Evaluation of Photosynthetic and Yield Traits in Ten Potato Clones and Cultivars Under Farming Conditions in Poland



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Abstract

Photosynthetic properties and tuber yield were compared in seven tetraploid potato (Solanum tuberosum L.) clones ('13-VIII-10', '13-VIII-27', '13-VIII-45', '13-VIII-49', '13-VIII-50', '13-VIII-60', 'TG-97-403') and three cultivars ('Jelly', 'Satina', 'Tajfun') at four localities in Poland under either integrated (Młochów, Boguchwała) or organic (Radzików, Chwałowice) fertilisation conditions applying the 'OJIP' analysis of chlorophyll fluorescence kinetics. The yield-relevant parameters of leaf pigment content and chlorophyll fluorescence were used to rank the tested clones and cultivars applying multidimensional comparative analysis. The results indicate that the clones 13-VIII-10 and 13-VIII-45 cannot be recommended for cultivation, while cv. Taifun performed the best. The assessment of the efficiency of the light reactions of photosynthesis produced a different ranking, indicating that the efficiency is not related to yield, but characterises the balance between light harvesting and dark reactions of photosynthesis. In this respect, the light reactions of photosynthesis were least balanced in clone 13-VIII-49 and cv. Jelly while those of cv. Taifun and clone 13-VIII-60 were the best. The effect of the production system was of minor significance for tuber yield, but local factors dominated. Only in the case of chlorophyll (Chl) and carotenoid (Car) contents of leaves did an effect of the production system became evident, favouring integrated over organic cultivation. By contrast, most of the chlorophyll fluorescence parameters were controlled by soil nitrogen content, including maximum quantum yield for primary photochemistry (φ_{P0}) and the absolute and total performance indices (PI_{Abs}, PI_{Total}). Within a production system precipitation affected the ratio Car/total Chl content.

Keywords Chlorophyll *a* fluorescence · Chlorophyll *b/a* ratio · OJIP transient · *Solanum tuberosum* L

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Introduction

Potato tubers are among the most important staple crops, which supply not only metabolic energy in the form of carbohydrates, but also additional valuable compounds. The nutritional value of potato tubers is characterised by the presence of essential amino acids (especially lysine) and their fatty acid profile, high starch content, dietary fibre and ascorbic acid as well as a low concentration of fats. Potato tubers also contain important amounts of bioactive compounds and antioxidants, including vitamin C, phenolic acids, carotenoids and flavonoids (Reddivari et al. 2007).

Even if potato breeding nowadays focuses on tuber quality, yield still represents an important aspect that has to be kept in mind during breeding programs. The Plant Breeding and Acclimatization Institute (IHAR-PIB) in Młochów, Poland, has bred seven new tetraploid clones with promising tuber quality traits. These clones were compared with three conventional cultivars ('Jelly', 'Satina', 'Tajfun') with respect to their effectiveness of the photosynthetic system and tuber yield under organic and integrated fertilisation. All seven new tetraploid clones are vegetatively propagated hybrids derived from crossbreeding programs between selections of IHAR-PIB and registered potato cultivars. Plants were cultivated under conditions that are representative of current practices at four experimental stations in Poland. At two of them, potato plants were fertilised organically (Radzików, Chwałowice); at the other two (Młochów, Boguchwała), integrated management was applied in order to determine how these two agricultural practices influence the effectiveness of the photosynthetic system. Another important aspect is to what extent the productivity of potato depends on additional, local environmental factors. Therefore, in the present 3-year study, the general effects of organic and integrated fertilisation and differences in nitrogen supply and precipitation on potato tuber yield were assessed.

Recent studies have shown that the measurement of Chl a fluorescence of photosystem (PS) II represents a significant improvement in the assessment of agricultural productivity and a powerful tool in agricultural, environmental and ecological studies (Kalaji et al. 2016). Under natural conditions, plants are exposed to many adverse environmental stress factors. These cause acclimatisation of the photosynthetic apparatus, which, as a consequence, affects plant development, growth, productivity and yield quantity and quality. Photosynthesis is particularly sensitive to environmental constraints (Kalaji et al. 2012), making Chl a fluorescence measurements an important component of studies on the suitability of potato cultivars for organic and integrated production systems. Because Chl a fluorescence kinetics represent a helpful tool for characterising differences among cultivars in their photosynthetic system (Kalaji et al. 2011a), this rapid and non-destructive technique was selected to compare the ten potato clones and cultivars. Due to the substantial role of photosynthesis in carbon metabolism, differences in Chl a fluorescence should reflect and contribute to differences in tuber yield. Chl fluorescence measurements should be complemented with analyses of leaf Chl content (either destructively or non-destructively using a reflectance-based technique) and, as in the present study, with the analysis of yield-relevant parameters, if these are important for the selection of new commercial cultivars. Phenotyping of Chl a fluorescence characteristics represents a promising practice in breeding programs aimed at finding physiological mechanisms related to yield and environmental stress resistance (Kalaji et al. 2011a, b; Brestic et al. 2012; Zivcak et al. 2014).

The assessment of the potato clones and cultivars represents a complex approach because different kinds of variables have to be combined. For this reason, a multidimensional comparative analysis (MCA) is introduced which can examine complex phenomena described by two or more variables. Using MCA, two categories of problems can be solved: similarity studies using the methods of classification and ranking studies with the use of linear ordering methods.

