

Higher yielding varieties of common buckwheat (*Fagopyrum esculentum* Moench) with determinate growth habit (single mutation *det*) manifest higher photosynthesis rate at stage of grain filling

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Abstract: Comparison of common buckwheat varieties with determinate vs. indeterminate growth habit reveals no differences in leaf photosynthesis rate at stage before flowering. However, at stage of seed filling the difference was significant. Maximal difference was 20 days after early flowering, i.e. in period of most intensive seed formation. These results show that determinate varieties have higher sink strength providing by developing seeds. It is correlated with higher yield ability of such varieties. Probably, growth limitation resulting from *det*-mutation leads to some shifts in system of sink priorities of buckwheat plant and allows initiate the development of additional seeds. One more possible cause of alteration of the physiological parameters in determinate varieties is some optimization of plant structure: in terms of physiology the determinate buckwheat is a plant which is more similar to cereals than indeterminate buckwheat. However, underlying physiological changes accompanying the transition from indeterminate toward determinate growth in buckwheat remain almost unknown. Assumption about strong effect of *det*-mutation *per se* on photosynthesis rate was not supported in our work. Alternative assumption about accumulation of additional genes enhancing the sink ability suggests opportunities for additional progress in the selection work using tools evaluating photosynthesis intensity at stage of grain filling.

Key words: *Fagopyrum esculentum*; buckwheat; photosynthesis rate; sink strength; growth habit

Bolj donosne sorte navadne ajde (*Fagopyrum esculentum* Moench) z determinantno rastjo (enojna *det* mutacija) imajo večjo fotosintezo v fazi polnjenja zrnja

Izvleček: Primerjava sort navadne ajde z determinantno in nedeterminatno rastjo ne kaže razlik v fotosintezi listov v fazi pred cvetenjem, vendar je razlika v fazi polnjenja zrnja značilna. Največja razlika je bila 20 dni po začetku cvetenja, to je v fazi najbolj intenzivnega oblikovanja semen. Ti izsledki kažejo, da imajo determinantne sorte večjo moč ponora, ki jo dajejo razvijajoča se semena. To je povezano tudi s sposobnostjo večjega pridelka teh sort. Verjetno je omejitve rasti posledica *det*-mutacije, kar vodi v nekatere premike v sistemu prioritete ponora v rastlinah ajde in, kar vzpodbudi razvoj dodatnih semen. Nadaljni možni vzrok v spremembi fizioloških parametrov determinatnih sort je v optimizaciji zgradbe rastline, determinatna ajda je v fiziološkem pogledu bolj podobna žitom kot pa nedeterminatni ajdi. Kljub vsemu, pa ostajajo fiziološke spremembe, ki spremljajo prehod od nedeterminatne k determinatni rasti skoraj popolnoma neznane. Domneva o močnem učinku *det*-mutacije *per se* na fotosintezo v našem delu ni bila potrjena. Alternativna domneva o kopičenju dodatnih genov, ki pospešujejo sposobnost ponora daje priložnosti za nadaljni napredek pri selekcijskem delu z uporabo ovrednotenja jakosti fotosinteze kot orodja v fazi polnjenja zrnja.

Ključne besede: *Fagopyrum esculentum*; navadna ajda; velikost fotosinteze; moč ponora; rastna oblika

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1 INTRODUCTION

Fagopyrum esculentum Moench (common buckwheat) is a species cultivated as groats or grain crop in many countries, mainly in Russia and China (Wang & Campbell, 2004; Fesenko et al., 2016). During a last half of century, crop evolution of common buckwheat have resulted the increasing of the species grain productivity. Physiological basis of the result is mainly unknown. Probably, it was associated with correction of source-sink relationships.

