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Are the fluorescence parameters of German chamomile leaves the first indicators of the anthodia yield in drought conditions?

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Abstract

7-day soil drought followed by 7-day rehydration was applied to potted German chamomile (*Chamomilla recutita*) plants at the beginning of their generative stage. Plants of a wild type (WT), plus two diploid (2n) and two tetraploid (4n) genotypes were studied, in order to examine the alterations in chlorophyll (Chl) and carotenoids (Car) contents, and chlorophyll fluorescence (CF) parameters during water shortage and rehydration. The fresh mass of the anthodia after the recovery was also studied.

WT plants adjust better to water stress than modern breeding genotypes, because drought resulted in the low fall in leaf water content of WT, the lowest decrease in the fresh mass of its anthodia (a 41% decrease from the control), and the most elastic response of the photosynthetic apparatus. 4n C11/2 strain plants suffered from the highest reduction in anthodia yield (87%), and had the lowest constitutive pigment contents. It was also the only genotype which revealed nontypical alterations in various CF parameters obtained on a dark- and light-adapted leaf. During drought, a big increase was noticed in minimal, maximal, and variable fluorescence of PSII reaction centres in the dark- adapted (F_0, F_m and F_v, respectively), and in the light-adapted state (F_0', F_m' and F_v'). It was accompanied by the biggest decline in linear electron transport rate (ETR), quantum efficiency of PSII electron transport (Φ_{PSII}) and photochemical quenching coefficient (q_P). These alterations were prolonged to the stage when the normal leaf water content was retained. On the contrary, C6/2 strain plants had the highest constitutive Chl and Car contents, which additionally increased after rehydration, similarly to the values of F_0, F_m and F_v, which reflects the high photosynthetic potential of this genotype. It was accompanied by the relatively high yield of its anthodia after drought. Considering the drop in the yield triggered by drought, it seems to be the only parameter which may be linked with the ploidy level.

Although the yield formation of chamomile strains cannot simply be estimated by CF assay, this technique may serve as an additional tool in the selection of plants to drought. The following circumstances should be submitted; namely: measurement at the proper developmental stage of plants, in different water regimes, and an analysis of various CF parameters. The increase in F_0 and F_0', and the reduction in ETR, F_v'/F_m', Φ_{PSII} and q_P values in response to water deficit should be an indicator of the impairment of the photosynthetic apparatus through drought.

Additional key words: carotenoids, chlorophyll, ploidy, wild type.

Introduction

Soil drought affects photosynthesis in various ways. Gas exchange is inhibited, as the stomata close due to a drop in turgorescence when the leaf water content is diminished (Cornic 2000). Photosynthetic electron trans-

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Abbreviations: Car – carotenoid, CF – chlorophyll fluorescence, Chl – chlorophyll, F_0, F_m – minimal and maximal fluorescence in the dark-adapted state, respectively, F_v – variable fluorescence in the dark-adapted state, F_v/F_m – photochemical efficiency of PSII in the dark-adapted state, F_0', F_m' – minimal and maximal fluorescence in the light-adapted state, respectively, F_v' – variable fluorescence in the light-adapted state, F_v'/F_m' – PSII maximum efficiency, ETR – linear electron transport rate, Φ_{PSII} – quantum efficiency of PSII electron transport, NPQ – nonphotochemical quenching of maximal CF, PSII – photosystem II, q_P – photochemical quenching coefficient.

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port decreases in response to an impaired CO_2 fixation (Cornic *et al.* 1989). Drought is often accompanied by excessive light, and this interaction leads to a drop in photosynthesis, a phenomenon known as photoinhibition (Huner *et al.* 1993). When reversible (dynamic photoinhibition), it is an adaptive feature. However, when prolonged, it may be dangerous for the photosynthetic apparatus (Critchley 2000, Lu *et al.* 2001, Jin *et al.* 2003). To avoid this, plants have evolved various mechanisms of energy dissipation. A biochemical mechanism known as nonphotochemical dissipation involves a xanthophyll cycle (VAZ cycle; Demmig-Adams and Adams 1996, Ort 2001). Another depends on β-carotene (β-Car), which quenches both triplet chlorophyll (^{3}Chl*) and singlet oxygen ($^1O_2$; Huner *et al.* 1993, Lavaud and Kroth 2006).

The resistance of photosystem II (PSII) to chronic photoinhibition may be estimated by the analysis of chlorophyll fluorescence (CF). The alterations in the values of individual CF parameters, allow one to establish the pool of energy which is used to photosynthates formation, either re-emitted, or dissipated (Maxwell and Johnson 2000). As noninvasive, CF measurements are often an alternative for photosynthetic assays performed *via* gas-exchange measurement (Kouřil *et al.* 2003, Ebbs and Uchil 2008). Some CF parameters depend on the Chl content, and it is noteworthy that homoiochlorophyllous desiccation-tolerant plants retain their Chl pool during a drought, whereas poikilochlorophyllous ones resynthesize it after the recovery (Proctor and Tuba 2002, Xu *et al.* 2008).

