REPRODUCTIVE BIOLOGY OF BUCKWHEAT

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ABSTRACT

The variability of a buckwheat inflorescence structure and a number of flowers in inflorescence and on a plant are discussed. The equation of a linear regress between the number of flowers in a thyrsus and its length is worked out. The way embryological processes in common buckwheat are going on in conditions of the Republic of Tatarstan is described. The pollen fertility has made on the average 80-85%. The abnormalities in the processes of megasporogenesis and in the development of female gametophyte, embryo and endosperm are found out. The cases of flower degeneration are revealed. The suspension of development of microspore mother cells, cytomixis, the disturbances in tapetum functioning, the formation of 4-celled pollen grains and setting of two-celled female archesporium for common buckwheat are shown. The coefficient of seed productivity (productivity index) is figured up.

INTRODUCTION

The basic problem in *Fagopyrum esculentum* Moench selection is low and unstable productivity of the culture. Thus it is known, that potential seed productivity of common buckwheat is realized only less than 10%, the rest 90% of being set flowers degenerate at various stages of their development (Soloviev, 1948). The study of reproductive biology of this plant and, in particular, its embryological features, makes it possible to reveal the reasons causing a gap between potential and real seed productivity, and to provide the information about the critical stages of ontogenesis, which are responsible for the abnormalities in development.

Reproductive organs of a buckwheat plant are placed in a zone of fruit formation of a stem (Krotov, 1975; Bochkarjeva, 1994). The type of lateral inflorescences in buckwheat is presented by single raceme located on long flower stalks, or racemes assembled in corymbs, less often in semiumbels. A buckwheat inflorescence consists of elementary inflorescences (bunches) (Krotov, 1975). The results of detailed investigations of a buckwheat inflorescence structure can be found in the research works, carried out by Soloviev (1947), Kobozeva (1964), Gorina (1976), Nagatomo (1989) etc. According to modern concepts a floral unit of common buckwheat represents an open frondescent raceme made up of open bracteose thyrsi (Kuznetsova, et al., 1992).

The flower structure has been described in many works, special attention of the researchers being given to the phenomena of heterostyly and entomophyly (Darwin, 1877; Knuth, 1899 etc.). The flower of buckwheat is complete, hermaphroditic, five-cyclic, and asymmetric. Usually it is formed by 5 tepals (two outer, two inner and one in the middle), 8 stamens, located in 2 whorls (5+3) and an ovary, formed as a result of a merge of three carpells. Depending on the position of a middle tepal, left-hand and right-hand flowers are marked out. The peculiarities in a flower structure and its position in the inflorescence give the possibility to identify each of its elements. Our previous researches have shown significant number of deviations of the buckwheat flower from a typical one. The number of tepals varies from 4 to 11, of stamens – from 3 to 13, carpells, as components of an ovary, – from 0 to 8. Thus, most frequently quantitative changes can be noted in androecium, less often – in perianth and rather rare – in gynoecium (Kadirova, Sitnykov, 2004).

Common buckwheat embryology is investigated rather thoroughly. The formation of a male generative sphere of a flower is described in works of Marjakhina and co-authors (1961), Pausheva (1988). Microsporegenesis in autotetraploid buckwheat has been studied by Frolova et al. (1946), Tkachev (1986). Nizovtseva (1970) has experimentally proved that in dry season deep pathological changes take place during the process of formation of microspores in diploid buckwheat and a significant reduction of fertility comes along. An ovule structure, megasporogenesis and magagametogenesis were studied by Mahony (1935), Modilevsky (1947), Marjakhina et al. (1961), Pausheva (1988). Pollination processes, fertilization, embryogenesis and endosperm formation have been in detail described in the works of Stevens (1912), Mahony (1936), Modilevsky (1947), Poddubnaya-Arnoldi (1948), Zhebrak (1960) and Pausheva (1988). It was stated, that environmental conditions influence upon the character of pollen and embryo sac development, growth of pollen tubes, pollination, fertilization, embryo and endosperm development, which, in the end, has an impact on the size of a crop.