Materials and Methods

The 3-year study (2014–2016) used seven tetraploid potato (Solanum tuberosum L.) clones ('13-VIII-10', '13-VIII-27', '13-VIII-45', '13-VIII-49', '13-VIII-50', '13-VIII-60', 'TG-97-403') of the IHAR-PIB (Poland) and three conventional cultivars ('Jelly', 'Satina', 'Tajfun'), which were originally selected for their tuber carotenoid content. All the tetraploid genotypes represented vegetatively propagated hybrids of a crossbreeding program with selection at the IHAR-PIB and established potato cultivars. Experiments were conducted at four experimental stations in Poland with two of them fertilised organically (Radzików, Chwałowice) and the other two according to integrated management (Młochów, Boguchwała). In each location, the potatoes were planted in a randomised complete block design, with two replicates and ten-plant plots (plus two plants at the margin of each side of the field), at the end of April and harvested at the end of August. After tuber harvest, fresh weight was determined. Then, tubers were cut in small pieces, frozen, stored at -18 °C and finally freeze-dried in order to determine dry weight and water content. Soil type, fertilisation and measures of plant protection are summarised for each locality and year of experiment in Table 1. For Młochów and Boguchwała, the amounts of fertilizer supplied were determined by the results of previously performed soil analyses, which were 0.063 ± 0.004 , 0.056 ± 0.001 and 0.044 ± 0.001 g N kg⁻¹ soil at Młochów in 2014, 2015 and 2016, respectively, and 0.120 ± 0.006 , 0.114 ± 0.001 and 0.115 ± 0.001 g N kg⁻¹ at Boguchwała in 2014, 2015 and 2016, respectively. The analyses for the other two sites were 0.088 ± 0.016 , 0.063 ± 0.001 and 0.085 ± 0.001 g N kg⁻¹ at Chwałowice in 2014, 2015 and 2016, respectively, and 0.100 ± 0.006 , 0.068 ± 0.001 and 0.068 ± 0.001 g N kg⁻¹ at Radzików in 2014, 2015 and 2016, respectively. Total soil nitrogen content of dried samples was determined by the Kjeldahl distillation and titration method according to the research procedure (PB) 37 ed. 3 dated 15/10/2009 (Trawczyński 2015). At both localities with integrated production, Młochów and Boguchwała, different amounts of nitrogen were supplied (Table 1). This experimental set-up was chosen in order to discuss effects with respect to the relative influence of the production system itself and the available nitrogen content.

The photosynthetic capacity of the clones and cultivars was assessed using Chl fluorescence measurements with the Pocket PEA Rapid Screening Chlorophyll Fluorimeter of Hansatech Instruments Ltd. (Norfolk, United Kingdom). Chl *a* fluorescence was measured at the basal part of the terminal leaflet of the youngest completely expanded leaf of each plant, usually the third-, and rarely the second-youngest. Leaflets were dark-adapted with a leaf clip for 30 min, and then, the Kautsky induction curves were recorded by applying a saturating light pulse of white light. The data were analysed in line with Strasser et al. (2000, 2004, 2010). Measurements were performed

Table 1InfoiBoguchwała (integrated	locality cultivat	v, soil type, fertilisation and of plant protection measures at the four experimental sta iion)	tions Radzików, Chwałowice (organic fertilisation) and Młochów,
Locality	Soil type	Year	Fertilizer kg ha ⁻¹	Plant protection measures
Młochów 52° 3' 0" N 20° 46' 7" E	Podzol	2014	90 N, 110 P_2O_5 , 180 K_2O (multi-component fertilizer Lagron 4-8-18 and urea 46%)	Tanos, Altima, Ridomil (6×) (pests); Apacz, Actara, Karate (6×) (beetles); Afalon before emergence, Titus (weeds)
		2015	90 N, 110 P_2O_5 , 180 K_2O (multi-component fertilizer Lagron 4-8-18 and urea 46%)	Tanos, Altima, Ridomil (3×) (pests); Apacz, Actara, Karate (3×) (beetles); Afalon before emergence, Titus (weeds)
		2016	90 N, 110 P_2O_5 , 180 K_2O (multi-component fertilizer Lagron 4-8-18 and urea 46%)	Tanos, Altima, Ridomil (3×) (pests); Apacz, Actara, Karate (5×) (beetles); Afalon before emergence, Titus (weeds)
Boguchwała 49° 58' 59" N 21° 56' 23" E	Cambisol	2014	120 N, 60 P ₂ O ₃ . 180 K ₂ O + 15 t composted manure (multi-component fertilizer Polifoska 6 (6-20-30) and urea 46%) + foliar feeding with Adob Cu, Adob Mn, Adob S and Basfoliar 36 Extra	Pyton Consento, Infinito, Revus (pests); Actara (beetles); Titus (weeds)
		2015	120 N, 60 P ₂ O ₃ . 180 K ₂ O (multi-component fertilizer Polifoska 6 (6-20-30) and urea 46%) + foliar feeding Basfoliar 36 Extra and Basfoliar 12-4-6+S+amino	Ridomil Gold, Infinoto, Pyton Consento, Valbon (pests); Actara (beetles); Plateen before emergence, Agil (weeds)
		2016	120 N, 60 P ₂ O ₅ , 180 K ₂ O (multi-component fertilizer Polifoska 6 (6-20-30) and urea 46% + foliar feeding with Basfoliar 36 Extra and Basfoliar 12-4-6 + S + amino	Ridomil Gold, Infinoto, Pyton Consento (pests); Actara, Proteus (beetles); Afalon & Command before emergence (weeds)
Radzików 52°13'38"N	Phaeozem	2014	composted manure 25 t ha ⁻¹	Miedzian 50WP (pests); weeds mechanically
20°36'55"E		2015	composted manure 25 t ha ⁻¹	Spintor 1× (beetles); weeds mechanically
		2016	composted manure 25 t ha ⁻¹	Spintor 1× (beetles); weeds mechanically
Chwałowice 51° 10' 56" N	Cambisol	2014	composted manure 25 t ha ⁻¹	Miedzian (pests); Spintor 2× (beetles); weeds mechanically
21° 18' 17" E		2015	composted manure 25 t ha ⁻¹	Miedzian (pests); Spintor 2× (beetles); weeds mechanically
		2016	composted manure 25 t ha-1	Miedzian (pests); Spintor 2× (beetles); weeds mechanically

on the 10th and 11th July 2014, the 22nd and 23rd June 2015 and 27th and 28th June 2016, respectively, in the interval 'end of the principal growth stage 5 (59)' to 'beginning of the principal growth stage 6 (61)' according to BBCH growth stage scale potato (Von Hack et al. 1993). On these dates, the photosynthetic capacities of the plants were evaluated under near-optimal environmental conditions.