The tolerance to water shortage and photoinhibition within the species and the adaptive strategies may be differentiated. German chamomile *Chamomilla recutita* (L.) Rauschert), a common weed, and medicinal plant present and cultivated in Europe, Asia, Northern America, and Australia (Šalamon 2004), is considered tolerant to drought (Razmjoo *et al.* 2008). However, its cultivars and strains may be susceptible to water deficit to differing extents, and this involves alterations in morphological changes, anthesis and gas exchange (Bączek-Kwinta and Seidler-Łożykowska. 2004, Bączek-Kwinta *et al.* 2006a, Bączek-Kwinta *et al.* 2010). The reason for different strategies among the species may be the breeding, which is oriented toward specific usable characteristics, mainly in order to adjust the plants to mechanical harvesting and provide the crude raw material of specific chemical compositions (Seidler-Łożykowska 2000). However, this may cause the gradual elimination of wild adaptive features (Johnston *et al.* 2001). Additionally, some of the cultivars and strains are di- or tetraploid, and one can surmise that the ploidy level may influence plant response. For this reason, it seems worthwhile elucidating the hypothesis that plants of cultivars and strains, which have been bred for pharmaceutical purposes, have different photosynthetic performance levels during stressful weather and climatic factors, than wild type (WT) plants. Studies on the influence of soil factors on German chamomile plants, covering nitrogen deficiency, heavy metal stress and selenium/cadmium interactions, have already been performed (Kovačik *et al.* 2006, 2009, Pavlovič *et al.* 2006, Král'ová *et al.* 2007, Šalamon *et al.* 2007). In a comparative work (Bączek-Kwinta *et al.* 2010), it was established that WT plants and a diploid strain of *Chamomilla recutita* close their stomata to a similar extent, although the response of WT to desiccation and rewatering is more elastic. Therefore, the aim of the study was to estimate the impact of soil drought on the photosynthetic apparatus of the wild type and four cultivated forms (genotypes) of German chamomile. It was borne in mind that the ploidy level (2n and 4n) and the degree of genetic modification (wild type, strain and cultivar), can determine the alterations of CF parameters and pigment composition during water shortage and rehydration. As the main goal for chamomile cultivation is to obtain a high yield of anthodia (although sometimes the whole herb is used) with a good essential oil content, we were also hoping to answer the question as to whether CF measurement can reflect the yield potential of this species.

Materials and methods

Plant material: Two cultivars, two strains and a wild type of German chamomile (*Chamomilla recutita* (L.) Rauschert) were used. The cultivar 'Promyk' and C6/2 strain were diploids (chromosome number 2n), whereas 'Złoty Łan' and the C11/2 strain were tetraploids (4n). WT seeds originated from the Malopolska region, Poland, and cultivars and strains from the Research Institute of Medicinal Plants (Poznań, Poland).

Initial plant growth: Seeds (approx. 100 seeds) were sown directly into the surface of the soil without covering, due to their photoblastic germination, into plastic pots 200 cm^3 in volume, containing a mixture of brown soil, peat (pH 5,5; Kronen Poland) and sand (3:1:1; v/v/v). Seedlings were grown at 20–25°C, with a relative humidity (RH) of 30–50% and a photoperiod of 14/10h; day/night. When plants were *ca.* 2–3 cm in height, they were transplanted into pots of 2,000 cm^3 containing the same soil mixture as described above. 4 pots were prepared for each treatment, and there were 5 plants in each pot. They were kept at a temperature of 20–22°/15-17°C, RH 30/50%, and a photoperiod of 14/10h (day/night). During the cloudy days, additional illumination was provided in order to maintain a minimal photosynthetic photon flux density (PPFD) of *ca.* 400 µmol(quantum) m^{-2} s^{-1}. Plants were watered every 2–3 days and fertilized once a week with Hoagland's solution of half strength, as in the preliminary experiment as we established that this was necessary to provide the plants with the proper amount of nutrients (Bączek-Kwinta *et al.* 2010, Bączek-Kwinta and Kozieł 2010).

Drought treatment: 7 weeks after sowing, when the plants of both genotypes were *ca*. 10–12 cm high and had begun their generative stage, the set of pots with the plants was divided into a control and drought-treated group (4 pots per treatment = 20 plants). Drought conditions were created through no watering for 7 days, whereas the control plants were watered (but not fertigated) every 2–3 days. This allowed to one to obtain a field water capacity of *ca*. 45% (drought) and 65% (control). Then the drought-treated plants were rehydrated (subjected to the same watering regime as the control plants). The duration of the drought stage and vegetation conditions were established on the basis of previous experiments (Bączek-Kwinta and Seidler-Łożykowska 2004, Bączek-Kwinta *et al.* 2006a).

Measurements and assays were conducted on the mature (developed but not senescing) leaves, taken from the 4th–8th nodes counting from the top of the plant). One or two plants were selected from each pot, to obtain the final number of 6 biological replicates (one replicate = an individual leaf from an individual plant). Biochemical assays were made in 2–3 analytical repetitions for each biological replicate. Sample collection and measurements were performed on the 7th day of drought treatment and on the 7th day of the rehydration (recovery).

For water content quantitation, a fresh mass of leaves was recorded immediately after cutting, then the tissue was dried to create a stable mass (70°C, 24 h), kept in a presence of silica gel for 24 h, and then weighed again (d = 0.001 g).

For pigment assays, leaves were quickly weighed and frozen in LN2, and then kept at –70°C until homogenization in 80% acetone (v/v). Chl *a*, *b* and Car contents were assayed spectrophotometrically (*LKB Biochrom*, UK) according to Lichtenthaler and Wellburn (1983).

