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Can we predict winter survival in plants using chlorophyll *a* fluorescence?

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Abstract

In the last years, JIP-test became to be a tool widely applied to assess the performance of photosynthetic apparatus of plants growing under environmental stresses. The objective of our work was to check whether JIP-test can help to predict winter survival in plants. An experiment with outdoor vertical garden was conducted in June 2015 on a south-oriented wall in Lublin city, Poland. Plants were cultivated in pockets made of polyester felt and irrigated by automatic controlled system. After winter period (2015/2016) only 16 species and cultivars from 23 initially planted taxa substantiated successful survival. Chlorophyll fluorescence measurements were performed twice in 2015 and six times in 2016. Survival rate of examined species did not show any significant correlation with performance indices of PSII (PI_{ABS} and PI_{total}) and parameters related to quantum yields. On the other hand, changes of some parameters related to specific energy fluxes per active reaction centres were found to be connected, to some extent, to plants winter survival. These changes could play a key role in plants ability to survive winter conditions.

Additional key words: green wall; JIP-test; perennials; plant winter hardiness; vertical garden.

Introduction

Since the first works describing the analysis of polyphasic fluorescence rise in photosynthetic material were published and so-called OJIP parameters for this analysis were introduced (Strasser and Strasser 1995, Strasser *et al.* 2000, 2004), numerous researchers applied this chlorophyll *a* fluorecence (ChF) method to examine leaf samples or behaviour of the whole plants under variable growing conditions and under the pressure of any kind of stress. The satisfying informative results were obtained in research detecting stress effects of drought (Živčák *et al.* 2008, Goltsev *et al.* 2012, Wang *et al*. 2012, Oukarroum *et al.* 2018, Dąbrowski *et al*. 2019), heat (Duan *et al.* 2015, Jedmowski and Brüggemann 2015), freezing or chilling (Parvanova *et al.* 2004, Rapacz *et al.* 2015), salinity (Bacarin *et al.* 2011, Dąbrowski *et al*. 2016, Kalaji *et al.* 2018a), contamination with metals and metal oxides (Tuba *et al*. 2010, Kalaji *et al*. 2016, Paunov *et al*. 2018, Rastogi *et al.* 2019), nutrient deficiency (Redillas *et al.* 2011, Živčák *et al.* 2014b, Kalaji *et al*. 2018b), plant infections (Christen *et al*. 2007, Keča *et al*. 2018), *etc.* in leaf or plant samples under laboratory conditions. Based on analysis of polyphasic fluorescence transient changes in PSII structure and function during ontogeny could be described (Jiang *et al.* 2006, Lepeduš *et al.* 2010). OJIP transient analysis, shortly named JIP-test (Strasser and Strasser 1995, Strasser *et al.* 2000), was introduced widely in agricultural sciences to screen crop plant sensitivity to various stress factors (Oukarroum *et al*. 2007, Brestič *et al*. 2012, Živčák *et al.* 2014a).

The essence of this method is illumination of an examined sample by strong actinic light after previous dark adaptation. Contemporary devices such as plant efficiency analysers (PEA) enable application of actinic photosynthesis-driving light also as a measuring light

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Abbreviations: ABS – photon absorption; ChF – chlorophyll *a* fluorescence; DI – energy dissipation; ET – electron transport; F_v/F_m – maximum quantum yield of PSII photochemistry in a dark-adapted sample; OJIP parameters – parameters calculated from fluorescence values in O, J, I, and P points obtained from prompt fluorescence transient plotted on a logarithmic scale; PI_{ABS} – performance index on absorption basis; PI_{total} – total performance index; RC – reaction centre; RE – reduction of end electron acceptors at the PSI acceptor side; TR – excitation trapping.

and allow to obtain high-time resolution records (with intervals of 10 μs). Such high-time resolution is necessary to visualise so-called prompt (fast) fluorescence rise from the point 0 to the maximal value after the rapid illumination. ChF transient plotted on a logarithmic time scale shows particular steps named O, J, I (at 0, 2, and 30 ms, respectively), and P (at maximum fluorescence) (Strasser and Govindjee 1992). Based on ChF values recorded at these steps, numerous JIP-test parameters can be calculated (Strasser *et al*. 2004, 2010). They describe energy fluxes occurring inside and around reaction centres (RCs) of numerous PSII localised in chloroplasts and enable to get an insight into particular phenomena concerning light absorption and its conversion to biochemical energy. The explanation of the origin and meaning of JIP-test parameters was published in numerous works by Prof. Reto J. Strasser. A great advantage of the analysis of prompt fluorescence transient results from its characteristics: rapid, automated, and nondestructive measurements may be performed both on living plants and on samples collected and delivered to a laboratory. This method is also suitable for continuous real-time *in-situ* monitoring. JIP-test parameters gave much information on plant performance when applied in field conditions in agriculture and horticulture (Tsonev *et al.* 2011, Swoczyna *et al*. 2019), forestry (Pollastrini *et al.* 2014, Bussotti and Pollastrini 2015), urban environment (Hermans *et al.* 2003, Ugolini *et al.* 2012, Swoczyna *et al.* 2015), ecological research (Bąba *et al.* 2016), *etc*.

One of the most interesting ways of OJIP analysis application is plant phenotyping (Kalaji *et al*. 2018c). Numerous parameters derived from the JIP-test have a great potential to indicate not only differences in PSII overall efficiency, but also they may indicate which steps of energy transitions in consecutive processes inside and around PSII are affected in particular species or cultivars (Oukarroum *et al.* 2007, Swoczyna *et al.* 2015). Strasser *et al.* (2000) pointed out that, at a given moment, the shape of a ChF transient is determined by the physiological state of the sample at the certain moment and all the states the sample went through in the past. Therefore, the analysis of particular JIP-test parameters seems to show the overall capacity of given samples to withstand environmental conditions which the samples were set to.