The interpretation of Chl fluorescence is usually based on the hypothesis that fluorescence is determined by the redox state of the first quinone electron acceptor of PSII (Q_A); hence, the net concentration of Q_A^- should be related to Chl *a* fluorescence yield (Govindjee 2004; Kalaji et al. 2011a). At the 'O' level of Chl fluorescence (or at F_0 in another terminology), all Q_A is considered to be in the oxidised state. The reaction centres (RCs) of PSII are open at F_0 , and hence, photochemical processes operate at the maximum level. By contrast, when Chl *a* fluorescence is maximal (F_m), all RC of PSII are closed and the first quinone electron acceptor of PSII is in the reduced state (Q_A^-). It is hypothesised that F_m is accompanied by a traffic jam of electrons at the electron acceptor side of PSI, resulting in a minimum of photochemical processes (Govindjee 2004; Kalaji et al. 2011a).

Strasser et al. in their pioneering works (2000, 2004, 2010) developed the so-called 'OJIP' analysis, where 'O', 'J', 'I' and 'P' define specific inflexion points of the measured curves. This analysis offers simple equations for energy fluxes for light absorption (ABS), trapping of excitation energy (TR) and electron transport (ET, RE) as well as quantum yields and efficiencies (φ_{P0} , ψ_{E0} , φ_{E0} , δ_{R0} , φ_{R0}), characterising energy absorption by PSII antenna pigments, energy trapping for the reduction of pheophytin and Q_A , electron transport after Q_A^- to intersystem electron acceptors, and reduction of electron acceptors at the PSI acceptor side (Table 2). Because Chl *a* fluorescence kinetics represent a helpful tool for characterising differences among cultivars in their photosynthetic system (Kalaji et al. 2011a), this rapid and non-destructive technique was selected to compare the ten potato clones and cultivars. Due to the substantial role of photosynthesis in carbon metabolism, differences in Chl *a* fluorescence should contribute to differences in tuber yield.

Immediately after measurements of Chl *a* fluorescence, leaves were harvested, placed in a cool-box and transported to the laboratory for pigment analyses. These leaf samples were frozen at -18 °C, freeze-dried and used for the spectrophotometric analyses of Chl and carotenoid contents in line with Wellburn (1994) using methanol as a solvent.

Data analysis was performed with the IBM SPSS STATISTICS version 21 (2017). Because the data were neither normally distributed according to Kolmogorov-Smirnov and Shapiro-Wilk tests nor did the Levene test indicate variance homogeneity, the results of the measurements were compared by nonparametric tests. Mann–Whitney–Wilcoxon tests were used to compare single measurements and the significance level was adjusted in line with Bonferroni ($P < \alpha/n$ with $\alpha = 0.05$ and n = 4 for locality or = 10 for clone or cultivar).

The final characterisation of the photosynthetic system of the tested clones and cultivars was evaluated using multidimensional comparative analysis (MCA), which is based on the comparison of multivariate objects (Grabiński et al. 1989; Mierowska 1996). For this purpose, parameters characterising the photosynthetic pigments and Chl fluorescence were evaluated separately after calculating the mean values from all measurements at the four localities collected during the 3 years of experiments. Using

Parameter	Meaning
RC/CS _m	Measure of the density of the reaction centres (RCs)
ABS/RC	Absorbed photons/energy per RC
TR ₀ /RC	Trapped energy per RC leading to QA reduction
DI ₀ /RC	Lost energy per RC
ET ₀ /RC	Electron transport flux per RC further than Q_A^-
RE ₀ /RC	Electron flux reducing end electron acceptors at the PSI acceptor side per RC
F ₀	Dark fluorescence
F _m	Maximum fluorescence of a dark-adapted leaf
ϕ_{P0}	Maximum quantum yield for primary photochemistry
ψ_{E0}	Probability that an electron moves further than Q _A ⁻
ϕ_{E0}	Quantum yield for electron transport
δ_{R0}	Probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side
ϕ_{R0}	Quantum yield for the reduction of end electron acceptors at the PSI acceptor side
PI _{Abs}	Absolute performance index characterising the energy conservation from photons absorbed by PSII to the reduction of intersystem electron acceptors
PI _{Total}	Total performance index characterising the energy conservation from photons absorbed by PSII to the reduction of end electron acceptors at the PSI acceptor side

 Table 2
 Abbreviations and explanations of the Chl fluorescence parameters calculated from the OJIP measurements

MCA, the genotypes were hierarchised and the method of linear ordering of the investigated objects was applied. A matrix was created implementing the diagnostic variables for each genotype. The procedure used is described in detail in Chrzanowska (2017); however, her final step 4 was modified and the normalisation of the measure was carried out using the following formula to calculate the MCA-variables:

$$MCA_i = o_i/(\bar{o} + 2 \times SD),$$

where o_i represents the distance of each object from the pattern, \bar{o} is the mean value of all objects o_i and SD is their standard deviation.

These MCA variables are the main criterion for organising the examined genotypes. Values vary between 0 and 1, and the smaller the MCA variables, the better the 'leaf pigments' and the 'Chl fluorescence' of the genotype is rated. During the creation of the synthetic measures, the assessed parameters were assigned as positively or negatively affecting tuber yield, which is here considered the goal for an optimisation of the photosynthetic system. So-called 'stimulants' are those characteristics where larger values are more desirable, whereas so-called 'de-stimulants' are parameters where smaller values are preferred. For the sake of completeness, it should be mentioned that 'nominants' are features which are characterised by an optimum value, the so-called 'nominal value', or values within a certain range. For the photosynthetic pigments, the leaf contents of total Chl, Chl a, Chl b and Car, as well as the ratios Chl b/a and Car/ total Chl, were selected and for the evaluation of the electron transport, the parameters

RC/CS_m, ABS/RC, TR₀/RC, ET₀/RC, RE₀/RC, DI₀/RC, F₀ and F_m, as well as the efficiencies φ_{P0} , ψ_{E0} , φ_{E0} , δ_{R0} and φ_{R0} and performance indices (PI_{Abs}, PI_{Total}), were tested (Table 2).

