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Changes in Vascular Tissues and Productivity of Buckwheat Plants after Impulse Pressure Treatment

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Authors' contributions

This work was carried out in collaboration between all authors. Author EEN designed the study, conducted experiments and wrote the first draft of the manuscript. Author VIL elaborated the method of treatment of seeds, designed and supervised the research. Author SD managed the analyses of the study and managed the literature searches. Author VAP performed the statistical analysis, wrote the protocol. All authors read and approved the final manuscript.

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ABSTRACT

Osmotic pressure, pressure gradients in the phloem, and mechanical forces influence different processes in plants. We have proposed the method of pre-sowing seed treatment by impulse pressure generated by a shock wave. It is possible to use the shock wave for different precision purposes due to the excellent parameter control that determine the intensity of the influence. Buckwheat (*Fagopyrum esculentum* Moench., cv. Saulyk) plants were treated by impulse pressure. The purpose of this work was to study following physiological processes, such as growth of plants, and development of phloem and xylem, which promote crop increases in buckwheat plants, treated by impulse pressure. The changes in the development of conductive tissues provided the growth of

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leaves and the redistribution of photosynthates to inflorescences and fruits. So, these experiments demonstrated that the total fruit weight increased at plants treated by 11 MPa, exceeding the control by 22.6%. Hence the treatment of seeds by impulse pressure provided more favorable conditions for the supply of forming fruits with photosynthates.

Keywords: Phloem; physical factor; redistribution; xylem.

ABBREVIATION

IP : Impulse pressure

1. INTRODUCTION

Plants are sensitive to different environmental factors. Mechanical stress is a critical signal affecting morphogenesis and growth. It is caused by a large variety of environmental stimuli such as touch, wind, and gravity in addition to endogenous forces generated by growth [1].

External mechanical forces resulting from the pressure exerted by wind or water movement are a major stress factor for plants. A plant's ability to resist these forces relies on minimizing the forces encountered by the plant (avoidance strategy), or on maximizing its resistance to breakage (tolerance strategy). The evolution and variation of both strategies may constrain many morphological, anatomical and architectural traits that underlie avoidance and tolerance [2].

Gravity resistance has played an important role in the evolution of land plants [3]. On the basis of studies dating from the early 19th century, there are plant mechanical sensors and response components related to gravity. Potential candidates for mechanosensitive channels have been identified in *Arabidopsis thaliana*. Classical physiological analyses and recent simulation studies also suggest involvement of the cytoskeleton in sensing/responding to long-term mechanoresponse independently of the biochemical signaling cascades triggered by initial graviperception events [1]. The cell wall is responsible for the final step of gravity resistance. Plants develop a tough body to resist the gravitational force via an increase in cell wall rigidity and the modification of growth anisotropy [3].

Sudden changes of osmotic pressure can promote some unspecific stress symptoms in plants, but normal osmotic pressure is an important factor for cell survival, cell growth and water uptake [4]. Plant cells can clearly sense their water status and respond in a variety of ways, including osmotic adjustment through accumulation of compatible solutes such as proline or glycine betaine, accumulation of abscisic acid, and changes in gene expression, development, and morphology [5].

The following processes such as phloem transport of substances [6], dynamics of physico-chemical properties of xylem sap [7], as well as gas transport in culms of emergent aquatic macrophytes [8] depend on pressure gradients.

Soil tightening is known to influence on plant growth since the end of 19th centuty [9]. An emerging shoot experiences mechanical impedance, when it needs to break through soil that has a surface crust. This is one of the first physical stresses that the shoot experiences. Mechanical impedance of the soil is important in limiting shoot growth [10].

Soil strength restricts the growth of a root system [11,12]. Soil strength is increased if it is compacted by machinery or animals, and can increase by an order of magnitude as the soil dries from field capacity to the wilting point. A slower rate of root extension occurred in mechanically impeded roots as a result of reduced axial cell extension and cell production. The reduction in cell extension was not associated with a reduction in turgor pressure, implying that cell wall properties were controlling cell extension. The thicker roots found under mechanical impedance were associated with wider cells [12]. A multiphase bio-mechanical response of elongation rate of roots to axial mechanical forces was revealed. The junction between the growing and the mature zones of roots was identified as a zone of mechanical weakness that seemed critical to the bending process [13].

Pressure and mechanical forces are also factors of plant growth and development control. The shape of an organism relies on a complex network of genetic regulations and on the homeostasis and distribution of growth factors. Shape changes also involve major changes in structure, which by definition depend on the laws of mechanics. Mechanical forces contribute in morphogenesis [14].