The idea of vertical gardens established on building facades became very attractive in the contemporary concept of a green city. This is because of scarcity of space for implementation of traditional greenery forms in urban high-density areas, such as squares, green courtyards, *etc*. When planting trees, shrubs, flowering plants, or even vines is impossible, vertical arrangement of greenery provides numerous advantages for improving air quality, thermal comfort, aesthetic values, and mental well-being for humans (Alexandri and Jones 2008, Wong *et al.* 2009, 2010). There are numerous types of so-called green walls and numerous plant cultivation manners ranging from full-soil boxes to hydroponic systems (Timur and Karaca 2013). In northern countries the most serious problem is winter survival of the plants. This is due to the exposure to wind and the lack of soil layer providing root insulation (Skarżyński *et al.* 2014). There is not much research on ornamental species selection for vertical gardens in northern countries (Medl *et al.* 2017). Most of information about proper plants comes from constructors' own experience, however, the information on physiological characteristics of plants suitable for vertical gardens is lacking. Plant phenotyping is a quantitative description of the plant's anatomical, ontogenetical, physiological, and biochemical properties and recently became a developing area of research focussed on agricultural purposes (Fiorani and Schurr 2013, Walter *et al.* 2015, Pietruschka *et al*. 2019). Contrary to agriculture, in ornamental horticulture, not final crop yield but longevity and durability of plants are expected. Nevertheless, methods used in agriculture may successfully be applied in this area of plant cultivation.

The main goal of our experiment was to evaluate the usefulness of several woody and non-woody perennial species for outdoor vertical gardens. The objective of this report is to assess the usefulness of chlorophyll fluorescence-based methods to plant phenotyping in vertical gardens.

Materials and methods

Plant material and experiment design: The experiment was established in June 2015 on a south-oriented wall of a university building of University of Life Sciences in Lublin (51°14'37''N, 22°32'26''E). A construction of an experimental vertical garden consisted of vertically arranged pockets made of polyester felt, 1,000 ± 10% g m^{-2}, attached to a metal frame. A root system of every plant together with 650–700 cm^3 of soil, was additionally wrapped with polyester felt of density of 200 ± 10% g m^{-2}. Controlled irrigation using tap water was applied to each pocket except temperatures below 2°C. Primarily 23 species and cultivars were planted in the pockets (Table 1). The species and cultivars used in the experiment are the most popular ornamental taxa which meet requirements of low size, spreading shape, and dense foliage, both ground-covering shrubs and herbaceous perennials. Due to the experiment design after the first winter 2015/2016 species and cultivars with less than 50% survival were eliminated and pockets were complemented with the remaining taxa in order to obtain 30 specimens of each taxon for the growing season 2016. However, *Pachysandra terminalis*, as a very popular species, was included additionally. After the winter 2016/2017, only seven taxa revealing 75% survival rate were included in the experiment and the other ones were excluded (Table 1).

Temperature on the surface of the vertical garden was measured by a *DHT 22* sensor (*Aosong Electronics Co., Ltd.*, Guangzhou, China). Data were recorded every 5 min. For this paper, the data were grouped and analysed as weekly data. The minimum and maximum weekly temperatures are shown in Fig. 1.

Chl *a* fluorescence measurements: In the growing season of 2015, ChF measurements were performed on 30 September and 30 October, at about 11:00 h using a *HandyPEA* fluorimeter (*Hansatech Instruments Ltd*., King's Lynn, Norfolk, UK). The measurements were

Table 1. Species and cultivars cultivated in vertical garden in consecutive growing seasons and their survival rate [%] after the winter seasons of 2015/2016 and 2016/2017.

Taxon	Symbol	Cultivated 2015	2016	2017	Survival rate [%] 2015/2016	2016/2017
Geranium × cantabrigiense P.F.Yeo 'Cambridge'	GCC	+	+	+	93.3	96.7
Armeria maritima (Mill.)Willd. 'Splendens Perfecta'	AMS	+	+	+	90.0	93.3
Potentilla fruticosa L.	PF	+	+	+	90.0	93.3
Heuchera L. 'Plum Royale'	HPR	+	+	+	86.7	83.3
Koeleria glauca (Spreng.) DC.	KG	+	+	+	83.3	86.7
Heuchera L. 'Marmalade'	HM	+	+	+	76.7	80.0
Lavandula angustifolia Mill. 'Hidcote Blue Strain'	LAH	+	+	+	76.7	80.0
Armeria maritima (Mill.)Willd. 'Alba'	AMA	+	+		66.7	70.0
Fragaria vesca L. 'Rugia'	FVR	+	+		66.7	73.3
Carex muskingumensis Schwein.	CM	+	+		56.7	66.7
Euonymus fortunei (Turcz.)Hand.-Mazz. 'Coloratus'	EFC	+	+		56.7	43.3
E. fortunei (Turcz.)Hand.-Mazz. 'Emerald'n Gold'	EFE	+	+		53.3	46.7
Iberis sempervirens L.	IS	+	+		53.3	60.0
Cotoneaster dammeri C.K.Schneid. 'Eichholz'	CDE	+	+		53.3	43.3
Cotoneaster dammeri C.K.Schneid.	CD	+	+		50.0	50.0
Hedera helix L.	HH	+	+		50.0	56.7
Vinca minor L. 'La Grave'	VMG	+			46.7	-
Vinca minor L. 'Illumination Cahill'	VMI	+			36.7	-
Pachysandra terminalis Siebold & Zucc.	PT	+	+		27.7	-
Saxifraga umbrosa L.	SU	+			13.3	-
Asarum europaeum L.	AE	+			13.3	-
Asplenium trichomanes L.	AT	+			13.3	-
Polypodium vulgare L.	PV	+			13.3	-