According to all the above stated the aim of the work – identification of specific characteristics of reproductive biology and, first of all, embryological processes in common buckwheat in the environmental conditions of the Republic of Tatarstan – has been formulated.

MATERIALS AND METHODS

A detailed study of an inflorescence structure was carried out on materials collected in 2008 and 2009. For the investigation buckwheat varieties of the Tatar Research and Development Institute for Agriculture selection were taken: Cheremshanka, Batyr and a perspective buckwheat variety “Nikolskaya”. Plants in three replications were selected from sample areas (total area – 0,5 m^2) for their investigation in the seed-field of buckwheat variety testing (non-selective line way of sowing with the norm of 2,0 million seeds for hectare) in a picking ripeness period. With the help of microscope (MBS-10) fully blown flowers and completely filled seeds, as well as the number and sizes of flower heads, were calculated in the laboratory.

The recognized buckwheat varieties Karakityanka, Saulyk and TVS have been chosen as an object for embryological research. The material was collected in 2000-2002 at Tatar Research and Development Institute for Agriculture selection farming rotation (Experimental Farm “Tsentralnoe”, situated in Laishevsky region of the Republic of Tatarstan). The weather conditions for plants vegetation in 2000 were rather moderate, whereas in 2001-2002 they were rather unfavorable because of a long soil and atmospheric drought in the second half of vegetation.

Inflorescences, buds, flowers and fruits were fixed in the early morning hours in a Chamberlain solution (formalin - 5 parts, acetic acid - 5 parts, 50% mutilated spirit - 90 parts). The fixed material was put into paraffin in accordance with a standard technique (Pausheva, 1988). In laboratory permanent preparations of embryological structures were produced. The cuts’ thickness was 14 microns, and they were stained with hematoxylin according to Heidenhein. The samples were put into Canadian balsam and were observed through the MBI-3 microscope. Fertility rate of buckwheat pollen in 2002 was determined by an iodic method. The analysis was carried out in field conditions with the help of MBD-2,5 microscope. Because of hot weather during mass buckwheat flowering anthers were taken out of those buds, which should have shot forth the next day. On each object-plate 5 selected at random fields were being inspected, and the correlation between fertile grains and sterile pollen grains was worked out. The fertility rate of pollen grains in 25 flowers was analyzed. The evaluation of seed productivity was carried out by use of methods that were offered by Vainagy (1974) and Levina (1981). The processing of received data was performed using the methods of variation, statistics, correlation and regressive analysis (Dospekhov, 1985) with use of a package of AGROS selection-guided programs, version 2.08 (1999).

RESULTS

The zone of seed formation of the main axis of a buckwheat plant represents a floral unit. There are the first order offshoots (paracladium) in a branching zone of the main axis in leaves sinuses. They reproduce the main axis in their structure, i.e. they also contain a floral unit. The first order offshoots in their turn in a zone of branching can have the second order offshoots, etc. A degree of branching of an offshoot is strongly modified by environment conditions (the area of plant nutrition, meteorological conditions of vegetative season, etc.).

A thyrsus in buckwheat is an unlimited, simplified one (a monothyrsus), since partial inflorescences are located directly on the main inflorescence axis; it is spike-like, poorly branched, spiral; according to the position in space a buckwheat thyrsus is either upright or curved. In bract axil on the axis of thyrsus simple inflorescences – monochasium – can be seen. In an upper part of the main axis and paracladia, internodes are strongly shortened. It results in the fact that thyrsi on tops pulled together. The capacity of thyrsi (their length and a number of partial inflorescences) decreases in an acropetal direction.

Fasciated buckwheat plants are actively involved in selection process in Tatar Research and Development Institute for Agriculture. Fasciations influence an inflorescence structure as well: they are manifested in the form of cohesion of bracts or pedicels with a thyrsus axis, in substantial shortening of thyrsus internodes. In those axils, where monochasia were located, single cases of rosette-like arrangement of bracts were recorded.