Chl *a* fluorescence was measured using a pulse-modulated fluorescence monitor system (*FMS-2* plant stress meter, *Hansatech*, UK). The source of the modulation beam (duration pulses 1.8 µs, 2.3 kHz) was the amber LED (peak wavelength 594 nm, PFD *ca*. 0.05 µmol(photon) m^{-2} s^{-1}). Actinic and pulse irradiations were provided by a halogen lamp (20 W). The signal detector was a *PIN* photodiode with a long-pass filter (>700 nm), and the sampling rate was 10–20 kHz (depending upon the instrument mode). A clip with optical fibre was fastened on the central part of the attached leaf for 20 min. Then the leaf was irradiated by a saturating light pulse to determine the F_m (intensity of 90 units, duration 0.9 s), after which the actinic light [25 units = 1,500 µmol(photon) m^{-2} s^{-1}] was switched on for 270 s. F_0’ was then measured after turning off the actinic light, by immediately irradiating the leaf for 3 s with a diode emitting far red radiation of about 15 W m^{-2}. The efficiency of excitation energy capture by the open photosystem II (PSII) reaction centres (F_v’/F_m’), the photochemical quenching (q_P), quantum yield of electron transport at PSII (Φ_{PSII}), and electron transport rate (ETR), were all determined according to Genty *et al.* (1989) and Schreiber *et al.* (1986).

Statistics: The significance of the genotype, treatment and the experimental stage was evaluated by two-way variance analysis (*ANOVA*, preceded by the *Kolmogorov-Smirnov* test). The differences within the stage were estimated using one-way *ANOVA*. For the comparison of two means of a particular genotype among the experimental stage, the Student *t*-test and median test were used. It was impossible to test the ploidy effect using *ANOVA*, as two genotypes were 2n, another two 4n, and WT probably 2n (Rutkowski 1998, Kubat *et al.* 2002). All analyses were carried out using the *Statistica 8.0* (*SPSS Inc*., Chicago, IL, USA).

Results

Drought effect on leaf water status: Drought treatment resulted in a drop in leaf water content of all the plant genotypes (Fig. 1). However, there were differences and the highest reduction (45% in relation to the respective control) was noticed for the diploid strain C6/2, and the lowest (25% of control) in WT and ‘Promyk’ cv. plants, which were also 2n. Rehydration treatment caused an increase in water content in all plants to the control level (*ca*. 90–95% of leaf fresh mass). The pattern of changes was neither related to the kind of genotype (cultivar or strain), nor to the ploidy level.

Photosynthetic pigments: Drought had no significant common effect on the Chl *a* and Chl *b* contents (Fig. 2*A*,*B*). The experimental stage was the main factor in case of Chl *a*, and the only one in case of Chl *b*, which affected the results (*ANOVA*, Table 1). This means that the Chls pools of both control and desiccated groups usually increased during rehydration. In the case of Chl *a*, the influence of genotype and stage × treatments were noticed. Genotypic effect means, that the highest content was established in the leaves of C6/2 strain plants, and the effect of stage × treatment relies on the reversed control/drought relations at the rehydration stage, when compared to the drought stage (Table 1, Fig. 2*A*). Tetraploid genotypes (C11/2 and ‘Złoty Łan’) revealed a common pattern of Chl *a* and *b* changes, although only one difference in Chl *b* at the drought stage was significant (Fig. 2*A*,*B*).

Chl *a*/*b* was directly increased by drought in

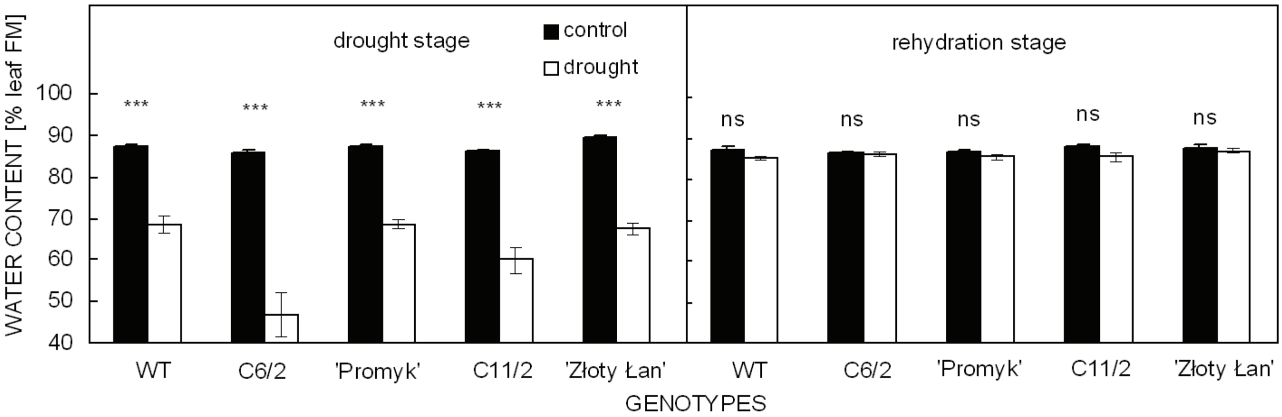

Fig. 1. The direct effect of 7-day drought, and the after-effect (after 7-day recovery) on water content in matured leaves of German chamomile plants. *** – p=0.001; ns – nonsignificant difference (n = 6 ± SE, Student's *t*-test).

'Promyk" but decreased in 'Złoty Łan' (Fig. 2*C*). After rehydration the response of these genotypes was reversed. Additionally, at this stage, WT and C11/2 plants revealed an increase in relation to their controls. Similarly to the tendencies in the contents of Chl *a* and Chl *b* themselves, alterations in Chl *a*/*b* were common for both tetraploids (tendency to decrease in drought-subjected plants, and the increase in relation to the control at the rehydration stage, Fig. 2*C*).