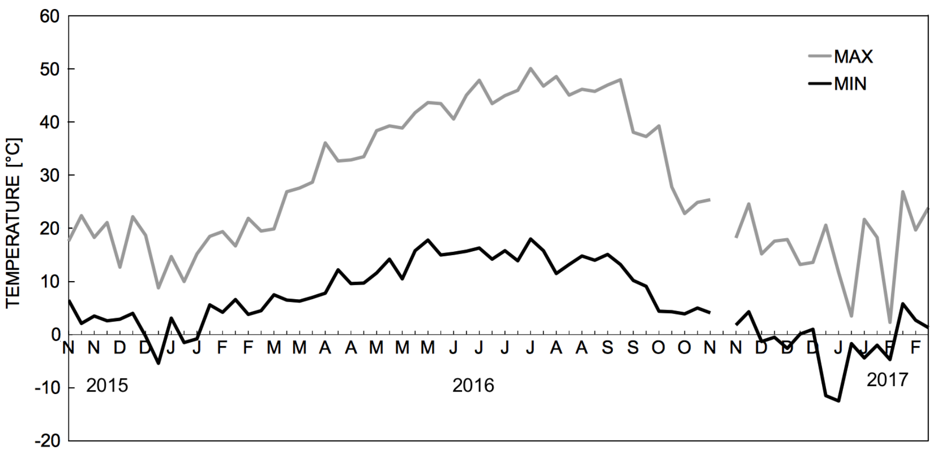

Fig. 1. The minimum and maximum weekly temperatures recorded on a construction of the vertical garden between 14 November 2015 and 28 February 2017.

conducted on five leaves from each taxon. We chose leaves from the middle part of a shoot or a rosette, not the youngest neither the oldest ones, being of similar size and representing the typical appearance. The leaves were dark-adapted using light-excluding clips for minimum 20 min. The dark-adapted leaf samples of 4-mm diameter within each clip were illuminated with 660-nm light of 3,500 μmol(photon) m^{-2} s^{-1}. During 2016, ChF was measured on leaves of older plants of remaining 17 taxa. The measurements were performed at about 11:00 h on 27 June, 27 July, 26 August, 27 September, 27 October, and 24 November.

In 2015, only maximum quantum yield of primary photochemistry, F_v/F_m, and a performance index of PSII on absorption basis, PI_{ABS}, were analysed. F_v/F_m is described also as a ratio of trapped energy to energy absorbed by antenna pigments, TR_0/ABS. In 2016, several additional ChF parameters were analysed, *i.e.*, total performance index, PI_{total}, efficiency of excited electron movement into the electron transport chain beyond Q_A, ψ_{E0}, (denoted also as ET_0/TR_0), as well as so-called 'specific energy fluxes', expressed per active RC, average photon absorption

(ABS/RC), exciton trapping (TR_0/RC), energy dissipation (DI_0/RC), electron transport (ET_0/RC), and reduction of end electron acceptors at the PSI acceptor side (RE_0/RC) (Strasser *et al*. 2004, 2010).

Statistical analysis: One-way analysis of variance (*ANOVA*) was used to analyse differences between taxa, separately for each measurement date and for the entire year, as well as to analyse differences between dates of measurements, separately for each taxon. A post-hoc *Tukey*'s test was performed in order to determine homogenous groups. Dependency of ChlF parameters and survival rate was analysed using *Pearson*'s correlation coefficient *r*. The correlation was considered to be significant when a significance level *p* was equal or lower than 0.05. In correlation analysis records from June were excluded in order to avoid disturbances caused by early phenological stage. As on 10–16 November 2016, the first ground frosts occurred (personal observation, data not available due to the temperature sensor malfunction) the data from November 2016 were analysed separately. All calculations were made using *STATISTICA version 13.0* software (*TIBCO Software Inc.*, http://statistica.io., USA).

Results

The winter season of 2015/2016 was not very severe with minimum temperature –5.4°C recorded on the construction surface. In the winter season of 2016/2017, severe frosts occurred in the beginning of January, up to –12.5°C. During the spring and the summer, the surface of the vertical garden was subjected to high solar radiation. In 2016, the maximum temperatures, recorded between 11–15 h, often exceeded 30°C since April and occasionally exceeded 40°C at noon since mid-May till mid-September 2016 (Fig. 1).

All the plants survived well during the growing season and no visible symptoms of damage or losses were noticed. Only in November and December, deciduous plants, such as *Potentilla fruticosa* (a deciduous shrub), *Carex muskingumensis*, *Koeleria glauca*, *Polypodium vulgare*, *Asplenium trichomanes*, *Fragaria vesca*, *Geranium*, and *Heuchera* cultivars showed leaf discolouration and gradual leaf losses. The most harmful seasons for plants were winters. After the winter of 2015/2016, only 16 species and cultivars revealed successful survival (minimum 50% of specimens) from 23 initially planted taxa. The similar results were obtained after the winter of 2016/2017 (Table 1).

In 2015 growing season, differences between the examined taxa were more pronounced in PI_{ABS} than that in F_v/F_m (Table 2). Species and cultivars showing better F_v/F_m results in September mostly performed better also in October, however, some species showed an increase or

Table 2. Changes in maximum quantum efficiency of PSII, F_v/F_m, and performance index, PI_{ABS}, in 23 species and cultivars during 2015 growing season. *Letters* indicate homogeneous groups due to *Tukey*'s *post-hoc* test after *ANOVA* performed on results from each date separately.