Results and Discussion

Effect of Locality and Production System

Temperature differences among localities were small (Figs. 1, 2, 3 and 4) with the mean values of the 3 years lowest at Chwałowice (14.4 °C), intermediate at Boguchwała and Młochów (14.5 °C) and highest at Radzików (14.7 °C). Precipitation varied among localities and years (Figs. 1, 2, 3 and 4) with the mean precipitation highest at Chwałowice, followed closely by Boguchwała. It was intermediate at Młochów and lowest at Radzików (Table 3). Nitrogen content was highest in the soil of Boguchwała, followed by Radzików and Chwałowice, while the content was lowest in Młochów (Table 3). Tuber yield and tuber dry weight were similar among the localities Młochów, Boguchwała and Radzików, but significantly lower at Chwałowice. By contrast, tuber water content was significantly lower at Młochów, but similar among Boguchwała, Radzików and Chwałowice (Table 3). Yield parameters were not consistently related to differences in soil nitrogen content, the production system or mean precipitation. Tuber dry weight was slightly higher under integrated production, but within each production system a high precipitation tended to reduce tuber dry weight. A lower yield under organic cultivation was also reported by Maggio et al. (2008), who found a reduction of 25% in fresh-weight marketable yield compared to integrated production at the experimental farm of the University of Naples (Italy) using the potato cultivars Agria and Merit.

The analysis of leaf pigments revealed significant differences among localities, which, in most instances, reflected significant differences between organic and



Fig. 1 Precipitation and temperature from March to September at Boguchwała during the years 2014, 2015 and 2016



Fig. 2 Precipitation and temperature from March to September at Radzików during the years 2014, 2015 and 2016

integrated fertilisation (Table 4). Organic fertilisation was accompanied by lower contents of total Chl (14.2 vs. 20.6 mg g⁻¹ DM), Chl *a* (10.1 vs. 14.3 mg g⁻¹ DM), Chl *b* (4.1 vs. 6.3 mg g⁻¹ DM) and Car (3.7 vs. 5.2 mg g⁻¹ DM) in potato leaves. The 31% lower total Chl content suggests interpretation of the results as indicative of a suboptimal availability of nitrogen in the plants fertilised organically, because a low Chl content is generally coupled with a low nitrogen content in leaves (Vos and Bom 1993; Mauromicale et al. 2006). However, a comparison of soil nitrogen content indicates that the highest and lowest contents were found in integrated production due to different amounts of nitrogen supplied (Table 1), proving that it is not the soil nitrogen content but the production system that limits leaf Chl content and, hence, the availability of



Fig. 3 Precipitation and temperature from March to September at Chwałowice during the years 2014, 2015 and 2016





nitrogen. Thus, the present result confirms Maggio et al. (2008) and Ierna and Parisi (2014) that organic fertilisation does not provide nitrogen in a form that is as readily accessible to plants as from conventional fertilizers.

Table 3Differences in soil nitrogen content after harvest, mean precipitation during the cultivation period(March–September), potato tuber yield, water content and dry weight, among different localities. 1. Młochów,2. Boguchwała, 3. Radzików, 4. Chwałowice. Different letters indicate significant differences by Mann–Whitney–Wilcoxon tests

	$Mean \pm SD$	Soil nitrogen content	Fertilisation	Precipitation
Soil N content (g kg ⁻¹ soil)	1. 0.55 ± 0.09 c 2. 1.16 ± 0.04 a 3. 0.79 ± 0.17 b 4. 0.79 ± 0.14 b		integrated integrated organic organic	"medium" "higher" "lower" "higher"
Mean precipitation (mm)	1. 351 ± 90 2. 390 ± 68 3. 321 ± 103 4. 406 ± 132	lower higher medium medium	integrated integrated organic organic	
Tuber yield (t/ha)	1. 34.2 ± 7.7 a	lower	integrated	"medium"
	2. 37.3 ± 10.9 a	higher	integrated	"higher"
	3. 35.5 ± 12.4 a	medium	organic	"lower"
	4. 14.5 ± 3.4 b	medium	organic	"higher"
Tuber water content (%)	1. 78.3 ± 2.8 b	lower	integrated	"medium"
	2. 81.0 ± 3.2 a	higher	integrated	"higher"
	3. 80.9 ± 4.1 a	medium	organic	"lower"
	4. 81.4 ± 4.3 a	medium	organic	"higher"
Tuber dry mass (t/ha)	1. 7.42 ± 2.61 a	lower	integrated	"medium"
	2. 7.09 ± 3.80 a	higher	integrated	"higher"
	3. 6.78 ± 6.43 a	medium	organic	"lower"
	4. 2.70 ± 1.71 b	medium	organic	"higher"

	$Mean \pm SD$	Soil nitrogen content	Fertilisation	Precipitation
Total Chl (mg g ⁻¹ DM)	1. 21.40 ± 7.02 a	lower	integrated	"medium"
	2. 19.84 ± 7.31 b	higher	integrated	"higher"
	3. 13.81 ± 6.37 c	medium	organic	"lower"
	4. 14.66 ± 7.07 c	medium	organic	"higher"
Chl a (mg g ⁻¹ DM)	1. 14.97 ± 4.56 a	lower	integrated	"medium"
	2. 13.66 ± 4.84 b	higher	integrated	"higher"
	3. 9.83 ± 4.39 c	medium	organic	"lower"
	4. 10.41 ± 4.95 c	medium	organic	"higher"
Chl b (mg g ⁻¹ DM)	1. 6.43 ± 2.52 a	lower	integrated	"medium"
	2. 6.18 ± 2.56 a	higher	integrated	"higher"
	3. 3.98 ± 2.02 b	medium	organic	"lower"
	4. 4.24 ± 2.15 b	medium	organic	"higher"
Chl b/a	1. 0.421 ± 0.050 b	lower	integrated	"medium"
	2. 0.446 ± 0.056 a	higher	integrated	"higher"
	3. 0.399 ± 0.046 d	medium	organic	"lower"
	4. 0.406 ± 0.037 c	medium	organic	"higher"
Car (mg g ⁻¹ DM)	1. 5.66 ± 2.82 a	lower	integrated	"medium"
	2. 4.84 ± 2.32 b	higher	integrated	"higher"
	3. 3.60 ± 1.90 c	medium	organic	"lower"
	4. 3.81 ± 2.35 c	medium	organic	"higher"
Car/total Chl	1. 0.262 ± 0.094 a	lower	integrated	"medium"
	2. 0.249 ± 0.076 b	higher	integrated	"higher"
	3. 0.271 ± 0.087 a	medium	organic	"lower"
	4. 0.257 ± 0.073 b	medium	organic	"higher"