A direct influence of drought on Car content was noticed (Table 1, treatment factor significant). It means that drought-subjected plants revealed a tendency to increase Car in relation to their respective controls. The direct comparison of means by the Student *t*-test confirmed the significance of such a tendency in the case of three forms. Interestingly, apart from WT there were also 4n genotypes (C11/2 and 'Złoty Łan'). However, during the rehydration stage only the diploid C6/2 plants revealed a significant increase, whilst 4n plants revealed only a tendency. Similarly to the Chl pools, that of Car was strongly affected by the stage of the experiment (Fig. 2*D,* Table 1). However, contrary to Chl *a* and *b*, Car absolute values were higher at the drought than rehydration stage, irrespective of the treatment. The genotypic differentiation was similar to that described for Chl, meaning that the highest Car content was noticed in the leaves of C6/2 plants.

Similarly to the previously described results concerning Chl *a*, *b*, and their ratio, Car/Chl (*a*+*b*) was strongly influenced by the stage of the experiment (Fig. 2*E*). As the Car pool decreased during the rehydration stage (Fig. 2*D*), and Chl increased (Fig. 2*A,B*), so Car/Chl (*a*+*b*) was diminished. The pattern of drought-resulting changes for individual genotypes was similar to that obtained for Car itself. At the rehydration stage, it was reversed (Fig. 2*E*).

Chl fluorescence (CF): CF parameters were influenced by all implemented factors as well as their interactions (Table 1, 2). The parameters obtained in the dark-adapted state, namely F_0, F_m, and F_v revealed a different pattern of changes than that of F_v/F_m (Table 2). During drought, the values of F_0, F_m,, and F_v obtained on the leaves of 2n genotypes (C6/2 and 'Promyk') and one 4n cultivar plants ('Złoty Łan'), were reduced to 40–50% of the level of the respective control. The response of another 4n genotype, the C11/2 strain, was opposite, posting a 129% increase in F_0, 61% in F_m, and 50% in F_v. After rehydration, the response of C11/2 was prolonged, but that of C6/2 was reversed (the increase in relation to the respective control, contrary to the drought stage). WT parameters were not affected during drought, but revealed an increase at the rehydration stage. 'Promyk' and 'Złoty Łan' plants gave no alterations after rehydration.

An additional effect of the stage and stage × genotype interaction was noticed, namely that F_0 values after rehydration were diminished in all control plants when compared to the previous stage (Table 1, 2). When analysed, the stage effect on drought-subjected and rehydrated plants, revealed the different response of WT and C6/2 plants compared to other genotypes. WT specimens did not change their absolute values of F_0, F_m, and F_v, in response to rehydration, when the leaves of C6/2 plants increased them. Interestingly, C6/2 plants were the most desiccated at the drought stage, but recovered after rehydration (Fig. 1), and had the highest Chl level, which was also increased over the stage (Fig. 2).

F_v/F_m values were slightly diminished by drought in WT and 'Złoty Łan' (a 2% decrease in relation to control), and more in C11/2 plants (8%, Table 2). After rehydration, WT maintained a decline.

The pattern of drought-related changes in fluorescence parameters obtained for light-adapted leaves (F_0', F_m', F_v' and F_v'/F_m'; Table 2), was partially similar to the analogous pattern of the parameters obtained for dark-adapted leaves. F_0' was increased by 139% of the control in the tetraploid strain C11/2. This increase was prolonged, but to a lesser extent, to the rehydration stage (Table 2). Contrary to F_v, which was increased during drought in the leaves of this strain, a decrease in F_v' was