Taxon	F_v/F_m September	F_v/F_m October	PI_{ABS} September	PI_{ABS} October
Carex muskingumensis	0.804[a]	0.798[a]	7.518[abcd]	5.878[ab]
Heuchera ‘Plum Royale’	0.804[a]	0.748[abc]	8.868[ab]	4.112[bcde]
Cotoneaster dammeri ‘Eichholz’	0.790[ab]	0.702[abcd]	9.950[a]	2.298[efgh]
Iberis sempervirens	0.776[abc]	0.724[abcd]	6.588[bcde]	5.506[ab]
Pachysandra terminalis	0.776[abc]	0.680[abcd]	8.000[abc]	4.314[bcd]
Cotoneaster dammeri	0.774[abc]	0.728[abcd]	7.774[abcd]	4.090[bcde]
Potentilla fruticosa	0.774[abc]	0.714[abcd]	5.484[cdefg]	2.936[def]
Armeria maritima ‘Alba’	0.772[abc]	0.728[abcd]	5.026[defgh]	6.390[a]
L. angustifolia ‘Hidcote Blue Strain’	0.772[abc]	0.726[abcd]	6.842[bcd]	2.382[efg]
Geranium × cantabrigiense ‘Cambridge’	0.770[abc]	0.728[abcd]	3.774[efghi]	3.142[def]
Armeria maritima ‘Splendens Perfecta’	0.754[abc]	0.760[ab]	5.758[cdef]	5.120[abc]
Vinca minor ‘La Grave’	0.752[abc]	0.638[bcde]	5.446[cdefg]	2.226[efghi]
Koeleria glauca	0.748[abc]	0.754[abc]	5.342[cdefgh]	4.750[abcd]
Fragaria vesca ‘Rugia’	0.746[abc]	0.676[abcd]	1.748[ikl]	0.878[ghi]
Asarum europaeum	0.742[abc]	0.640[bcde]	3.754[efghi]	1.370[fghi]
Vinca minor ‘Illumination Cahill’	0.740[abc]	0.612[cdef]	3.278[fghik]	0.736[ghi]
Polypodium vulgare	0.728[abc]	0.772[ab]	3.304[fghik]	3.452[cde]
Hedera helix	0.694[abc]	0.522[ef]	2.796[ghikl]	0.356[i]
Euonymus fortunei ‘Emerald'n Gold’	0.692[abc]	0.638[bcde]	1.782[ikl]	1.456[fhig]
Asplenium trichomanes	0.688[bc]	0.596[def]	0.802[kl]	0.442[hi]
Saxifraga umbrosa	0.680[bc]	0.720[abcd]	2.478[hikl]	3.068[def]
Heuchera ‘Marmalade’	0.672[c]	0.660[abcde]	1.474[ikl]	0.556[ghi]
Euonymus fortunei ‘Coloratus’	0.382[d]	0.481[f]	0.318[l]	0.550[ghi]

a decrease of F_v/F_m. This was reflected to some extent by PI_{ABS} which showed more distinct differences between taxa. During the 2016 growing season, F_v/F_m varied between the examined taxa only to a minor extent or did not differ at all in the case of August (Table 3). Likewise, differences between dates were not significant in the majority of cases (Fig. 2); however, a depletion was visible in July and August in most taxa. The greatest differences between species were visible in November. *Potentilla fruticosa*, *Carex muskingumensis*, and *Koeleria glauca* showed the lowest values which may be ascribed to autumn leaf senescence. In *Potentilla*, the November values were significantly lower than that in October, while in other species it was not apparent. However, in most taxa, we noticed a visible tendency to diminish quantum efficiency of PSII at the end of the growing season (Fig. 2). On the contrary, PI_{ABS} and PI_{total} varied in the examined taxa considering both species and dates (Table 4). Moreover, some species, such as *Armeria maritima* and *Cotoneaster dammeri*, improved their efficiency during the growing season, while others showed decreasing values, *e.g.*, *Carex muskingumensis* and *Heuchera*.

Survival ability of examined species and cultivars was not correlated with performance indices of PSII, PI_{ABS}, and PI_{total}. Likewise, F_v/F_m (TR_0/ABS) and ψ_{E0} (ET_0/TR_0) were not linked to the winter survival of plants (Table 5).

On the contrary, particular parameters describing specific energy fluxes per active RC were linked to some extent with winter survival rates. ET_0/RC and RE_0/RC were the most related to winter survival parameters. The correlation significance here was below 0.05 in all cases of analysed survival rates and high *r* values were noted only in November 2016, 0.622 and 0.533 for ET_0/RC and RE_0/RC, respectively, and 0.717 and 0.600, respectively, in November 2017 (Table 5). TR_0/RC average annual values from 2016 growing season were more or less even, while ABS/RC differed to a greater extent (Fig. 3*A*). Nevertheless, the differences were species specific rather than linked with winter hardiness. Contrary to this, ET_0/RC and especially RE_0/RC reflected the difference between the best and the moderate survivors (Fig. 3*B*).

Discussion

In case of vertical gardens, the main goal of the cultivation is to provide aesthetic value. Therefore, the ability of plants to maintain good and healthy condition of leaves is crucial. In practice, a visual assessment of plant vitality is good enough to make decisions about replacing poorly performing specimens. However, this is time- and cost-consuming, particularly, taking into account that vertical gardens are sometimes established on high facades. Our experiment aimed to evaluate the usefulness of several woody and non-woody perennial species for outdoor vertical gardens using physiology-based methods.

Both performance indices showed high differences between the examined taxa, but the pattern of differences was rather not repeatable on consecutive dates of measurements. Moreover, PI_{ABS} records did not show the same pattern in two years of measurements. This suggests that PI_{ABS} and PI_{total} records reflected a temporary plant condition rather than overall tendencies (Živčák *et al.* 2014a). These parameters are very sensitive to different kinds of stress, *e.g.*, excess or insufficient light (Kalaji *et al*. 2012) or lower but not chilling temperatures (Zushi *et al.* 2012, Snider *et al.* 2018). Performance indices are

Table 3. Changes in maximum quantum efficiency of PSII, F_v/F_m, in 17 species and cultivars during 2016 growing season. *Letters* indicate homogeneous groups due to *Tukey*'s *post-hoc* test after *ANOVA* performed on results from each date separately; ns, nonsignificant differences.

