well as leaf water potential appear to be an important factor contributing to the reduced CO₂ assimilation that has been reported (Reddy et al., 2004; Miyashita et al., 2005). The most sensitive changes resulting from water deprivation relate to rubisco metabolism, although the details of the mechanism are not known. Se lowered transpiration rate in the third measurement in cv. Adora (Fig. 1, Table 3). In contrast, Kuznetsov et al. (2003) found, in wheat, that under conditions of water limitation Se did not inhibit, but slightly increased transpiration rate. Cv. Bard behaved similarly: it exhibited a higher transpiration rate in Se treated plants in the third measurement. Se also caused higher leaf water potential and fresh/dry mass ratio in the leaves of cv. Bard (Table 2), that could enable higher transpiration rate. Cv. Adora exhibited the lower potential (F_v/F_m) and effective ($\Delta F/F_m'$) quantum yield of PSII as well as photosynthetic rate comparing to cv. Bard (Figs. 1,2, Table 3). Thus, cv. Adora is not a desirable cultivar for growing in an area that has experienced limitation of water, especially in recent years. However, it should be noted that our plants were growing in pots. Therefore, some physical as well as chemical components and biological interactions that occur in the fields might be not present. Plants of both cultivars exhibited the lowest photosynthesis rate during drought conditions, while F_v/F_m was maintained mainly on the same level (Figs. 1,2). The similar results were obtained in potato cv. Desiree by Germ et al. (2007). The relative maintenance of F_v/F_m values throughout the experiment demonstrated that drought did not cause damage to the flow of electrons in PSII, as previously reported for potato (Tourneux and Peltier, 1995), kidney bean (Miyashita et al., 2005), sunflower (Panković et al., 1999; Germ et al., 2005) and some other species (Jiménez et al., 1999; Chaves et al., 2002). It was concluded (Cornic and Briantias, 1991) on the basis of chlorophyll *a* fluorescence, that the potential rate of electron transport in thylakoids was maintained, even at low relative water content. Present research supports the idea that photodamage to PSII reaction centres is not the main factor in the depression of CO₂ assimilation of the leaves induced by water stress. However, the large decreases in F_v/F_m observed in lavender and rosemary leaves exposed to drought indicates that either PSII reaction centres had been damaged, or slowly relaxing quenching had been induced (Nogues and Baker, 2000). Values of $\Delta F/F_m'$ were lowest in drought exposed specimens (Fig. 2, Table 3). Down regulation of PSII activity due to drought stress, causing an imbalance between generation and utilization of electrons, apparently results in changes in quantum yield (Foyer and Noctor, 2000; Reddy et al., 2004). Even though $\Delta F/F_m'$ was lowest in the drought exposed plants, the relative closeness of the potential photochemical quantum yield to the theoretical maximum (0.8-0.83) (Fig. 2) indicated reversible inactivation, rather than damage to the reaction centre.

Se treatment did not affect the potential and effective quantum yield of PSII (Fig. 2, Table 3). The impact of Se on potential quantum yield of PSII was also absent in the study in common buckwheat (Breznik et al., 2005).

Packard (1985) stated that when organisms are stressed and demand more energy, ATP production and O₂ consumption in the mitochondria are increased. However, water limitation was found to lower ETS activity in the potato plants (Fig. 3, Table 3). Similarly, when the relative content of water was reduced from 100 to 80%, again in potato, O₂ uptake increased, then remained relatively constant at ca. 60%, until it finally fell in parallel with O₂ evolution (Tourneux and Peltier, 1995). We assumed that the damage caused by drought was sufficiently strong that plants could not overcome the stress, leading to lower respiratory potential. Mitochondrial structure has been reported to be affected by water deficit (Giles et al., 1976). Pb led to lower respiratory potential in the roots of *Picea abies* (L.) Karst. (Vodnik et al., 1999). Unfavourable conditions for growth also lowered ETS activity in *Phragmites australis* (Cav.) Trin. ex Steud. (Urbanc-Berčič and Gaberščik, 2001). Se did not affect ETS activity in cv. Adora (Fig. 3, Table 3), pumpkins and common and tartary buckwheat (Germ et al., 2005; Breznik et al., 2005), in keeping with the results of Seppänen et al. (2003), in which Se application on potato did not suppress or promote mitochondrial reactions. ETS activity was reduced by Se in cv. Bard in the third measurement (Fig. 3, Table 3). Valkama et al. (2003) reported a decreased density of mitochondria in barley in response to Se, that could be attributed to alteration of mitochondrial division. The latter might also be the reason for Se induced lower respiratory potential in cv. Bard.