 Table 4
 Differences in leaf pigment content among studied localities.
 1. Młochów,
 2. Boguchwała (both integrated cultivation),
 3. Radzików,
 4. Chwałowice (organic fertilisation).
 Different letters indicate significant differences by Mann–Whitney–Wilcoxon tests

Chl. chlorophyll, Car. carotenoids

Generally, leaf Chl content is coupled with leaf nitrogen content, and according to the theory of optimal nitrogen partitioning within a leaf, the Chl b/a ratio is expected to decrease when leaf N content decreases (Kitajima and Hogan 2003). In principal, this relationship is confirmed by the observation that the Chl b/a ratio is reflected in the impact of the production system such as total Chl content (Table 4). In addition, the Chl b/a ratio is, together with the ratio Car/total Chl, also affected by the mean precipitation (Table 4). Within a production system, the Chl b/a ratio was higher when the precipitation was high. It is generally known that under drought stress, the reduction of Chl b is greater than that of Chl a, resulting in a decrease in the Chl b/a ratio. However, the opposite response of the Chl b/a ratio has also been documented (Ashraf and Harris 2013). It is, therefore, suggested to interpret the dependency of the Chl b/a ratio on precipitation as a consequence of a temporarily occurring water shortage at Młochów and Radzików.

The increase in the ratio Car/total Chl under a medium or low precipitation regime within a production system may be interpreted similarly. Carotenoids not only contribute to light harvesting, but they may also contribute to quenching of excessive light energy (Demmig-Adams and Adams III 1996). This characteristic of the xanthophyll cycle may be involved in the case of an imbalance of water and light availability and results in an increase of carotenoids content relative to total Chl content if water

becomes a temporarily limiting factor. In addition, carotenoids are also present in the plant cellular membranes, where they protect from light-dependent oxidative damage. The role of carotenoids in scavenging reactive oxygen species has been studied by Davison et al. (2002) and is summarised in Ashraf and Harris (2013).

The light-use efficiency of the photosynthetic system is difficult to predict, because the partitioning of leaf N between ribulose bisphosphate carboxylase oxygenase (Rubisco) and the light harvesting complex consisting of Chl and attached proteins is likely to be genotype-dependent (Veres et al. 2017), balancing the harvesting of light energy and its utilisation in the dark reactions of photosynthesis in relation to environmental factors such as water availability. For the studied potato clones and cultivars, the Chl a fluorescence parameters, such as RC/CS_m, φ_{P0} , φ_{E0} , φ_{R0} , PI_{Abs} and PI_{Total}, followed in most cases the soil nitrogen content (Table 5), ABS/RC was inversely correlated with soil nitrogen content. The listed parameters best characterise the efficiency of the light reactions. While it is not unexpected that they follow soil nitrogen content, it is worth noting that leaf Chl content, in contrast, is strongly affected by the production system (Table 4). However, F_m is also influenced by the production system (Table 5) and F_m has indeed been reported by Miranda et al. (1981) and Netto et al. (2005) as proportional to total chlorophyll content. However, Netto et al. (2005) observed a linear relationship between total Chl content and F_m only up to a Chl content of about 150-200 µmol m⁻². For a further increase in total Chl content, a stable behaviour in the F_m values was observed.

It was suggested previously to interpret the relationship between Chl content and production system as indicative of a sub-optimal availability of nitrogen in the plants fertilised organically. However, the observed relationship of the majority of the chlorophyll fluorescence parameters with soil nitrogen content questions this general conclusion. If these chlorophyll fluorescence parameters are not related by the production system to leaf Chl content, they may be influenced by other compounds affected by the soil nitrogen content, for example, the activity of Rubisco, which is the dominating enzyme of leaves. If this hypothesis is correct, the effectiveness of the light reactions of photosynthesis should be strongly coupled to the energy needs of the dark reactions of photosynthesis. Since neither leaf nitrogen content nor Rubisco activity were assessed in the present study, it remains unsettled, in what different ways the soil nitrogen content and the production system affected leaf nitrogen and Chl contents as well as chlorophyll fluorescence and Rubisco activity.

If chlorophyll fluorescence and Rubisco activity were well coordinated, it would be reasonable that the density of the reaction centres (RC/CS_m) is controlled by Rubisco activity. Likewise, the measure of absorbed photons per RC (ABS/RC) may be inversely correlated with Rubisco activity and RC/CS_m. In a light-exposed location as in the case of potato production, there is always the danger of an excessive amount of light energy transferred to a single RC. As a consequence, the density of RCs may be increased while the absorbed energy per RC may be reduced in order to protect the light harvesting system and optimise light harvesting. Further steps to balance electron transport to the end electron acceptors at the PSI acceptor side are best characterised by the efficiencies φ_{P0} , ψ_{E0} , δ_{R0} and φ_{R0} . It is worth noting that φ_{P0} , φ_{E0} and δ_{R0} are all related to soil nitrogen content (Table 5), while the single steps ψ_{E0} and δ_{R0} cannot be related with certainty to one of the considered factors (soil nitrogen content, cultivation system, precipitation). Since φ_{R0} is the product of φ_{P0} , ψ_{E0} and δ_{R0} , it is