Taxon	F_v/F_m June	July	August	September	October	November
Heuchera 'Plum Royale'	0.706^{a}	0.674^{a}	0.646^{ns}	0.648^{ab}	0.736^{ab}	0.692^{abc}
Potentilla fruticosa	0.686^{a}	0.678^{a}	0.582^{ns}	0.690^{ab}	0.698^{ab}	0.528^{cd}
Euonymus fortunei 'Emerald'n Gold'	0.682^{ab}	0.636^{a}	0.628^{ns}	0.632^{ab}	0.598^{bcd}	0.564^{abcd}
Iberis sempervirens	0.680^{ab}	0.674^{a}	0.620^{ns}	0.772^{a}	0.774^{a}	0.706^{abc}
Fragaria vesca 'Rugia'	0.674^{ab}	0.608^{a}	0.660^{ns}	0.698^{a}	0.662^{abc}	0.634^{abcd}
Koeleria glauca	0.672^{ab}	0.574^{ab}	0.512^{ns}	0.684^{ab}	0.742^{ab}	0.544^{bcd}
Carex muskingumensis	0.666^{ab}	0.642^{a}	0.612^{ns}	0.490^{b}	0.482^{d}	0.408^{d}
L. angustifolia 'Hidcote Blue Strain'	0.654^{ab}	0.634^{a}	0.722^{ns}	0.710^{a}	0.664^{abc}	0.732^{abc}
Cotoneaster dammeri	0.632^{ab}	0.590^{a}	0.682^{ns}	0.718^{a}	0.722^{ab}	0.736^{abc}
Geranium × cantabrigiense 'Cambridge'	0.592^{abc}	0.530^{ab}	0.600^{ns}	0.604^{ab}	0.762^{a}	0.612^{abcd}
Cotoneaster dammeri 'Eichholz'	0.588^{abc}	0.694^{a}	0.692^{ns}	0.758^{a}	0.740^{ab}	0.678^{abc}
Armeria maritima 'Alba'	0.552^{abc}	0.330^{b}	0.522^{ns}	0.660^{ab}	0.812^{a}	0.782^{a}
Euonymus fortunei 'Coloratus'	0.546^{abc}	0.512^{ab}	0.608^{ns}	0.636^{ab}	0.526^{cd}	0.574^{abcd}
Armeria maritima 'Splendens Perfecta'	0.544^{abc}	0.540^{ab}	0.612^{ns}	0.724^{a}	0.784^{a}	0.762^{ab}
Pachysandra terminalis	0.544^{abc}	0.672^{a}	0.600^{ns}	0.706^{a}	0.690^{ab}	0.670^{abc}
Hedera helix	0.476^{bc}	0.480^{ab}	0.466^{ns}	0.610^{ab}	0.592^{bcd}	0.582^{abcd}
Heuchera 'Marmalade'	0.422^{c}	0.600^{a}	0.458^{ns}	0.634^{ab}	0.602^{bcd}	0.590^{abcd}

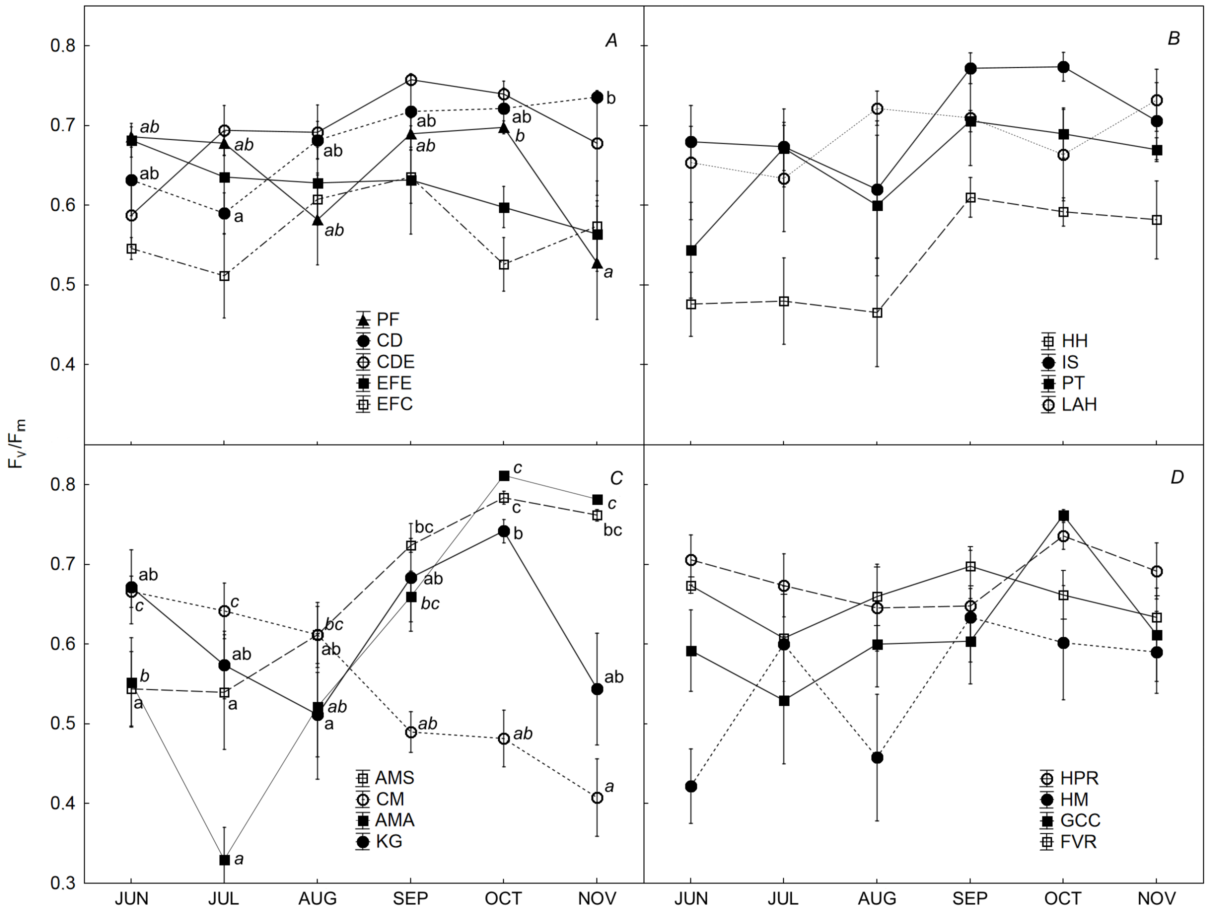

Fig. 2. Maximum quantum efficiency of photosystem II (F_v/F_m) during the growing season 2016. Examined taxa were grouped in order to facilitate reading the graphs (*A–D*). Species/cultivar symbols are explained in the Table 1. Means ± SE, *small letters* indicate homogenous groups based on *ANOVA* and post-hoc *Tukey*'s test, *regular* in AMS, CD, KG, *italics* in AMA, CM, PF; *lacking letters* denote nonsignificant differences.