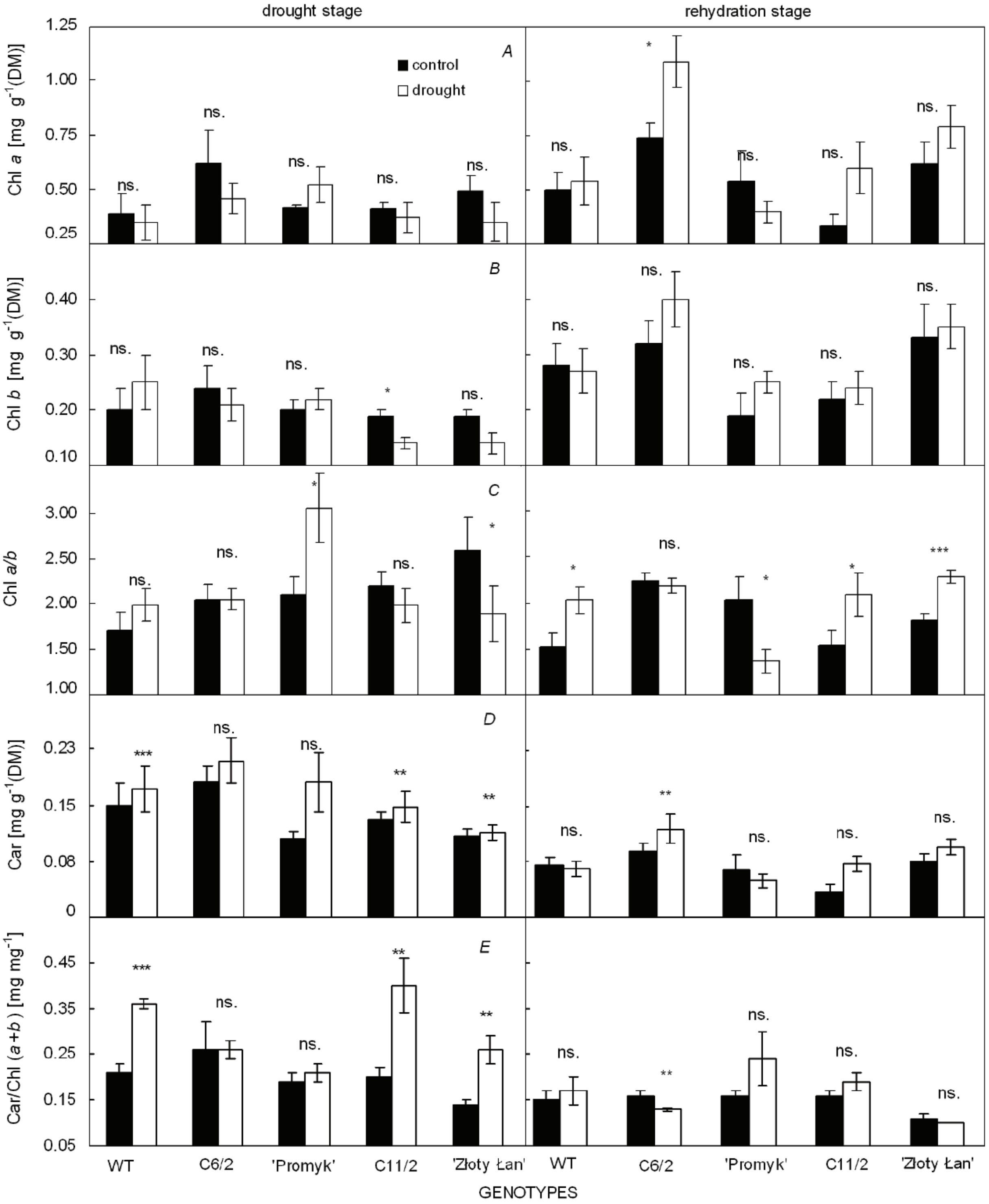

Fig. 2. The direct effect of 7-day drought, and the after-effect (after 7-day recovery) on chlorophyll *a* (*A*) and *b* (*B*) contents and their ratio (*C*), and carotenoid content (*D*) and their ratio to chlorophyll (*E*) in matured leaves of German chamomile plants. *** – p=0.001; * – p=0.05; ns – nonsignificant difference (n=6 ± SE, Student's t-test).

observed in all genotypes. Similarly to F_v/F_m values,those of F_v'/F_m' were diminished by drought in WT plants and both tetraploids. At both stages, the biggest drop in this parameter (41% of the reduction during drought, 15% at the rehydration stage) was noticed in the C11/2 strain.

The pattern of changes of electron transport rate (ETR), as well as two other parameters; namely the quantum efficiency of PSII electron transport (Φ_{PS2}) and photochemical quenching coefficient (q_P), was identical for all genotypes, but that of non-photochemical fluorescence quenching of maximal CF (NPQ) was reversed (Table 2). That means that the ETR, Φ_{PSII} and q_P of drought-treated plants revealed a 30–80% reduction in relation to the respective control, and the treatment was the main factor affecting these results (Table 1). Similarly to previously described fluorescence parameters, the response of the C11/2 genotype was the strongest (77% of reduction in ETR value, 69% in Φ_{PSII} and 50% in q_P when compared to the control), and the strongest decreasing tendency was prolonged to the rehydration stage. Non-photochemical fluorescence quenching (NPQ) was increased by drought in all plants, but the highest, a *ca*. 60% increase in relation to the respective control, was noticed in the case of the C11/2 strain. During the recovery, NPQ values only increased significantly in C6/2, and corresponded with the decrease in ETR and Φ_{PS2} obtained on the plants of this strain.

Drought effect on anthodia formation: Anthesis was affected by the stress conditions, and the fresh mass of the anthodia was differentially reduced by drought in the studied genetical forms. The pattern of changes was partially comparable to the physiological alterations which were previously described. That means, the lowest decrease in anthodia mass (41% reduction in relation to the control), was noticed for WT plants, the highest for C11/2 plants, whilst the 2n genotypes revealed a reduction of *ca*. 50% from the control total (Table 3). The drop in the yield corresponded to the ploidy level, in that its range was similar in both 2n modern breeding genotypes, and close to 2n WT, whereas in 4n plants it was much bigger. The absolute yield values obtained from controls reflected the type of development represented by the studied genotypes. It means, both studied diploids, C6/2 and 'Promyk' are the early genotypes, which initiate their anthesis earlier than WT or 'Złoty Łan'.

Discussion

Water content changes: WT plants adjust best to water stress, because drought causes a low fall in leaf water content and the lowest decrease in fresh mass of the anthodia. However, the superior water status of WT partially results from its relatively short shoots, which means these plants have a shorter water transport pathway compared to the specimens of other studied genotypes, *e.g*. diploid C6/2 strain (Bączek-Kwinta *et al.* 2006a, Bączek-Kwinta *et al.* 2010). Plant size often induces different ecophysiological response (Ramírez *et al.* 2008). After rewatering, the plants of all studied forms retain their proper water status, as the stress response of water management is elastic. However, the response of the photosynthetic apparatus is not identical to the changes in leaf water content.

Pigments and their ratios: Pigment composition deserves analysis for two purposes. First, the Chl content may be lowered by drought in poikilochlorophyllous plants (Bradford and Hsiao 1982, Montanaro *et al.* 2007, Xu *et al.* 2008). Second, the alterations in the Chl and Car pool affect CF parameters. As shown in Fig. 2, German chamomile is an homoiochlorophyllous plant, in which Chl *a* and *b* contents do not change during drought, especially for a short drought period as adopted in the study. The Chl *a* and Car pools are strongly determined by the genotype. Interestingly, the highest Chls and Car values are represented by the C6/2 strain, and although its plants are the most highly desiccated, they recover and exhibit the lowest drop in anthodia yield among the studied modern genotypes. The lowest pigment contents belong to C11/2 plants, which suffer the biggest drop in anthodia yield. The simple relationship between pigment content and the yield is impossible, but one can speculate that photosynthetic centres in C6/2 leaves are more abundant than in C11/2 leaves, and the phloem pathways, which allow the photosynthates to be transported from their source (leaf) to the developing anthodia, operate more efficiently in C6/2 specimens.