	$Mean \pm SD$	Soil nitrogen content	Fertilisation	Precipitation
RC/CS _m	1. 21,742 ± 6465 c	lower	integrated	"medium"
	2. 26,569 ± 3891 a	higher	integrated	"higher"
	3. 24,497 ± 7659 b	medium	organic	"lower"
	4. 23,370 ± 6571 b	medium	organic	"higher"
ABS/RC	1. 1.680±0.331 a	lower	integrated	"medium"
	2. 1.348±0.203 c	higher	integrated	"higher"
	3. 1.461±0.270 b	medium	organic	"lower"
	4. 1.474±0.223 b	medium	organic	"higher"
TR ₀ /RC	1. 1.292±0.213 a	lower	integrated	"medium"
	2. 1.108±0.156 c	higher	integrated	"higher"
	3. 1.160±0.171 b	medium	organic	"lower"
	4. 1.178±0.153 b	medium	organic	"higher"
ET ₀ /RC	1. 0.629 ± 0.081 b	lower	integrated	"medium"
	2. 0.648 ± 0.122 ab	higher	integrated	"higher"
	3. 0.610 ± 0.092 c	medium	organic	"lower"
	4. 0.656 ± 0.098 a	medium	organic	"higher"
RE ₀ /RC	1. 0.333 ± 0.062 a	lower	integrated	"medium"
	2. 0.301 ± 0.039 b	higher	integrated	"higher"
	3. 0.304 ± 0.064 b	medium	organic	"lower"
	4. 0.301 ± 0.054 b	medium	organic	"higher"
F ₀	1. 7920 ± 1988 a	lower	integrated	"medium"
	2. 6258 ± 1014 c	higher	integrated	"higher"
	3. 6784 ± 1554 b	medium	organic	"lower"
	4. 6546 ± 1202 b	medium	organic	"higher"
F _m	1. 35,747 ± 9740 ab	lower	integrated	"medium"
	2. 35,466 ± 5680 a	higher	integrated	"higher"
	3. 34,475 ± 9040 b	medium	organic	"lower"
	4. 33,602 ± 7912 b	medium	organic	"higher"
φ _{P0}	1. 0.774 ± 0.038 c	lower	integrated	"medium"
	2. 0.823 ± 0.013 a	higher	integrated	"higher"
	3. 0.799 ± 0.033 b	medium	organic	"lower"
	4. 0.802 ± 0.024 b	medium	organic	"higher"
ψ_{E0}	1. 0.496 ± 0.085 c	lower	integrated	"medium"
	2. 0.584 ± 0.064 a	higher	integrated	"higher"
	3. 0.530 ± 0.064 b	medium	organic	"lower"
	4. 0.563 ± 0.089 a	medium	organic	"higher"
ϕ_{E0}	1. 0.386 ± 0.078 d	lower	integrated	"medium"
	2. 0.481 ± 0.056 a	higher	integrated	"higher"
	3. 0.424 ± 0.060 c	medium	organic	"lower"
	4. 0.453 ± 0.080 b	medium	organic	"higher"
δ_{R0}	1. 0.539±0.117 a	lower	integrated	"medium"
	2. 0.478±0.098 c	higher	integrated	"higher"
	3. 0.501±0.090 b	medium	organic	"lower"
	4. 0.470±0.117 c	medium	organic	"higher"
φ _{R0}	1. 0.204 ± 0.048 b	lower	integrated	"medium"
	2. 0.226 ± 0.036 a	higher	integrated	"higher"
	3. 0.209 ± 0.030 b	medium	organic	"lower"
	4. 0.206 ± 0.037 b	medium	organic	"higher"
PI _{Abs}	1. 2.544 ± 1.594 d	lower	integrated	"medium"

Table 5 Differences in Chl *a* fluorescence parameters (for abbreviations, see Table 2) among studied localities. 1. Młochów, 2. Boguchwała (both integrated cultivation), 3. Radzików, 4. Chwałowice (organic fertilisation). Different letters indicate significant differences by Mann–Whitney–Wilcoxon tests

	$Mean \pm SD$	Soil nitrogen content	Fertilisation	Precipitation
	2. 5.252 ± 1.745 a	higher	integrated	"higher"
	3. 3.586 ± 1.708 c	medium	organic	"lower"
	4. 4.195 ± 2.015 b	medium	organic	"higher"
PI _{Total}	1. 2.998±1.997 c	lower	integrated	"medium"
	2. 4.917±1.918 a	higher	integrated	"higher"
	3. 3.504±1.573 b	medium	organic	"lower"
	4. 3.567±1.665 b	medium	organic	"higher"

Table 5 (continued)

concluded that the relationship between ϕ_{R0} and soil nitrogen content is determined by ϕ_{P0} , the first step of electron transport.

The parameters RC/CS_m , φ_{P0} , PI_{Abs} and PI_{Total} may be regarded as the most important for the characterisation of Chl fluorescence. RC/CS_m , the efficiency of light harvesting, was highest in Boguchwała, intermediate in Radzików and Chwałowice, and smallest in Młochów (Table 5). The efficiency of chlorophyll fluorescence has traditionally been described using the parameters φ_{P0} PI_{Abs} and PI_{Total} . With respect to these parameters the same ranking was found as in case of RC/CS_m . However, in case of PI_{Abs} , potatoes cultivated at Chwałowice performed better than those grown at Radzików, which might reflect an influence of precipitation, which was higher at Chwałowice than at Radzików (Table 5).

Evaluation of the Photosynthetic System of the Potato Clones and Cultivars

Since the leaf pigment content was mainly affected by the production system and the chlorophyll fluorescence parameters were influenced most by soil nitrogen content, both components of the photosynthetic system were studied separately using MCA.

The analysis, where leaf pigment parameters were related to tuber dry weight, revealed that concentrations of total Chl, Chl a, Chl b and carotenoids were significantly and positively correlated, and hence stimulants (Table 6). The ratios Chl b/a and Car/total Chl were not related to tuber yield.

From total Chl, Chl *a*, Chl *b* and Car contents, the MCAs of yield-relevant leaf pigment properties were calculated for cultivars and clones and correlated with their tuber dry weights (probability = 0.002). The ranking from best to worst leaf pigment parameters started with cv. Tajfun, followed by the clones 13-VIII-27, TG-97-403, 13-

Table 6 Pearson correlation coefficient and probability level of the relationships of single Chl fluorescence parameters and tuber dry weight. Based on these results, the parameters were rated as 'stimulant' or 'de-stimulant' or not related (–)

Parameter	Pearson correlation coefficient	Probability	Evaluation
Total Chl	0.852	0.002	Stimulant
Chl a	0.860	0.001	Stimulant
Chl b	0.821	0.004	Stimulant
Chl b/a	0.490	0.151	_
Car	0.824	0.003	Stimulant
Car/total Chl	-0.561	0.092	_

VIII-50, then cultivars Jelly and Satina, then clones 13-VIII-49, 13-VIII-60 and 13-VIII-10 and finally 13-VIII-45 (Fig. 5).