In Russia, breeding of this crop on scientific basis was started in 1900s on Shatilov's Experimental Station (Orel region, Russia). First Russian commercial variety, Bogatyr, was bred by selection of heavier (i.e. larger and better filled) fraction of grain from cultivated local buckwheat. Beginning from 1960s buckwheat breeding in Russia is based on application of several morphological mutations (Fesenko, 1983; Fesenko et al., 2006). Agricultural practice has chosen mainly determinate varieties based on a mutation *d* (*det*) (Fesenko, 1968; Ohnishi, 1990) that limits the generative development of shoots by 3-5 inflorescences without possibility for development of any additional ones (Fesenko, 1983; Fesenko et al., 2009)(Fig. 1). First variety of this type was registered in 1985. Since the beginning of 21st century the share of the determinate varieties in the buckwheat sowing area in Russia was increased from 8.2 % to 56.2 %, which led to an increase in average buckwheat yield by 1.5 times (FAO, 2014). Breeding and research work with determinate type buckwheat was conducted also in Slovenia (Bohanec & Kreft, 1981; Luthar et al., 1986; Kreft, 1989), Serbia (Nešković et al., 1990) and Japan (Kasajima et al., 2016).

The steady increase in productivity of determinate

varieties compared to traditional ones implies, among others, changes in their physiology, which probably include correcting some processes associated with regulation of photosynthesis. Although the results of experiments evaluating correlation between photosynthesis rate and plant productivity are not always unambiguous (Peng et al., 1991; Long et al., 2006; Driever et al., 2014), the intensification of the assimilate synthesis looks as one of major factors in plant productivity growth.

Since changes in the intensity of photosynthesis are one of the supposed reasons for a higher grain productivity of buckwheat with determinate growth, we compared the common buckwheat varieties of indeterminate, i.e. traditional, and determinate types on seasonal dynamics of the photosynthesis rate. Also, we evaluated the influence of *det*-mutation itself on photosynthesis rate in buckwheat. The aim of this article was to describe results of this work and to discuss it.

2 MATERIAL AND METHODS

2.1 PLANT MATERIAL

Two local cultivars from Orel region represented by accessions k-406 and k-1709 from collection of Vavilov's Institute of Plant Industry, St.-Petersburg; three varieties of traditional type with indeterminate growth habit (genotype *DET/DET*) Bogatyr (registered in 1938), Kalininskaya (1954) and Shatilovskaya 5 (1967); four varieties with determinate growth (genotype *det/det*) Demetra (1995), Dozhdik (1998), Dikul (1999) and Devyatka (2004). All the varieties are similar in characteristics of vegetation period and manifest similar time of flowering beginning. F₂ hybrids 'Dikul



Figure 1: Shoots of a) determinate and b) indeterminate buckwheat shoots

Table 1: Some essential dates of the experiment

Year	Sowing date	Date of seedlings appearance	Varieties groups	*Dates of early flowering
2013	May 23	May 29	Indeterminate	June 19-20
			Determinate	June 19-22
2014	May 21	May 27	Indeterminate	June 15-19
			Determinate	June 18-20
2015	May 29	June 4	Indeterminate	June 28
			Determinate	June 28-29

* 10-15 % of plants have any opened flowers

Table 2: Weather conditions in days when photosynthesis rate was measured

Year	Date	Air temperature, °C		Air humidity, %	
		average	max	average	min
2013	June 13	19.5	24.4	61	41
	June 26	21.8	30.9	81	49
	July 6	23.9	31.1	64	34
	July 16	17.1	21.6	90	73
2014	July 3	21.8	26.5	39	22
	July 14	13.6	18.0	81	61
	July 24	13.6	19.2	74	49
2015	June 20	15.6	18.0	93	90
	July 6	21.2	27.1	60	42
	July 16	17.4	24.2	76	43
	July 26	26.3	33.8	57	37
2018	July 13	22.1	28.8	69	39

× Bogatyř' were used to evaluate the influence of *det*-mutation itself on photosynthesis intensity.

2.2 EXPERIMENTAL DESIGN

The experiment was conducted in 2013-2015 in crop rotation of buckwheat breeding laboratory of the All-Russia Research Institute of Grain Legumes and Groats Crops, Orel, Russia. A plot area was 10m². The plots locations were random, with fourfold replication. Sowing rate was 300 seeds per square meter. Dates of sowing and early flowering are presented in Table 1.