The Nikolskaya variety plants under study showed approximately equal number of thyrsi on the main axis and on the paracladia, on the average - 8,8. As a whole the number of thyrsi on a plant varied within a wide range - from 4 up to 90 pieces. A thyrsus length varied from 0,2 up to 2,6 sm. The figure of the amount of partial inflorescences in a thyrsus fluctuated from 1 up to 16. In a monochasium there were from 1 up to 7 flowers, on the average – 3 or 4. The capacity of thyrsi on the main axis of a shoot has appeared to be greater, than on paracladia (tab. 1).

Table 1. Characteristic features of thyrsi on the main axis of a shoot and on the paracladia.

	$X \pm S_x$ of the feature			
	The length of a thyrsus	The number of monochasia per thyrsus	The number of flowers per thyrsus	The number of plump seeds per thyrsus
The main axis of a shoot	1,06 ± 0,02	7,07± 0,17	20,66± 0,68	1,18± 0,12
Paracladia	0,92± 0,03	6,07± 0,22	16,27± 0,81	0,74 ±0,11

The number of flowers in a thyrsus and the length of a thyrsus have turned out to be two closely interconnected features. The rate of correlation between them was + 0,80 (being authentic on 1% level of significance). The equation of linear regress was worked out on the basis of the analysis of a structure of more than 400 thyrsi, which looks as follows:

$$y = 23{,}38\ x - 3{,}94,$$

where “y” is the number of flowers in a hyrsus, and “x” is the length of a thyrsus.

The character “a number of flowers on a plant” is strongly subjected to environmental influence. In 2008 Nikolskaya variety gave on the average 968,6 flowers on a plant, in 2009 -

only 386,8 flowers. This feature showed high individual variability: in one and the same variety in 2008 the number flowers on a plant varied from 163 up to 5541 flowers.

Characteristic features of buckwheat embryological structures are described on an example of Karakityanka variety. A young anther in cross section has a weak-bladed form. In the process of the anther's development primary archesporium cells under the epidermis start to stand out because of their larger sizes. They get divided in the periclinal direction, forming parietal and sporogenous tissues. The sporogenous cells subsequently turn into microspore mother cells. The parietal tissue cells get divided in the periclinal direction, forming a cell layer under the epidermis, which subsequently is differentiated in a fibrous layer, and then into a more inner cell layer, which in its turn also by periclinal divisions gives a beginning to a centre layer and a tapetum. Concurrently with periclinal cell divisions anther's walls undergo anticlinal division as well – the anther grows in length. The tapetum cells, originally mononuclear, to the moment of the introduction of pollen mother cell (microsporocyte) in meiosis become binuclear. By this the formation of an anther wall is finished which, thus, occurs centripetally, i.e. corresponds to a monocotyledonous type.

The sporogenous cells also get divided in the anticlinal direction, the process of division is simultaneous with first periclinal divisions of anther wall cells. As a result a single-layer of cells, which are closely linked to each other, is formed in every pollen sac. They become microspores' mother cells. The number of microsporocytes in a pollen sac is rather unstable. Usually we observed 8-10, maximum 16 microsporocytes.

To the moment of introduction of microspore mother cells into miosis their sizes become considerably larger, there are changes in an anther wall too: gradual destruction of cells in the centre layer begins, in endothecium and epidermis cells vacuoles can be observed, besides, nuclei in the epidermis cells are getting distorted. To this moment in the connective a vascular bundle can clearly be seen, in some anther cells the deposition of secondary metabolites is observed.

At Karakityanka variety miosis proceeds as usual, no abnormalities were observed. At the end of the first division of the miosis between nuclei no cell walls are formed. Telophase II ends with the initiation of the microspore cell walls (simultaneous type of cytokinesis). An arrangement of microspores in a tetrad is tetrahedral. Already in the period of a metaphase I the change of the form of cells which have entered the miosis is evident: they become more round-form and are covered by a callosal membrane.