The relationships between pigments reveal some physiological alterations. The range of the Chl *a*/*b* ratio obtained during our experiment is 2–2.5, which corresponds to the values of plants grown in low light intensities (Lichtenthaler *et al.* 2006), which holds true for such greenhouse conditions. However, the pattern of changes in Chl *a*/*b* is not equal among the studied genotypes. The increase observed in 'Promyk' plants at the drought stage, as well as that in WT and 4n forms in the recovery phase, indicate an increase in PSII reaction centres when the antennae size decrease (Wentworth *et al.* 2006). However, after rehydration the pattern is reversed. Considering the fact that neither Chl *a* itself nor Chl *b* is affected in a special way by drought, we suggest the partial and temporary conversion of Chl *a* into *b* or Chl *b* into *a* (Ohtsuka *et al.* 1997, Ebbs and Uchil 2008).

CF parameters response: F_v/F_m is a widely used CF parameter in the study of plant response to stress, but alterations in its values may be misinterpreted. To establish whether the F_v/F_m decline means chronic or dynamic photoinhibition, we have to analyse other fluorescence parameters and relate them to pigment alterations. In our experiment, F_v/F_m was slightly changed at the drought stage. The biggest decrease was for the C11/2 strain, although it was only 8% in relation to the control. On the other hand, a slight decline noticed for WT specimens was maintained at the recovery stage. One should remember that if F_v/F_m declines according to the stress factor, it suggests the diminished photochemical capacity of PSII (Demmig and Björkmann 1987, Bączek-

Table 1. The *F*-values of two-way *ANOVA* expressing the influence of the factors implemented in the study on the effect of drought on German chamomile plants. * – $p<0.05$, ** – $p<0.01$, *** – $p<0.001$. Chl – chlorophyll; Car – carotenoids; F_0, F_m, F_v – minimal, maximal and variable fluorescence in the dark-adapted state, respectively; F_v/F_m – photochemical efficiency of PSII in the dark-adapted state; F_0’ – minimal fluorescence in the light-adapted state; F_v’/F_m’ – PSII maximum efficiency; q_P – photochemical quenching coefficient; NPQ – nonphotochemical quenching of maximal fluorescence; ETR – linear electron transport rate; (e^-) – electron.

	Water content [% leaf FM]	Chl *a* [mg g^{-1}(DM)]	Chl *b* [mg g^{-1}(DM)]	Car [mg g^{-1}(DM)]	F_0	F_m	F_v	F_v/F_m	F_0'	F_v'/F_m'	q_P	NPQ	ETR [mmol(e^-) m^{-2} s^{-1}]
Genotype	12.60***	6.21**	1.58	6.05**	20.14***	15.12***	15.42***	11.74***	18.79***	7.59***	3.60*	1.82	6.73***
Treatment	413.71***	0.00	0.25	3.33*	6.45*	0.21	0.02	18.88***	3.98*	81.65***	118.51***	54.73***	78.09***
Genotype × treatment	4.82**	0.55	0.68	0.96	8.61***	3.88*	3.60*	5.26**	10.84***	8.73***	9.23***	0.96	12.75***
Stage	290.81***	12.07**	17.21**	89.56***	20.84***	15.04**	15.97***	2.61	43.96***	52.92	58.32***	27.41***	70.35***
Stage × genotype	9.24***	1.70	2.09	2.07	6.59**	5.36**	6.04**	3.39*	16.42***	5.36**	14.42***	8.24***	21.63***
Stage × treatment	294.91***	4.13*	0.99	0.28	1.09	13.96**	18.49***	2.81	0.36	19.63***	59.42***	7.66**	35.71***
Stage × genotype × treatment	6.70	1.78	0.31	2.65	8.82***	2.81	2.45	5.33**	12.25***	1.65	2.54	0.49	3.20*

Table 2. The direct effect of 7-day drought on CF parameters of mature but non-senescing leaves of German chamomile plants and the after-effect (after 7-day recovery). *** – *p*=0.001; ** – *p*=0.01; * – *p*=0.05; ns – nonsignificant difference (*n*=6 ± SE, Student's *t*-test or median test). In case of statistical significance, % of reduction (–) or increase (+) in relation to the respective control is given.