The mass of tubers was the highest (except under Se0W0 treatment) in cv. Bard, largely the consequence of high canopy expansion and light interception (Table 5). Se lowered the mass of the tubers in watered and drought exposed plants in cv. Adora and in watered plants of cv. Bard. It appears that, in cv. Adora, which expressed the lowest quantum yield of PSII and photosynthetic rate, Se treatment itself could be a stress factor that resulted in lower tuber biomass.

5 CONCLUSIONS

Of the two potato cultivars cv. Adora showed the lower level of adaptation to growth conditions and least ability to cope with drought stress. The findings should be taken into account when choosing cultivars for growing in conditions likely to suffer water limitation. Under water limited conditions, photosynthesis,

transpiration rate, effective quantum yield of PSII, and ETS activity were the lowest of both cultivars. Se lowered photosynthesis in cvs. Bard and Adora and also the mass of tubers in cv. Adora. The effects of drought and Se treatment are different in different potato cultivars, thus the results from certain cultivar can not be extrapolated to the whole species. This could be expected, since both effects have a complex, direct, or more probably indirect impact on traits and parameters of plants.

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Table 1. Starting values of physiological parameters in cvs. Bard and Adora. Means±SD ($n = 5$).

	Bard	Adora
Net photosynthetic rate	8.53±6.80	8.26±5.67
Transpiration rate	7.01±0.71	6.72±0.31
F_v/F_m	0.77±0.04	0.62±0.03
$\Delta F/F_m'$	0.35±0.05	0.25±0.05
ETS activity	6.35±0.51	5.75±0.36

Net photosynthetic rate was measured in [$\mu\text{mol}(\text{CO}_2)\text{m}^{-2}\text{s}^{-1}$], transpiration rate in [$\text{mmol}(\text{H}_2\text{O})\text{m}^{-2}\text{s}^{-1}$], fluorescence parameters in relative units, and ETS activity in [$\mu\text{L}(\text{O}_2)\text{mg}^{-1}(\text{DM})\text{h}^{-1}$]. F_v/F_m - potential quantum yield of PSII, $\Delta F/F_m'$ - effective quantum yield of PSII, ETS - electron transport system.

Table 2. Values of fresh/dry mass ratio and leaf water potential in cvs. Bard and Adora, and the level of significance of the treatments or interaction. Means±SD ($n = 5$).

	Se0W0	Se0W1	Se1W0	Se1W1	W	Se	WxSe
Fresh/ dry mass							
Bard	6.22±0.31	6.92±0.61	6.69±0.48	7.45±0.87	**	*	n.s.
Adora	7.33±0.44	6.92±0.87	7.22±0.41	8.19±1.60	n.s.	n.s.	n.s.
L. water potential (MPa)							
Bard	-0.67±0.10	-0.58±0.09	-0.60±0.14	-0.54±0.12	*	**	n.s.
Adora	-0.64±0.10	-0.54±0.06	-0.48±0.07	-0.53±0.08	n.s.	*	n.s.

Legend: Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. W - water, Se - selenium, and WxSe - interaction. L. water potential - leaf water potential. Influences of factors are presented as: n.s. - non-significant $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3. The significance of influences of factors on physiological parameters in cvs. Bard and Adora.

		Photosynthetic rate		Transpiration rate		F_v/F_m		$\Delta F/F_m'$		ETS activity	
		II	III	II	III	II	III	II	III	II	III
Bard	Water	n.s.	***	***	**	n.s.	**	***	**	n.s.	*
	Se	n.s.	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***
	Water x Se	n.s.	**	n.s.	*	n.s.	n.s.	n.s.	n.s.	*	*
Adora	Water	n.s.	*	n.s.	*	n.s.	n.s.	n.s.	**	***	*
	Se	n.s.	*	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Water x Se	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.

Legend: II stands for the second measurement and III for the third measurement, Se - selenium, and Water x Se - interaction. F_v/F_m - potential quantum yield of PSII, $\Delta F/F_m'$ - effective quantum yield of PSII, ETS - electron transport system.

Influences of factors are presented as: n.s. – non-significant $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 4. The number and dimensions of leaf stomata in cvs. Bard and Adora, and the level of significance of the treatments or interaction. Means \pm SD ($n = 5$).