Soon after their formation the tetrads break into separate microspores. After that the microspores grow significantly in size, large central vacuoles are formed in them. Around the microspores a spore membrane starts its formation. A microspore turns into a pollen-grain. To this time the central layer on the anther wall disappears. The tapetum cells continue to disintegrate, the process of their stripping begins. Fibrous thickenings occur on endothecium cell walls.

A pollen grain remains mono-celled for rather a long period of time. During further development the nucleus of a pollen grain is shift in the direction of the membrane and enters the first mitosis. The spindle of the division is situated in transversal position to the pollen grain membrane. As a result of division two unequal cells are formed: a large vegetative one with rich cytoplasm, and a small generative one. When the division is over, the generative cell invaginates inside the vegetative one and detaches from its membrane. The generative cell is divided once again, and male gametes - sperms are formed. Buckwheat sperms – are tiny cells of an ellipsoid form. Pollen grains with three sperms are found rather seldom. Thus, a mature pollen grain is three-celled. It is richly filled with starch grains and is covered with a pollen membrane of two kinds of layers: a thick outer layer - exine and a thin inner one - intine. The exine of a pollen grain have small arms in the form of spinelets. A pollen grain is subcircular, slightly extended, with three pores and three furrows. Mature pollen is found in the buds, ready to flowering. The anther wall to this time consists only of endothecium and epidermis.

Apart from a normal course of embryological processes in the buckwheat varieties under study a significant amount of abnormalities in a course of microsporo- and microgametogenesis were revealed.

1) numerous cases of a break in the process of normal development of sporogenous tissue prior to the beginning of microsporogenesis, sometimes accompanying by the destruction of anther wall cells were found out.

2) the cytomixis phenomenon, which occurred after the division of sporogenous cells, was defined. The given infringement results in a degeneration of part of microspirocytes or all of them in a pollen sac, happening rather often in all loculi of one stamen or even in all stamens of a flower. Sometimes chromatin clots, divided by cell walls, can be connected with each other with the help of so called chromatin bridges. The given infringement is found out more often in partial inflorescences, located in the thyrsus base.

3) cases of infringement of tapetum functioning, resulting in the formation of defective pollen were determined. In this case early dieback of tapetum cells was observed, finally, there was no possibility for a normal development of a pollen membrane, so that the agglutination of pollen in a pollen sac takes place.

Besides, in Saulyk variety and TVS numerous disturbances in the course of miosis were observed, and as a consequence of it incomplete microspore tetrads and micronuclei, chromatin bridges, tetrads with unequal microspores, microspore octads were found out. As a result of infringements in miosis pollen grains of different size were formed. These grains have different, not similar with haploid ones, chromosome numbers in nuclei - the pollen of this kind is partially or completely sterile. A small pollen and a huge pollen were found out also in Karakityanka variety alongside with a pollen of a normal size.

The identified abnormalities made it possible to note, that partial pollen sterility is common in buckwheat. In the summer of 2002 field definition of pollen fertility was worked out. Karakityanka variety showed $84{,}76 \pm 1{,}93$ %, and TVS - $79{,}55 \pm 2{,}05$ %.

A single buckwheat ovule is orthotropous, bitegmic and crassinucellar. At early stages of its development an initial archesporial cell is laid down subepidermically on the top of an ovule primordium. This cell differs from others by its larger size and thick cytoplasm. It happens, when growing carpells have not yet reached the top of an ovule primordium. An initial archesporial cell is divided periclinally, thus a secondary archesporial and a parietal cells are formed. The secondary archesporial cell grows up; the parietal cell is divided in an anticlinal direction. At the same time periclinal division of a subepidermic layer of cells begins, and the place of foundation of an inner integument is being marked. A growing carpell and an ovule are approximately equal in length. At this stage of development ovules with two secondary archesporial cells and two pairs of parietal cells were discovered.