Parameter reduction/increase [%]	WT		C6/2		'Promyk'		C11/2		'Złoty Łan'	
	control	drought	control	drought	control	drought	control	drought	control	drought
Drought stage										
F_0	124^{ns}	130	107**	59 45 (–)	114*	61 46 (–)	114**	261 129 (+)	222**	162 27 (–)
F_m	798^{ns}	763	692**	401 42 (–)	702**	381 46 (–)	706**	1138 61 (+)	1425***	928 35 (–)
F_v	675^{ns}	634	585*	342 42 (–)	587*	320 45 (–)	592*	889 50 (+)	1201***	766 36 (–)
F_v/F_m	0.847*	0.834 2 (–)	0.849^{ns}	0.856	0.840^{ns}	0.839	0.841**	0.774 8 (–)	0.843**	0.825 2 (–)
F_0'	108^{ns}	116	94*	55 41 (–)	92*	47 49 (–)	108*	258 139 (+)	195*	146 25 (–)
F_m'	294*	202 31 (–)	300**	134 55 (–)	262*	117 55 (–)	296***	353 19 (+)	499***	269 46 (–)
F_v'	206**	113 45 (–)	201***	76 62 (–)	190**	70 63 (–)	212***	146 31 (–)	304***	154 49 (–)
F_v'/F_m'	0.658***	0.488 26 (–)	0.678^{ns}	0.611	0.636^{ns}	0.586	0.656***	0.387 41 (–)	0.609***	0.492 19 (–)
ETR [mmol(e$^-$) m^{-2} s^{-1}]	2.406***	1.125 53 (–)	2.28**	1.397 39 (–)	1.485**	1.009 32 (–)	2.652***	0.618 77 (–)	2.038***	1.102 46 (–)
Φ_{PSII}	0.413***	0.201 51 (–)	0.460***	0.274 40 (–)	0.410***	0.233 43 (–)	0.444***	0.138 69 (–)	0.323***	0.178 45 (–)
q_P	0.626***	0.411 34 (–)	0.676***	0.443 34 (–)	0.642***	0.392 39 (–)	0.674***	0.336 50 (–)	0.530***	0.359 32 (–)
NPQ	1.683***	2.343 39 (+)	1.433**	1.956 36 (+)	1.82*	2.302 26 (+)	1.259***	2.017 60 (+)	1.830*	2.272 24 (+)
Rehydration stage										
F_0	72*	124 72 (+)	70**	128 83 (+)	53^{ns}	62	94*	150 60 (+)	129^{ns}	125
F_m	455**	716 57 (+)	463**	798 72 (+)	355^{ns}	394	530*	839 58 (+)	804^{ns}	758
F_v	383**	592 55 (+)	393**	668 70 (+)	302^{ns}	334	436*	688 58 (+)	675^{ns}	633
F_v/F_m	0.850**	0.825 3 (–)	0.845^{ns}	0.843	0.850^{ns}	0.849	0.832^{ns}	0.822	0.843^{ns}	0.835
F_0'	65*	105 62 (+)	65*	105 62 (+)	53^{ns}	52	72*	121 68 (+)	113^{ns}	109
F_m'	198*	281 42 (+)	221^{ns}	274	157^{ns}	158 –1	212*	335 58 (+)	371^{ns}	317
F_v'	111*	156 41 (+)	145^{ns}	153	105^{ns}	92	145^{ns}	171	258^{ns}	210
F_v'/F_m'	0.660^{ns}	0.609	0.664*	0.603 9 (–)	0.685^{ns}	0.717	0.685***	0.582 15 (–)	0.691^{ns}	0.659
ETR [mmol(e$^-$) m^{-2} s^{-1}]	1.505*	2.083 38 (+)	2.046*	1.623 21 (–)	2.778^{ns}	3.079	2.559***	1.055 59 (–)	2.796^{ns}	2.936
Φ_{PSII}	0.383^{ns}	0.396	0.378*	0.299 21 (–)	0.427^{ns}	0.464	0.455***	0.251 45 (–)	0.494^{ns}	0.463
q_P	0.575^{ns}	0.648	0.568^{ns}	0.493	0.622^{ns}	0.702	0.662***	0.416 37 (–)	0.715^{ns}	0.699
NPQ	1.580^{ns}	1.792	1.441**.	2.048 42 (+)	1.507^{ns}	1.689	1.467***	1.826 24 (+)	1.253^{ns}	1.419

Table 3. The yield of the anthodia of German chamomile plants subjected to 7-day drought stress, obtained at the rehydration stage (mean ± SE; *n* = 20). *** – p=0.001; ** – p=0.01; * – p=0.05 ; (n = 6 ± SE, Student's *t*-test and median test).

	WT control	drought	C6/2 control	drought	'Promyk' control	drought	C11/2 control	drought	'Złoty Łan' control	drought
Fresh mass of anthodia [g plant^{-1}]	0.141 ± 0.042	0.083 ± 0.011*	0.287 ± 0.040	0.152 ± 0.022**	0.230 ± 0.081	0.116 ± 0.031***	0.722 ± 0.081	0.091 ± 0.013***	0.097 ± 0.018	0.019 ± 0.005**
Reduction from respective control [%]		41		47		50		87		80

Kwinta and Kościelniak 2003), but also alterations in the photosynthetic pigments (Krause and Weis1991), and adaptive processes. The adaptive response may be linked to an increase in the Car/Chl ratio, which is, in fact, the largest in the case of the C11/2 genotype. However, it is also noteworthy that at the drought stage, F_0 of C11/2 leaves increases, whereas other modern genotypes reveal a decrease and WT no response. Elevation in F_0 may result from inhibition of the acceptor side of PSII (Bertamini and Nedunchezhian 2003), Q_A reduction, and dissociation of LHCII from PSII (Yamane *et al.* 2000 and references therein).