The correlation between the single parameter Chl *a* content and tuber dry weight was slightly stronger than that between the MCA-variables of yield-relevant leaf pigment properties and tuber dry weight (Table 6, Fig. 6). The ranking was similar to that based on the MCA-variables of yield-relevant leaf pigment properties; however, the clones 13-VIII-49 and 13-VIII-60 exchanged their positions.

From Figs. 5 and 6, it can be deduced that the yield of cv. Taifun and clone 13-VIII-49 was distinctly larger than could be expected from the regression line. Other additional parameters could have significantly affected tuber yield in addition to Chl a and leaf pigment contents, respectively; for example, differences in the efficiencies of the light and dark reactions of photosynthesis, differences in assimilate partitioning resulting in the development of a larger photosynthetic area that later contributed more assimilates to tuber growth, or a higher sink strength of the developing tubers.

Testing the Chl fluorescence parameters for their applicability to yield predictions revealed that only the measure of the density of the reaction centres (RC/CS_m) and the electron flux reducing end electron acceptors at the PSI acceptor side per RC (RE₀/RC), were significantly correlated with tuber yield, the first acting as a stimulant, the second as a de-stimulant (Table 7). RC/CS_m can be related to Chl *a* content per leaf area, because the heart of the reaction centre of the photosynthetic system is a pair of Chl *a* molecules (Dashek and Miglani 2017). This hypothesis was tested, indicating a significant correlation (P = 0.003) between RC/CS_m and Chl *a* content, if clone TG-97-403 was excluded (Fig. 7). Including the latter clone resulted in an insignificant relationship (P = 0.087).

The negative correlation of RE_0/RC with tuber dry weight is best explained by linking RE_0/RC with the energy absorption per reaction centre (ABS/RC), the ratio of both being



Fig. 5 Relationship between the MCA-variable of yield-relevant leaf pigment properties and tuber dry weight in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-49 (\diamondsuit), 13-VIII-50 (\diamondsuit), 13-VIII-60 (\circ), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\Box) and Tajfun (\blacklozenge)



Fig. 6 Relationship between the Chl *a* content of leaves and tuber dry weight in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-45 (\bigtriangleup), 13-VIII-49 (\blacklozenge), 13-VIII-50 (\diamond), 13-VIII-60 (\circ), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\Box) and Tajfun (\blacklozenge)

 $\phi_{R0}~(0.21\pm0.01$ for the cultivars and clones studied). The amount of energy absorbed depends on the balance between the light harvesting complexes and core complexes of the photosynthetic system. In the case of a larger ratio of light harvesting vs. core complexes, relatively more energy is absorbed by a single RC, while a smaller ratio would result in less energy absorbed. In a light saturated environment typical of potato cultivation, a smaller ratio could be expected than for say plants growing on a forest floor. Thus, a

Parameter	Pearson correlation coefficient	Probability	Evaluation
RC/CS _m	0.647	0.043	Stimulant
ABS/RC	-0.482	0.158	_
TR ₀ /RC	-0.488	0.153	-
DI ₀ /RC	-0.452	0.190	_
ET ₀ /RC	-0.382	0.276	-
RE ₀ /RC	-0.673	0.033	De-stimulant
F ₀	0.205	0.569	_
F _m	0.477	0.163	-
ϕ_{P0}	0.392	0.263	_
ψ_{E0}	0.135	0.711	_
ϕ_{E0}	0.176	0.628	_
δ_{R0}	-0.519	0.124	_
ϕ_{R0}	-0.402	0.249	_
PI _{Abs}	0.306	0.390	-
PI _{Total}	-0.084	0.818	_

Table 7 Pearson correlation coefficient and probability level of the relationships of single Chl fluorescence parameters and tuber dry weight. Based on these results, the parameters were rated as 'stimulant' or 'de-stimulant' or not related (–)



Fig. 7 Relationship between the measure of the density of the reaction centres (RC/CS_m) and leaf Chl *a* content in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-45 (\bigtriangleup), 13-VIII-49 (\blacklozenge), 13-VIII-50 (\diamond), 13-VIII-60 (\circ), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\square) and Tajfun (\bullet). The regression line was calculated without clone TG-97-403

smaller energy absorption per RC would represent a strategy to avoid the absorption of excessive energy per RC in a light exposed environment. Higher ratios of RE₀/RC could, thus, be interpreted as indicative of an imbalance of energy absorption and transfer per RC. However, if this interpretation was correct, a negative correlation between ABS/RC and tuber dry weight should be expected, which was not confirmed (Table 7). Consequently, additional modulatory aspects must be involved, described by the efficiencies of electron transport (ϕ_{P0} , ψ_{E0} , ϕ_{E0} , δ_{R0} and ϕ_{R0}).

From RC/CS_m and RE₀/RC, the MCA-variable of yield-relevant Chl fluorescence properties was calculated and found to be significantly correlated with tuber dry weight (probability = 0.021). The ranking from best to worst Chl fluorescence properties of the studied clones and cultivars started with cv. Tajfun, followed by the clones 13-VIII-60, 13-VIII-50, 13-VIII-49, cv. Jelly, clone 13-VIII-27, cv. Satina, and the clones TG-97-403, 13-VIII-10 and 13-VIII-45 (Fig. 8). This ranking differs from that established from the leaf pigment properties. However, cv. Taifun performed best and clones 13-VIII-10 and 13-VIII-45 worst in both approaches. As a consequence of this sophisticated result, in order to draw a general conclusion for the photosynthetic systems of the potato clones and cultivars studied, it was decided to combine both approaches.