During the further development a secondary archesporial cell turns into a megaspore mother cell. It is a cell of the large oblong form with a large nucleus and rich cytoplasm. The parietal tissue capacity usually makes one layer of cells. The initiation of an outer integument corresponds in time to a stage of a mother cell. It should be noted as well that one case of an ovule with two megaspore mother cells was recorded in the variety under study.

As a result of division of a mother cell the tetrad of megaspores is formed. No abnormalities were found in miosis. Chalazal megaspore, which receives further development, already at a stage of a tetrad differs by larger sizes. The form of a tetrad is linear. At this stage cells of future hypostasis begin to be differentiated in a chalazal part of an ovule. Integuments to this time reach significant sizes: the length of inner makes approximately 15 cells, outer integument - 8 cells.

Chalazal megaspore increases greatly in size; it crushes other megaspores, which gradually degenerate. Its cytoplasm became vacuolized, in a chalazal part of a megaspore large vacuole is formed, with its nucleus being in a micropylar part of a cell. Integuments enlarge even more in size, to this time they already overgrow a nucellus.

As a result of the first division of a mother cell nucleus of an embryo sac a binuclear coenocyte is formed. The nuclei turned out to be separated from each other by a large vacuole. The coenocyte continues to grow in a micropyle direction. Gradually nucellar cells around an immature embryo sac adjacent to its micropylar part also begin to degenerate. Together with coenocyte growth a considerable growth in the size of an ovule itself takes place. The next division of coenocyte nuclei results in the formation of four-nucleate embryo sac. Pairs of nuclei appear divided by a large central vacuole. To this time nucellar cells around the embryo sac are already destroyed, without changes remain only cells that are placed close to the embryo sac from its chalazal end.

As a result of the third division of coenocyte nuclei a seven-celled and eight-nucleate embryo sac is formed. It consists of two groups of haploid cells, located along the embryo sac's poles, and a central two-nucleate cell. Later two polar nuclei of the latter merge and give birth to a secondary nucleus of the central cell. To this moment embryo sac increased in size. In micropylar part of a nucellus cells, surrounding the embryo sac, appear smashed and destroyed. Nucellus also considerably expands in central and chalazal parts by divisions of meristematic cells located close to its epidermis. A strong hypostasis, is situated under the chalazal part of the nucellus with a vascular bundle adjoining it. The nucellar cells, situated close to antipodes, remain unbroken, the inflow of nutritious substances to the embryo sac passes through them. The antipodes are placed one above another in one line, they soon get distorted. Inner integument due to periclinal and anticlinal divisions of the cells strongly expands above the micropylar part of the nucellus and closes the line, forming a narrow channel – a micropyle. An outer integument does not get closed and remains consisting of two layers of cells. In epidermis cells of nucellus near its micropylar part periclinal divisions can take place. It remains whole for quite a long period of time until an embryo with distinct cotyledons is formed.

Egg apparatus cells are inside a micropylar part of an embryo sac: an egg cell and 2 synergids. They are of a pear-shaped form, differ in size and structure. An egg cell is larger, has a larger nucleus and a large vacuole in a micropylar part. In synergids nuclei are located in the central part of cells, and in micropylar and chalazal parts there are large vacuoles. In mature embryo sac the secondary nucleus of central cell is found in a part of a cytoplasm in immediate proximity to an egg cell. The central cell is strongly vacuolated.

In a female part of the buckwheat the following abnormalities in the course of embryological processes are also determined.

1) in prophase I dying cells of nucellus tissue are detected around the megasporocytes on the side of chalaza. Finally, the megaspore mother cell also dies out.

2) the case of a break in the development at a stage of formation of female gametophyte in Karakityanka variety can also be mentioned, that may result in destruction of an ovule even before an embryo sac is formed.