the calculation of three (PI_{ABS}) or four (PI_{total}) parameters of efficiencies describing different processes in energy conversion. Thus, when analysing PIs solely, a decrease in one efficiency may be not visible when another efficiency increases (Swoczyna *et al.* 2019). This is the reason why the order of homogenous groups in PI_{ABS} and PI_{total} does not reflect the order in F_v/F_m, although mathematically transformed F_v/F_m is the component of PI_{ABS} and PI_{ABS} is a component of PI_{total}. In fact, PI_{ABS} and PI_{total} may show opposite reactions as Zushi *et al.* (2012) found in tomato under chilling stress. Performance indices were formerly used to rank varieties or provenances according to given traits or stress reactions (Bussotti *et al.* 2010, Jedmowski and Brüggemann 2015). Maximum quantum efficiency of PSII, F_v/F_m, the most known ChF parameter, showed the lowest differences between taxa (Table 3). On the other hand, plants in the vertical garden showed low F_v/F_m in both growing seasons, the optimal values exceeding 0.8 were recorded only in *Carex muskingumensis* and *Heuchera* 'Plum Royale' in September 2015. In 2016, F_v/F_m hardly exceeded 0.7. This may result from the time of measurements which were done about noon time. F_v/F_m is usually affected by midday depression (Valentini *et al*. 1995). F_v/F_m was previously mentioned as a good indicator of high light stress (Kalaji *et al.* 2012, Dąbrowski *et al*. 2015). All the plants grew on a south-oriented wall and faced the same light conditions. Most of the species of shaded habitats (*Asarum europaeum*, *Asplenium trichomanes*, *Polypodium vulgare*, *Hedera helix*, *Pachysandra terminalis*, *Vinca minor*) showed lower F_v/F_m and within the taxa of higher F_v/F_m, the species from open, light-exposed habitats dominated (*Iberis sempervirens*, *Koeleria glauca*, *Lavandula angustifolia*, *Potentilla fruticosa*). ET_0/TR_0 records did not show any clear pattern (data not shown); however, in former works higher ET_0/TR_0 values were found in plants of higher environmental plasticity or better adaptability to stress (Bussotti *et al.* 2010, Kalaji *et al.* 2011, Swoczyna *et al.* 2015). In our experiment, performance indices, F_v/F_m and ET_0/TR_0, did not correlate with survival rates after both preceding and following winters (Table 5). This suggests that the efficiencies of PSII performance were adjusted to temporary conditions of the plant growth.

On the contrary, parameters describing specific energy fluxes per active RC were connected to some extent with the winter survival rates. The most related to winter

Table 4. Changes in performance indices PI_{ABS} and PI_{total} in 17 species and cultivars during 2016 growing season. *Letters* indicate homogeneous groups due to *Tukey*'s *post-hoc* test after *ANOVA* performed on results from each date separately.