		Se0W0	Se0W1	Se1W0	Se1W1	W	Se	WxSe
Bard	NoS	94.37 \pm 60.42	270.85 \pm 81.33	313.90 \pm 128.45	271.98 \pm 69.55	n.s.	n.s.	n.s.
	LeS	34.4 \pm 2.5	31.4 \pm 3.4	33.6 \pm 3.1	34.0 \pm 3.3	n.s.	n.s.	*
	WiS	24.6 \pm 2.5	24.8 \pm 2.3	25.3 \pm 2.0	25.0 \pm 1.9	n.s.	n.s.	n.s.
Adora	NoS	47.37 \pm 37.26	263.67 \pm 96.57	262.60 \pm 67.95	226.18 \pm 53.84	n.s.	n.s.	n.s.
	LeS	32.2 \pm 3.6	36.2 \pm 5.4	33.6 \pm 3.4	34.7 \pm 3.0	n.s.	n.s.	n.s.
	WiS	22.2 \pm 2.6	24.4 \pm 3.2	23.4 \pm 2.7	22.3 \pm 2.6	n.s.	n.s.	n.s.

Legend: NoS – number of the stomata [mm^2], LeS - length of the stomata [μm], WiS – width of the stomata [μm]. Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. W - water, Se – selenium, and WxSe – interaction. Influences of factors are presented as: n.s. – non significant $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 5. The number and mass of the tubers in cvs. Bard and Adora, and the level of significance of the treatments or interaction on the mass of tubers. Means \pm SD ($n = 5$).

		Se0W0	Se0W1	Se1W0	Se1W1	W	Se	WxSe
Mass	of the tubers	[g]						
Bard		64.78 \pm 14.23	94.98 \pm 10.69	120.88 \pm 22.04	68.06 \pm 20.20	n.s.	n.s.	***
Adora		76.65 \pm 15.10	68.20 \pm 17.07	47.46 \pm 7.28	44.62 \pm 12.01	n.s.	**	n.s.
No.	of tubers							
Bard		3.2 \pm 0.4	3.0 \pm 1.0	4.2 \pm 1.9	3.8 \pm 1.6			
Adora		3.2 \pm 1.8	2.6 \pm 0.9	2.3 \pm 0.5	3.0 \pm 0.8			

Legend: Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. W - water, Se – selenium, and WxSe – interaction. Influences of factors are presented as: n.s. – non significant $p \geq 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

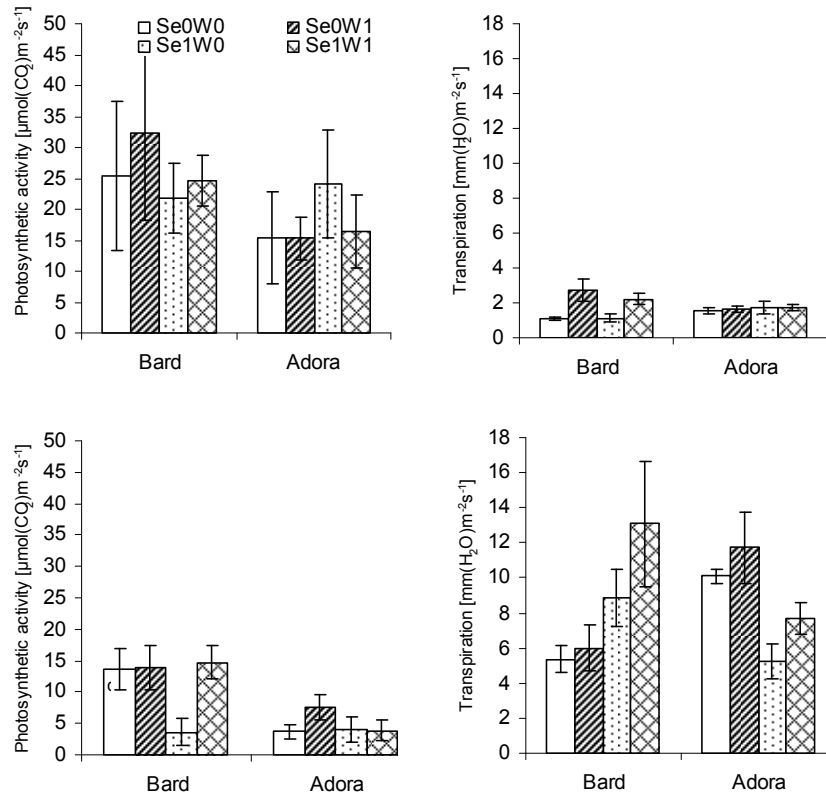


Fig. 1. Net photosynthetic rate (*left panels*) and transpiration rate (*right panels*) in the second measurement (*upper panels*) and in the third measurement (*lower panels*) in cvs. Bard and Adora grown under different drought and Se treatments. Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. Means \pm SD ($n = 5$).