The photosynthesis intensity was evaluated on intact plants in real-time regime with a portable gas analyzer Li-COR – 6400 using the original methodology of the company Li-COR. The evaluations were conducted three times in 2014 and four times in both 2013 and 2015 at different developmental stages (see Results). Fifteen plants of every determinate variety and twelve plants of every indeterminate one were analyzed every

time of the experiment (60 plants of every type in sum). The measurements were made in order "indeterminate - determinate - indeterminate - etc" with alteration every five plants.

Yield data were obtained by weighting of the grain yield from each plot. All these parameters were used to compare the two groups of varieties, i.e. indeterminate (traditional) vs. determinate. Significance of the differences between the groups was evaluated using t-statistics.

2.3 WEATHER CONDITIONS

Weather conditions deviate during experiments, but in permissible range (Table 2). In addition, gas exchange was evaluated in morning time, 9AM – 11AM, when conditions were maximally suitable. They did not notably influence the results of gas exchange evaluation. For example, photosynthesis rate was not decreased in 2014 July 14, the coldest day of the work, in comparison

with results at this developmental stage in two other years.

3 RESULTS

3.1 GRAIN PRODUCTIVITY OF VARIETIES IN THE EXPERIMENT

In this experiment the determinate varieties manifest higher grain productivity than the indeterminate varieties, on average; the difference was significant in all years of the study (Table 3).

3.2 PHOTOSYNTHESIS RATE AT DIFFERENT DEVELOPMENTAL STAGES

At stage before flowering the photosynthesis rate was measured only in 2013 and 2015. In a season scale, in 2013 this stage values of photosynthesis rate were maximal, but in 2015 – minimal. Comparison between 2013 and 2015 reveals at least twice difference (Table 4), but comparison between indeterminate and determinate varieties in every year reveals no any differences.

During period of flowering, i.e. 10, 20 and 30 days followed to early flowering, the measuring of photosynthesis rate was conducted in 2013, 2014 and 2015. Determinate varieties manifest significantly higher mean values of CO₂ exchange in all cases with an exception of 10 days after early flowering in 2014 (Table 4). In all years of the experiment the maximal differences between determinate and indeterminate varieties were at stage of 20 days after early flowering.

Maximal values of photosynthesis rate among determinate and indeterminate varieties sometimes were almost identical, and sometimes were even higher for indeterminants. Therefore, really, the possible maximal CO₂ exchange at level of individual plant of determinate varieties is not always higher, but CO₂ exchange at population level is always sufficiently more consistent

at stage of seed filling. It correlates with the sufficiently higher and more consistent grain productivity of determinate varieties in Russia.

3.3 THE *DET*-MUTATION *PER SE* DOES NOT AFFECT THE PHOTOSYNTHESIS RATE

The differences between varieties with indeterminate and determinate growth habits in the photosynthesis rate at stage of grain filling may be due to either the effect of the *det*-allele *per se* or the accumulation of additional genes affecting the intensity of gas exchange. We analyzed F₂ hybrids between indeterminate (Bogatyř) and determinate (Dikul) varieties. As expected, all F₁ hybrids were indeterminate; F₂ segregation was Mendelian, 182 indeterminate : 67 determinate ($\chi^2 = 0.48$; $p = 0.49$). For the test 55 plants of each type were selected and labeled. Measurements were made alternately: one determinate plant, one indeterminate plant etc. The experiment shown no differences in photosynthesis rate between the indeterminate and determinate groups of F₂ hybrids: photosynthesis rate was 10.89 ± 0.51 with range 1.32 - 18.22 for indeterminate sample and 10.07 ± 0.57 with range 1.00 - 20.12 for determinate sample from F₂ population ($t = 1.07$; $p > 0.1$). Therefore, the advantages of determinant varieties in photosynthesis rate are not directly conditioned by *det*-allele. Obviously, some other genes were accumulated which increase the photosynthesis rate at stage of grain filling. This indicates the possibility of selection for the intensity of photosynthesis.