Taxon	PI_{ABS} June	July	August	September	October	November
L. angustifolia ‘Hidcote Blue Strain’	3.866^{a}	2.090^{ab}	2.228^{b}	3.712^{bc}	2.786^{defg}	4.538^{a}
Euonymus fortunei ‘Emerald'n Gold’	3.664^{a}	0.498^{de}	0.282^{e}	2.750^{bcd}	1.748^{efgh}	1.492^{cd}
Heuchera ‘Plum Royale’	2.564^{b}	0.300^{e}	0.550^{de}	2.254^{cde}	3.294^{cde}	1.640^{c}
Koeleria glauca	2.490^{b}	0.476^{de}	0.164^{e}	2.822^{bcd}	1.622^{efgh}	0.154^{e}
Potentilla fruticosa	1.496^{c}	1.242^{cd}	1.108^{cd}	2.138^{cdef}	1.566^{efgh}	0.158^{e}
Iberis sempervirens	1.382^{cd}	2.246^{a}	3.350^{a}	10.804^{a}	5.890^{ab}	0.900^{cde}
Cotoneaster dammeri	0.872^{cde}	0.388^{e}	0.560^{de}	3.924^{bc}	4.552^{bcd}	4.840^{a}
Armeria maritima ‘Alba’	0.788^{cde}	0.604^{cde}	0.394^{de}	1.468^{def}	7.980^{a}	4.744^{a}
Fragaria vesca ‘Rugia’	0.716^{cde}	0.368^{c}	1.648^{bc}	0.738^{ef}	1.496^{efgh}	0.272^{de}
Carex muskingumensis	0.704^{cde}	0.630^{cde}	0.570^{de}	0.212^{f}	0.136^{h}	0.030^{e}
Armeria maritima ‘Splendens Perfecta’	0.682^{cde}	0.030^{e}	0.872^{de}	3.126^{bcd}	4.734^{bcd}	3.276^{b}
Pachysandra terminalis	0.544^{de}	2.038^{ab}	0.360^{de}	1.552^{def}	5.564^{abc}	1.530^{cd}
Geranium × *cantabrigiense* ‘Cambridge’	0.454^{e}	0.052^{e}	0.568^{de}	0.652^{ef}	2.442^{defgh}	0.542^{cde}
Cotoneaster dammeri ‘Eichholz’	0.302^{e}	2.532^{a}	1.726^{bc}	4.228^{b}	5.458^{bc}	4.152^{ab}
Hedera helix	0.250^{e}	0.312^{e}	0.502^{de}	0.502^{ef}	0.486^{gh}	0.346^{de}
Euonymus fortunei ‘Coloratus’	0.174^{e}	0.196^{e}	0.398^{de}	0.488^{ef}	0.290^{h}	0.208^{e}
Heuchera ‘Marmalade’	0.048^{e}	0.450^{e}	0.386^{de}	0.614^{ef}	0.752^{fgh}	0.610^{cde}
	PI_{total}					
Koeleria glauca	4.584^{a}	1.856^{ab}	0.926^{bcde}	3.486^{bcd}	1.930^{defg}	0.374^{ef}
Heuchera ‘Marmalade’	4.059^{ab}	2.096^{ab}	1.048^{bcd}	1.234^{defg}	0.836^{fghi}	0.439^{ef}
L. angustifolia ‘Hidcote Blue Strain’	3.415^{abc}	2.113^{ab}	1.058^{bcd}	5.081^{bc}	5.716^{b}	6.355^{a}
Euonymus fortunei ‘Emerald'n Gold’	3.062^{bcd}	2.459^{a}	1.230^{ab}	3.125^{cde}	1.918^{defgh}	0.718^{ef}
Iberis sempervirens	2.882^{bcde}	2.223^{ab}	1.110^{bc}	18.993^{a}	10.826^{a}	2.658^{cd}
Geranium × *cantabrigiense* ‘Cambridge’	2.865^{bcde}	1.315^{bc}	0.660^{cdef}	2.869^{cdefg}	1.702^{efghi}	0.533^{ef}
Armeria maritima ‘Alba’	2.408^{cdef}	1.408^{abc}	0.702^{bcdef}	2.611^{cdefg}	3.308^{cde}	4.004^{bc}
Cotoneaster dammeri	2.310^{cdef}	1.420^{abc}	0.712^{bcdef}	2.926^{cdef}	3.434^{cd}	3.938^{bc}
Heuchera ‘Plum Royale’	1.919^{defg}	0.408^{cd}	0.204^{fg}	1.835^{defg}	1.270^{fghi}	0.699^{efc}
Cotoneaster dammeri ‘Eichholz’	1.468^{efgh}	0.763^{cd}	0.380^{efg}	4.609^{bc}	4.632^{bc}	4.656^{b}
Potentilla fruticosa	1.147^{fgh}	0.585^{cd}	0.442^{efg}	1.428^{defg}	0.816^{fghi}	0.200^{f}
Pachysandra terminalis	1.066^{fgh}	0.521^{cd}	0.260^{fg}	1.456^{defg}	1.744^{efghi}	2.031^{de}
Fragaria vesca ‘Rugia’	0.834^{gh}	0.408^{cd}	0.202^{fg}	0.293^{fg}	0.260^{hi}	0.230^{f}
Armeria maritima ‘Splendens Perfecta’	0.823^{gh}	0.549^{cd}	0.532^{defg}	6.133^{b}	4.316^{bc}	2.500^{cd}
Carex muskingumensis	0.649^{gh}	0.416^{cd}	0.208^{fg}	0.213^{g}	0.134^{i}	0.052^{f}
Euonymus fortunei ‘Coloratus’	0.268^{h}	0.141^{d}	0.072^{g}	0.513^{efg}	0.488^{ghi}	0.458^{ef}
Hedera helix	0.056^{h}	0.033^{d}	1.758^{a}	0.359^{fg}	0.538^{fghi}	0.713^{ef}

survival parameters were ET_0/RC and RE_0/RC. The correlation significance here was below 0.05 in all cases of analysed survival rates. However, we should point out that during the growing season (July–September) the *Pearson*'s correlation coefficient *r* was below or close to 0.4, thus ET_0/RC and RE_0/RC were probably adjusted to temporary conditions in the summer. Higher *r* values were noted only when analysing the correlation of November measurements (Table 5). The similar results were found by Fan *et al.* (2015) while, simultaneously, quantum yield of electron transport (φ_{E0}) was diminished. These results may suggest that species with high electron transport rates through electron transport chain beyond plastoquinone, Q_A, referred to a pool of active RCs, are more resistant to chilling or freezing stress. Probably, they are fitted out with mechanisms for effective electron transport beyond PSII RCs. This adaptation seems to be necessary in species which prolong their photosynthetic activity till frosts while growing in open landscape. Cold sensitive plants, like tomato, may reveal a depletion of ET_0/RC under chilling stress (Zushi *et al.* 2012). The highest average ET_0/RC was found in evergreen species (*Armeria maritima*, *Lavandula angustifolia*, and *Koeleria glauca*). Also Rapacz *et al.* (2015) ascertained ET_0/RC correlated with winter field survival in wheat, while ABS/RC and TR_0/RC were not or even sometimes adversely

Table 5. Correlation between survival rates and parameters obtained from chlorophyll *a* fluorescence [performance index of photosystem II on absorption basis, PI_{ABS}; total performance index, PI_{total}; maximum quantum yield of primary photochemistry, F_v/F_m; efficiency of excited electron movement into the electron transport chain beyond Q_A, ψ_{E0}; specific energy fluxes expressed per active RC, average photon absorption (ABS/RC), energy dissipation (DI_0/RC), exciton trapping (TR_0/RC), electron transport (ET_0/RC), and reduction of end electron acceptors at the PSI acceptor side (RE_0/RC)], *Pearson*'s correlation coefficient *r* and *p*-value. *Bold letters* indicate statistically significant *p*-value and *Pearson*'s correlation coefficient *r* values when $p<0.05$.