After the pollination the pollen on the stigma spurs, and several pollen tubes can be observed in tissues of style. The pollen tubes in a case of legitimate pollination grow up to a micropyle, but only one of them gets into an embryo sac. The pollen tube bursts in one of synergids, which dies out. After its disintegration 2 X-bodies are found in it: a degenerating nucleus of the synergid and nucleus of a vegetative cell of a pollen grain. The second synergid remains unchanged for rather a long period of time. One of sperms gets nearer to an egg cell and fuse with it, the other fuse with the nucleus of a central cell. A premitotic type of karyogamy is characteristic for the buckwheat.

The primary endosperm nucleus begins to divide earlier, than a zygote. The embryo develops according to an Asterad-type. The endosperm is nuclear, at later stages a cell-formation on the micropylar end starts. In ripening fruits the embryo with well developed cotyledons, a stem apex and an embryo root is observed. To this time the endosperm is already cellular. Later cotyledons of an embryo become plicate.

The break in development at various stages of formation of an embryo and endosperm, including the destruction of large embryos with quite advanced cotyledons, is specified. In all cases the primary reason for it was a break in the development of an endosperm, implicating the process of dying out and disintegration of the embryo.

Besides, the cases of degeneration of all flowers in an inflorescence are made clear. Flowers, which appear first in partial inflorescences underwent the strongest disintegration.

As a result of all the above listed infringements, the productivity index in the year 2008 (for example) changed from 5,5 up to 8,2% (tab. 2).

Table 2. Seed productivity of buckwheat varieties in Tatarstan

Variety	Number of flowers per plant	Number of fruits per plant	Productivity index
Cheremshanka	1142,1±187,6	83,4±21,9	7,3
Batyr	992,9±161,0	54,7±7,0	5,5
Nikolskaya	968,6±161,0	79,5±12,5	8,2

DISCUSSION

In the carried out research we have revealed a very low productivity index of the buckwheat, grown in the conditions of the Republic of Tatarstan. The similar data are presented by Tkachev (1986), who shows, that 3516 flowers open on average on a diploid common buckwheat plant. He also marks out high variability in the number of fruits and seed formation and high dependence of these parameters on environmental conditions.

Problems with pollination are frequently indicated as basic reasons for low productivity of the buckwheat. A limiting factor here can be a lack of insects-pollinators. However, as it is specified in the experiments, carried out by Fesenko and Naumova (1976), the pollen conditions in buckwheat populations is biologically adequate and cannot be stated as a factor, limiting an output yield.

It is obvious, that the productivity of a buckwheat plant is closely connected with the morphology of reproductive structures at all stages of their development. Being aware of the fact, that there are from 8 to 16 microsporocytes in a pollen sac, we have calculated, that in one flower from 1024 to 2048 pollen grains can be formed. This estimated data coincide with those figures that are given in the literature (Doida, 1958; Fesenko, 2000). According to Frolova et al. (1946) in diploid buckwheat the percentage of abortive pollen very seldom exceeds 1%. In our research pollen sterility reached 20%. However, taking into account high pollen production of a buckwheat flower, we believe, that even such essential decrease in pollen fertility does not have any significant influence on the efficiency of pollination and, finally, on real seed production of the plant.

A considerable amount of pollen grains and embryo sacs at different stages of development, as well as whole flowers are eliminated long before the florescence begins. Investigations, made by Soloviev (1947) confirm the fact that dying out of flower-buds in inflorescence is observed at the most various stages of development. Indeed, if a setting up of 5-6 flower-buds were observed in partial inflorescence, then during picking maturity in partial inflorescence very seldom more than 3-4 flowers were observed. Even after successful pollination and fertilization a substantial part of already formed ovaries stop their development at different stages. In the above described cases of flower degeneration the productivity of a whole thyrsus tends to zero.

The reason for appearing of disturbances in the course of embryological processes must be in high sensitivity of these processes to environmental conditions. High atmospheric temperature and moisture deficiency in air and soil during corresponding stages of development can lead to significant abnormalities in structure of reproductive organs of buckwheat.

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