The combination of yield-relevant leaf pigment and Chl fluorescence properties revealed that the tested clones and cultivars can be grouped into three distinct clusters (Fig. 9), with cv. Taifun performing best and clones 13-VIII-10 and 13-VIII-45 performing worst. The remaining clones and cultivars grouped in a distinct cluster, so that it is difficult to rank them according to their photosynthetic properties. Still, cv. Taifun and clone 13-VIII-49 plot distinctly above the regression line, indicating that tuber yield is positively affected by other parameters (for discussion see above). Remarkably, clone TG-97-403 plots above the regression line as well, which may be



Fig. 8 Relationship between the MCA-variable of yield-relevant Chl fluorescence properties and tuber dry weight in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-45 (\bigtriangleup), 13-VIII-49 (\blacklozenge), 13-VIII-50 (\diamondsuit), 13-VIII-60 (\bigcirc), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\Box) and Tajfun (\bullet)

due to the comparatively inefficient yield-relevant Chl fluorescence properties when compared to tuber dry weight (Fig. 8). With respect to clone TG-97-403, it is obvious that Chl *a* content and tuber dry weight are well correlated as in the other studied potato clones and cultivars (Fig. 6). However, the relationship between RC/CS_m and leaf Chl *a* content was not typical for clone TG-97-403 (Fig. 7). This may be interpreted as an indication of a non-optimally adjusted Chl fluorescence in this clone, but an inaccurate measurement cannot be excluded.

In order to rank the tested potato clones and cultivars based on their efficiencies of the light reactions of Chl fluorescence, the generally applied parameters φ_{P0} , PI_{Abs} and PI_{Total} for such kind of assessment (Strasser et al. 2000, 2004, 2010; Murchie and Lawson 2013) were used to calculate MCA-variables of Chl fluorescence efficiency. These allowed the tested clones and cultivars to be arranged into three groups (Fig. 10): cv. Tajfun and clone 13-VIII-60 performed most efficiently, followed by a medium rated group with the clones 13-VIII-10, 13-VIII-27, 13-VIII-49, 13-VIII-50, 13-VIII-45, and cv. Satina, finally clone TG-97-403 and cv. Jelly performing least efficiently. It should, however, be kept in mind that the efficiencies of Chl fluorescence of the studied clones and cultivars cannot be compared immediately, because they depend on both energy absorption per RC and ATP and NADPH+H⁺ consumption in the dark reactions of photosynthesis, which may differ among clones and cultivars.

A comparison of the MCA-variable of combined leaf pigment and Chl fluorescence yield-relevant properties and the MCA-variable Chl fluorescence efficiency revealed that in the low yielding clones 13-VIII-10 and 13-VIII-45 light reactions of photosynthesis were sufficiently efficient. Hence, yield of these clones could potentially be increased by promoting leaf Chl content and/or tuber induction in combination with sink strength of the developing tubers. By contrast, electron transport efficiency of the light reactions of photosynthesis was below average in clone TG-97-403 and cv. Jelly.



Fig. 9 Relationship between the MCA-variable of combined leaf pigment and Chl fluorescence yield-relevant properties and tuber dry weight in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-45 (\bigtriangleup), 13-VIII-49 (\blacklozenge), 13-VIII-50 (\diamondsuit), 13-VIII-60 (\circ), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\square) and Tajfun (\blacklozenge)

While for clone TG-97-403, this inefficiency has already been deduced from the MCAvariable of yield-relevant fluorescence properties (Fig. 9), the negative rating of cv. Jelly was unexpected. This latter result emphasises, in line with the correlation



Fig. 10 Relationship between the MCA-variable of combined leaf pigment and Chl fluorescence yieldrelevant properties and the MCA-variable Chl fluorescence efficiency in the tetraploid potato clones 13-VIII-10 (\blacktriangle), 13-VIII-27 (\blacksquare), 13-VIII-45 (\bigtriangleup), 13-VIII-49 (\blacklozenge), 13-VIII-50 (\circlearrowright), 13-VIII-60 (\circlearrowright), TG-97-403 (+) and conventional cultivars Jelly (x), Satina (\Box) and Tajfun (\blacklozenge). The dotted line represents the positions where the data points would be situated if Chl fluorescence efficiency followed the MCA-variables of the yieldrelevant properties

coefficients in Table 7, that less efficiently operating light reactions of photosynthesis do not necessarily impair potato tuber yield but describe an unbalanced relationship between light harvesting and dark reactions of photosynthesis. It may, however, increase the risk for the generation of reactive oxygen species and could, in the worst case, reduce the lifespan of leaves, although this development is non-compulsive.

Conclusion

The present study characterised seven new tetraploid potato clones of the IHAR-PIB in comparison with three established cultivars with respect to their photosynthetic capacities, as determined by leaf pigment content and Chl fluorescence parameters as well as tuber vield under integrated and organic fertilisation at four different locations. Based on the yield-relevant aspects of the present results, the clones 13-VIII-10 and 13-VIII-45 cannot be recommended. The commercially available cv. Taifun behaved best with respect to yield and photosynthetic properties. This Polish cultivar is recommended as one of the best for cultivation in climate change areas, as it is resistant to heat and drought. In addition, plants remove moisture from the deeper layers of the soil but limit foliar transpiration. Last but not least, a change of drought and rain does not cause cracking, hollowing and germination of tubers (pers. communications). Altogether, these characteristics of cv. Taifun may have contributed to the highest tuber yield and photosynthetic capacity observed among the studied clones and cultivars. The remaining clones and cultivars do not differ distinctly from each other in yield and yield-relevant photosynthetic properties. For clone TG-97-403 and cv. Jelly this rating should be considered with care, because the Chl fluorescence measurements suggest that the light reactions of photosynthesis may not be as harmonised or efficient as in the other potato clones and cultivars.

The four localities, where the potato clones and cultivars were cultivated, affected yield and photosynthetic properties in different ways. An unambiguous effect on tuber yield could not be detected, but yield was rather low at Chwałowice when compared with the other localities. Chlorophyll and carotenoid contents of leaves were affected by the production system and were generally lower under organic fertilisation. By contrast, most of the chlorophyll fluorescence characteristics followed soil nitrogen content, while F_m followed the production system, as could be expected due to the, albeit weak, relationship between F_m and Chl content reported in literature. Precipitation affected the ratio Car/total Chl, especially within a production system, which suggests that temporary water shortage in combination with excessive light energy could have led to the enhanced production of reactive oxygen species inducing carotenoid synthesis.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

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