Parameters	Successful survival after the winter 2015/2016				Successful survival after the winter 2016/2017			
	July–October 2016		November 2016		July–October 2016		November 2016	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*
PI_{ABS}	–0.122	0.3360	–0.130	0.6323	–0.104	0.4138	–0.186	0.4916
PI_{total}	–0.098	0.4431	–0.188	0.4850	–0.055	0.6667	–0.206	0.4439
F_v/F_m	0.087	0.4964	0.066	0.8105	0.040	0.7547	0.017	0.9504
ψ_{E0}	–0.059	0.6411	0.068	0.8061	–0.029	0.8212	–0.103	0.7057
ABS/RC	0.207	0.1007	0.156	0.5637	**0.262**	**0.0366**	0.281	0.2911
DI_0/RC	0.111	0.3830	0.087	0.7476	0.166	0.1901	0.157	0.5621
TR_0/RC	**0.257**	**0.0402**	0.380	0.1463	**0.322**	**0.0094**	0.488	0.0554
ET_0/RC	**0.332**	**0.0073**	**0.622**	**0.0101**	**0.401**	**0.0010**	**0.717**	**0.0018**
RE_0/RC	**0.340**	**0.0060**	**0.533**	**0.0336**	**0.383**	**0.0018**	**0.600**	**0.0141**

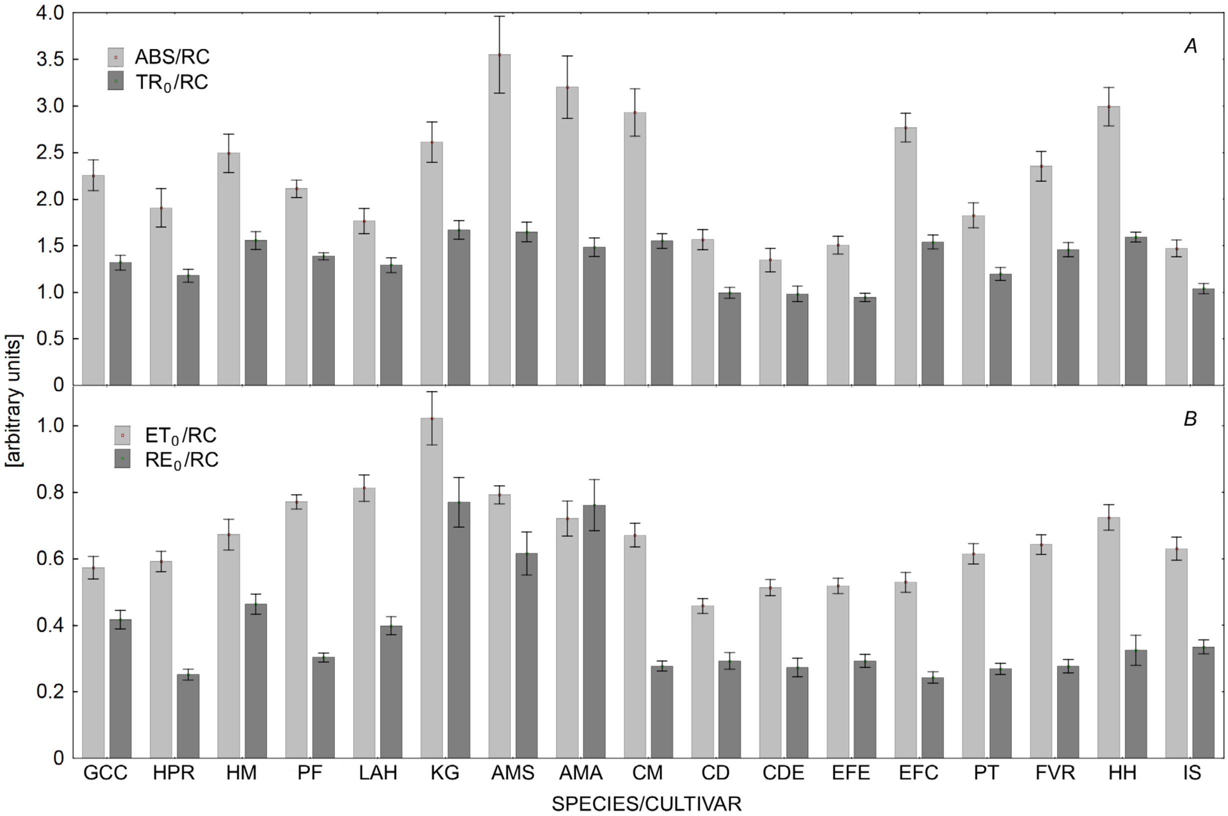

Fig. 3. Specific energy fluxes expressed per active RC: average photon absorption, ABS/RC, and excitation trapping, TR_0/RC (*A*); electron transport, ET_0/RC, and reduction of end electron acceptors at the PSI acceptor side, RE_0/RC (*B*). Averages of the records from June–October 2016, ± SE. Symbols of species and cultivars on the *x*-axis are explained in the Table 1.

correlated. We found significant positive correlation in ABS/RC and TR_0/RC in the summer and early autumn but it was not strong (r = 0.26 and 0.32, respectively). The examined species differed much in average annual light absorption per a pool of active RCs, but not much in average annual trapping per RCs pool. This suggests the higher antenna size in both *Armeria maritima* cultivars, *Carex muskingumensis*, and *Hedera helix*. In *Euonymus fortunei*, the higher ABS/RC was found in green-leaved cultivar 'Coloratus' but not in gold-edged 'Emerald'n

Gold'. It should not be referred only to chlorophyll scarcity in variegated leaves as the leaf clips were positioned on green parts of leaves. Moreover, it seems that leaf colours had no influence on ChF results, yellow-pink *Heuchera* 'Marmalade' showed higher ABS/RC than that of purple-leaved *Heuchera* 'Plum Royale' or green-leaved *Geranium* × *cantabrigiense* and *Iberis sempervirens*.

Conclusions: Winter survival capability in woody and non-woody perennial plants grown in a vertical garden was linked, to some extent, with rearrangement of particular processes related to light phase of photosynthesis process. The most highly correlated parameters with plants survival ability were electron transport flux per RC (at t = 0) (ET_0/RC) and electron flux reducing end electron acceptors at the PSI acceptor side per RC (RE_0/RC). The performance parameters, PI_{ABS} and PI_{total}, as well as efficiencies of energy trapping and electron transport beyond primary electron acceptors at PSII RCs, reflected the condition of the photosynthetic apparatus during the growing season, but had no link to the species resistance to winter stress.

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