4 DISCUSSION

Photosynthesis rate is regulated by sink strength (assimilate demand) and source strength (assimilate supply) (King et al., 1967; Marcelis et al., 2004; Wubs et al., 2009; Borrill et al., 2015; Zhang et al., 2015; White et al., 2016). Obviously, there are limitations for the photosynthesis intensity, which are various between crops. So, maximal values of CO₂ assimilation was $42.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for sorghum (Salas-Fernandes et al., 2015) and $30\text{-}33 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a high-yielding *indica* cultivar of rice (Adachi et al., 2014). Sometimes, photosynthesis rate is restricted by CO₂ concentration in air: several studies on rice revealed polymorphism for reaction on increasing of CO₂ concentration in air that was interpreted as differences in sink ability of filling grain between different varieties (Chen et al., 2014; Zhu et al., 2014).

However, photosynthetic apparatus usually does not work at full capacity. So, reported maximum indi-

Table 3: Grain yield (t ha⁻¹) of varieties with indeterminate and determinate growth habits

Year	Varieties group	X±m	t	P
2013	Indeterminate	1.02±0.12	2.21	0.05
	Determinate	1.38±0.11		
2014	Indeterminate	1.49±0.06	5.21	0.001
	Determinate	1.97±0.07		
2015	Indeterminate	1.25±0.09	2.24	0.05
	Determinate	1.52±0.08		

Table 4: Leaf photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of buckwheat plants at different stage of their life cycle in field conditions

Year	Developmental stage	Date	Indeterminate varieties	Determinate varieties	t	P
			X \pm m (range)	X \pm m (range)		
2013	Before flowering	June 13	14.04 \pm 0.75 (8.54 – 21.85)	14.78 \pm 1.05 (8.45 – 21.97)	0.57	-
	10 days after early flowering	June 26	9.59 \pm 0.62 (4.14 – 17.30)	11.84 \pm 0.64 (5.77 – 16.25)	2.53	0.02
	20 days after early flowering	July 6	9.03 \pm 0.80 (4.25 – 15.69)	14.68 \pm 0.51 (10.75 – 18.60)	5.96	0.001
	30 days after early flowering	July 16	9.54 \pm 0.47 (5.32 – 12.98)	12.08 \pm 0.43 (8.43 – 15.47)	3.96	0.001
2014	10 days after early flowering	July 3	10.24 \pm 0.60 (6.23 – 17.30)	11.04 \pm 0.51 (7.98 – 14.67)	1.02	-
	20 days after efflorescence	July 14	11.76 \pm 0.62 (5.77 – 17.62)	13.56 \pm 0.57 (8.81 – 17.54)	2.14	0.05
	30 days after early flowering	July 24	8.55 \pm 0.27 (6.05 – 11.99)	9.63 \pm 0.46 (6.44 – 14.00)	2.02	0.05
2015	Before flowering	June 20	6.50 \pm 0.09 (5.87 – 6.96)	6.24 \pm 0.13 (5.58 – 6.78)	1.64	-
	10 days after early flowering	July 6	11.44 \pm 0.19 (10.48 – 12.96)	12.57 \pm 0.27 (11.21 – 14.28)	3.42	0.001
	20 days after early flowering	July 16	12.19 \pm 0.18 (11.14 – 13.10)	14.07 \pm 0.17 (13.33 – 14.70)	7.59	0.001
	30 days after early flowering	July 26	8.27 \pm 0.19 (6.97 – 9.30)	9.38 \pm 0.15 (8.32 – 10.17)	4.59	0.001

vidual leaf net CO_2 assimilation rates for *V. vinifera* L. and other *Vitis* species approach $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Roper & Williams, 1989; Gamon & Pearcy, 1990). But more commonly reported maximum rates fall in the range of 8 to $13 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (Downton et al., 1987; Correia et al., 1990). On *Eucalyptus globulus* Labill. excision of several leaves causes increased photosynthesis in the remained leaves (Eyles et al., 2013). In addition, the increased assimilate demand also enhances photosynthesis (Aranjuelo et al., 2013). Finally, total sink strength can be increased as result of interactions with other organisms: for example, soybean plants inoculated with two different strains of *Bradyrhizobium japonicum* (Kirchner, 1896) Jordan, 1982 had 14–31 % higher rates of photosynthesis than N-fertilized plants (Kaschuk et al., 2012).