Consequently, F_0' of drought-treated C11/2 plants strongly increases. This means in effect, that the impairment in utilisation of the energy of excited Chl by the PSII leaves of this strain (Schreiber and Bilger 1993, Baker and Rosenqvist 2004). On the other hand, a lowering in F_0' values, established in 2n genotypes and 'Złoty Łan' cultivar (4n), means energy dissipation by the VAZ cycle (Verhoeven *et al.* 1997). Additionally, ETR during drought suffers its greatest decline in C11/2, and the response is prolonged to the rehydration stage. At a strong water deficit, in C11/2 leaves, the ETR decrease may result from decreased water photodissociation, but if it also occurs during normal water conditions, this suggests a disruption in functionality of the thylakoid-bound electron transport chain from PSII to PSI (Papadakis *et al.* 2007). Another parameter – the coefficient of photochemical quenching of fluorescence (q_P) corresponds to the part of the energy reaching PSII, that is directed towards further photochemistry. This reflects the degree of using radiation energy in photosynthesis (Öquist and Huner 1993, Sofo *et al.* 2009), as alterations in q_P correlate to that of the net photosynthesis (P_N), and the amount of the energy depends on the ratio of oxidized to reduced electron acceptors. In our experiment, at the drought stage, q_P declines in all studied forms of chamomile. This reflects the small energy transfer to PSII photochemistry, and that may, in turn, diminish the light phase of photosynthesis. However, at the rewatering stage, q_P is lower only in the C11/2 strain, and this confirms the previous conclusion concerning the stable photoinhibitory impairments in PSII, of plants of this genotype (Sofo *et al.* 2009). This corresponds to the greatest increase in NPQ, which reflects energy dissipation by heat *via* an xanthophyll (VAZ) cycle and other carotenoids, as well as PSII antennae (LHC) conformational changes (Maxwell and Johnson 2000, Montanaro *et al.* 2007, Sofo *et al.* 2009).

Potential linkage between CF parameters, drought resistance and anthodia yield: The study of CF parameters are widely used in ecophysiological and agricultural studies (Montanaro *et al.* 2007, Xu *et al.* 2008, Ramírez *et al.* 2008, Zhang *et al.* 2009, Sofo *et al.* 2009). The link between the CF parameters of chamomile leaves and the anthodia yield was suspected by Bączek-Kwinta and Kozieł (2010). Both in the cited and present work, CF measurements reveal a decline in drought adaptation and tolerance of photosynthetic apparatus of modern breeding genotypes, when compared to the wild type. From the present data, it is noteworthy that the PSII of WT plants is characterized by the most elastic response to soil drought. Tetraploid C11/2 strain is the most sensitive, as the photosynthetic apparatus of its plants operates less efficiently, even after soil rehydration. The diploid C6/2 strain deserves special attention, because the loss of its yield is the lowest, and the pigment pool the biggest among the studied genotypes.

Taking into account all the circumstances, the question arises whether the CF technique may directly help one to select drought-adapted chamomile strains, and to predict the anthodia yield during a dry summer. The absolute values of anthodia yield obtained from controls reflect the specific type of development which is represented by plants of individual genetical forms. It means, both studied diploids, C6/2 and 'Promyk' are the early genotypes, which initiate their anthesis earlier than WT and 'Złoty Łan' (Bączek-Kwinta *et al.* 2010). The drop in the yield triggered by drought is deemed to be the only parameter, which may be linked with the ploidy level. From the data obtained in this work, as well as from Bączek-Kwinta and Kozieł (2010), it is clear that yield formation cannot be simply estimated by CF measurement. Flowering is a complex process, depending on photosynthates, as well as hormonal factors (Bernier *et al.* 1993). In chamomile it is probably dependent on specific utilization of sugars in anthodia formation in 2n plants, because a drop in their yield is less than twice that of 4n specimens, as was mentioned earlier. However, CF assay seems to be an additional tool in the selection of chamomile strains to drought, but under the following circumstances: at the proper developmental stage of plants, various parameters should be analysed and the measurements should be repeated in different water regimes. Considering the stage, the type of growth of the genotype (early, fast-growing, or late) should be mentioned. It is noteworthy that after rehydration, 'Złoty Łan' plants reveal no alterations in CF parameters, which means no disturbances in the photosynthetic apparatus. However, the drop in the yield is high, and the reason is that 'Złoty Łan' is a late, slow-growing cultivar, which produces a high biomass of leaves, contrary to C6/2 and 'Promyk' (Bączek-Kwinta and Seidler-Łożykowska 2004, Bączek-Kwinta *et al.* 2006a). In considering F_v/F_m, its interpretation should be accompanied with that of F_v'/F_m' and other parameters. The increase in F_0 and F_0', and the reduction in ETR, Φ_{PSII} and q_P values in response to water deficit, should be of special interest. From the present data it is clear that the C11/2 genotype, which suffers from the highest reduction in anthodia yield, is the only one which reveals such nontypical alterations in various CF parameters obtained on dark- and light-adapted leaves. On the other hand, constitutive (obtained at the proper water regime) high values of F_0, F_m, and F_v of C6/2 plants, reflect their high photosynthetic potential which may be utilized for obtaining a relatively high yield, as was established.

Additional observations confirm the interesting properties of the C6/2 strain. When compared separately, the direction of changes in the mean for the control and drought-treated plants, it is visible that some changes happen irrespective of the water regime, and are common for all studied cultivars and strains. It is distinct in the case of Chl *a*, *b* and CF parameters: F_0, F_m, and F_v (and corresponding parameters obtained on a light-adapted leaf). Control values decrease at the rehydration stage when compared to the drought stage, which reflects a constitutive programme of the species. Similar effect was established for antioxidative enzymes in drought-treated triticale cultivars (Bączek-Kwinta *et al.* 2006b). However, in the case of chamomile the observation is disturbed by the comparison of the mean values for drought-treated C6/2 plants. At the recovery stage, the values are increased. This probably reflects the ability of this strain to enhance the metabolism of its plants to overcome the effect of drought, as was established earlier by Bączek-Kwinta *et al.* (2010). The advantages of the C6/2 strain must have been noticed by the breeders, as its plants were used when a new Polish cultivar 'Mastar' was bred (Seidler-Łożykowska 2007).

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