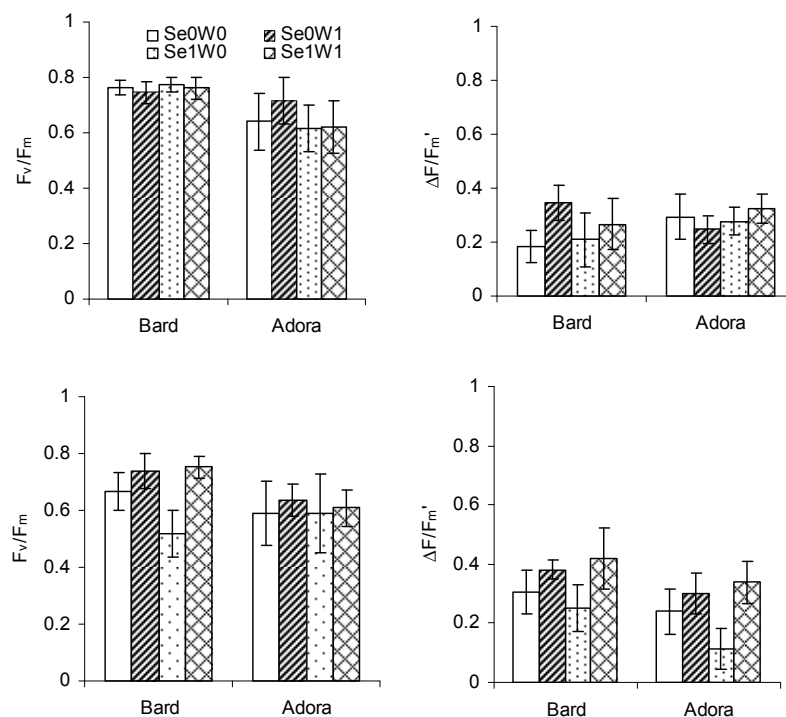


Fig. 2. Potential – F_v/F_m (left panels) and effective – $\Delta F/F_m'$ (right panels) photochemical quantum yield of PSII in the second measurement (upper panels) and in the third measurement (lower panels) in cvs. Bard and Adora grown under different drought and Se treatments. Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. Means \pm SD ($n=8$).

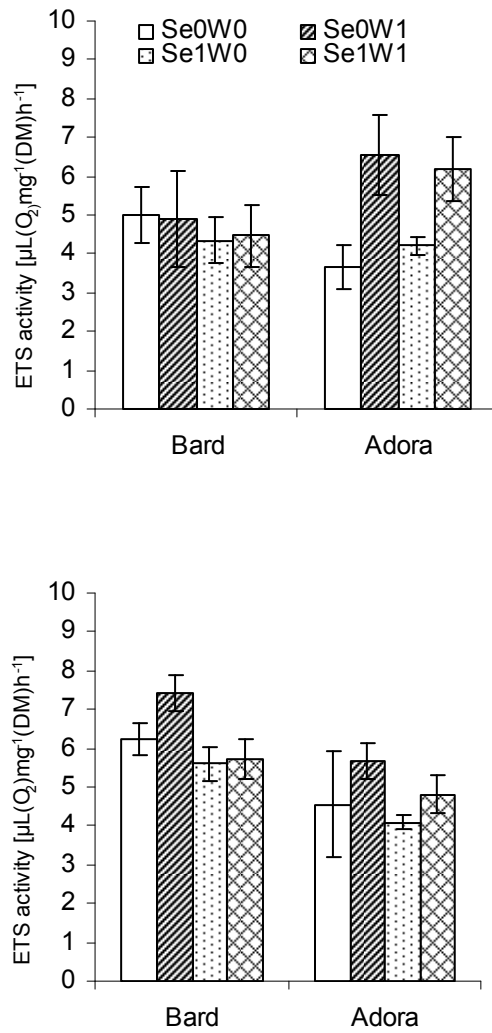


Fig. 3. Terminal electron transport system (ETS) activity in the second measurement (*upper panel*) and in the third measurement (*lower panel*) in cvs. Bard and Adora grown under different drought and Se treatments. Se0W0 - drought exposed without added Se, Se0W1 - well-watered without added Se, Se1W0 - drought exposed with added Se, Se1W1 - well-watered with added Se. Means \pm SD ($n = 4$).