Different groups of buckwheat varieties were not different in both sink and source strength at stage of vegetative development. However, at stage of seed filling the significant differences in photosynthesis rate were revealed between varieties with determinate vs. indeterminate growth habits. At present time the varieties with determinate growth habit cover more than a half of sowing area under buckwheat in Russia. Earlier, the higher productivity of such varieties was interpret-

ed only in terms of shift in balance between competitive sinks, i.e. vegetative growth and seed development. Our work elucidates that grain filling in buckwheat is limited by itself sink capacity rather than source capacity of leaves and competitive interactions with other growing organs.

All buckwheat varieties produce redundant number of flowers. Obviously, not all of the flowers produce seeds. It was discussed that there is often a hierarchy among sinks (Wardlaw, 1990), i.e. some organs have priority and suffer less from a reduction in assimilate supply than other organs. Such hierarchy usually is resulted from evolution of certain strategy of a species adaptation (Wardlaw, 1990). Since main adaptive property of common buckwheat is ability to continuous intensive growth, primary sinks in buckwheat plant are shoot meristems; seed production is only secondary sink (Fesenko, 1983). It explains the very little increasing of buckwheat seed productivity due to selection of most vigorous and productive plants. Progeny of such plants also had vigorous growth (maybe more vigorous than parental population), but competition between plants in the canopy was also very strong, and seed production was poor: only few plants produce sufficient num-

ber of seeds, and productivity of whole canopy remains low (Fesenko et al., 2006).

Determinate varieties manifest higher and more consistent yield obviously due to set several additional seeds per plant in comparison to indeterminate varieties. Setting the additional seeds on determinate plants could be explained by essentially reduced competition from vegetative growth at time of seed formation in comparison to indeterminate ones. However, this hypothesis does not explain why seed filling together with indeterminate growth in varieties of traditional type drive less sink strength than seed filling together with reduced vegetative growth in varieties of determinate type. Besides, it does not answer a question, why indeterminate varieties do not set additionally seeds with possible following growth of photosynthesis rate?

Probably, growth limitation resulting from *det*-mutation leads to some shifts in the priorities and allows initiate the development of additional seeds. One more possible base of the alteration of physiological and grain yield parameters in determinate varieties is some optimization of plant structure: determinate buckwheat is a plant, which is more similar with cereals than indeterminate buckwheat (*det*-mutation is a first step of buckwheat to became "cereal" in terms of physiology). However, underlying physiological changes accompanying the transition from indeterminate toward determinate growth in buckwheat remain almost unknown.

Attempting to determine any genes influencing photosynthesis rate led to discovering QTLs affecting, for example, chlorophyll content, stomatal resistance, transpiration rate (Teng et al., 2004; Wang et al., 2015), mesophyll conductance, and root surface area determining hydraulic conductance (Adachi et al., 2014). A mutation of rice *erect panicle 3 (ep3)* decreases photosynthesis due to reducing stomatal conductance (Yu et al., 2015).

Assumption about strong effect on photosynthesis rate of *det*-mutation *per se* was not supported in our work. Possible alternative explanation for higher photosynthesis rate together with higher seed productivity of the determinate varieties is accumulation of some additional genes enhancing the sink ability of filling seeds. The mechanisms of functioning of these genes are currently unknown. However, such assumption suggests opportunities for additional progress in the selection work using tools evaluating photosynthesis intensity at stage of grain filling.

5 CONCLUSION

The present study revealed the buckwheat varieties

with determinate growth habit (a mutation *det*) manifested higher photosynthesis rate at stage of grain filling compared to varieties with indeterminate growth habit. The mutation *det* itself is not determining the difference. Perhaps, some other genes increasing photosynthesis rate at stage of grain filling, i.e. sink strength of developing seeds pool, were accumulated in determinate varieties. Probably, there are some possibilities to continue the selection for photosynthesis rate in buckwheat.

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