The generative region in the sunflower capitulum corresponds to a zone of compression that could control the initiation of new primordia by means of buckling of the tunica layer [15]. The cell wall apoplasm of shoot apical meristem is most likely involved in a mechanical integration mode, in which mechanical stress and strains are putative signaling factors [16]. Mechanical strain can regulate auxin transport and accumulation in the shoot apex, where new leaves emerge and rapidly grow. The plasma membrane acts as a sensor of tissue mechanics that translates the cell wall strain into cellular responses, such as the intracellular localization of membrane-embedded proteins. One implication of this fundamental mechanism is the mechanical enhancement of auxin-mediated growth in young organ primordia [17].

On the principle that pressure is known to be external and internal factor of ontogenesis of plants we propose the method of presowing treatment of seeds by impulse pressure (IP) generated by a shock wave. It is characterized by high intensity and accuracy of dosage. IP has unique physical properties due to the excellent parameter control that determine the intensity of the influence [18].

The aim of this work was to study those physiological processes which promote crop increases in plants, treated by the IP. The following objectives were solved: to get dependence of germination and yield on the value of IP; to assess the distribution of photosynthates which influences the yield; to search development of vascular system, and sink-source dynamics. The choice of contrasting variants for the assessment would be useful to determine stress strategies of plants after the treatment of IP.

2. METHODOLOGY

2.1 Presentation of Buckwheat (*Fagopyrum esculentum* Moench., cv. Saulyk)

Buckwheat (*Fagopyrum esculentum* Moench., cv. Saulyk) plants were used for the experiments.

Buckwheat (*Fagopyrum esculentum*) is an important crop grown throughout the world. It has the origin of domestication thought to be the eastern Tibetan plateau, bordering the Chinese province of Yunnan. The main producers of buckwheat are China, Russian Federation, Ukraine, and Kazakhstan [19]. The crop is not a cereal, but the seeds (fruits) are usually classified among the cereal grains because of their similar usage [20].

Taxonomy: Division Magnoliophyta, class Magnoliopsida, order Polygonales, family Polygonaceae, genus Fagopyrum, species esculentum Moench. The plant has a branching root system with one primary root that reaches deeply into the moist soil [21]. Buckwheat has triangular seeds and produces a flower that is usually white, although can be pink or yellow [21, 22]. Buckwheat branches freely, as opposed to tillering or producing suckers, causing a more complete adaption to its environment than other cereal crops. Buckwheat has a growing period of only 10–12 weeks and it can be grown in high latitude or northern areas. It grows 75 to 125 cm tall [21].

Buckwheat grain is a rich source of valuable chemical compounds such as starch, protein, fat, dietary fiber, vitamins, minerals, fagopyritols, and flavonoids. Buckwheat flour contains significantly more proteins than rice, wheat, millet, sorghum, and maize but less than oat. Buckwheat proteins have a well-balanced amino acid composition and a high content of lysine [23].

The grain is generally used as human food and as animal or poultry feed, with the dehulled groats being cooked as porridge and the flour used in the preparation of other meals [20]. There is a variety of buckwheat foods produced on a global basis, such as noodles in Asian countries, cake, bread, and pasta in Europe, crepe and galette in France, kasha in Europe and Russia, zlevanka in Slovenia, and blini in Russia [24]. It is also a multipurpose crop. The small leaves and shoots are used as leafy vegetables. The crop produces honey of a very good quality [20].

This is reported to aid in increasing the elasticity of the blood vessels and therefore prevent hardening of the arteries [20]. *F. esculentum* is also a medicinal plant because of its antioxidative polyphenolic compounds (flavonoids) with potential benefits to human health. The most well-known drug is rutin [25].

Buckwheat has been used as a smother crop, owing to the lack of good herbicides for broad-leaved weed control. It is generally a very good competitor as it germinates rapidly and the dense canopy that it produces soon shades the soil [20].

Buckwheat is generally considered a short-day plant. It is a short-duration crop (3-4 months) and requires a moist and cool temperate climate to grow. Buckwheat has little tolerance to frost. It thrives well on sandy, well-drained soils. When moisture is limiting, buckwheat is very sensitive to high temperature and hot dry winds. This usually results in the loss of flowers. Seed size increased with increased soil moisture content. Buckwheat wilts badly and grows very slowly when affected by low soil moisture. If moisture is received, the plants will often start to grow again but maturity is delayed [20,21].

2.2 Methods

One of the major limitations in buckwheat appears to be the high amount of seed abortion that occurs. The causative factors for the abortion are not fully understood [20]. Due to heterostyly and open-pollination by insects the seed-set is only 12% [25].

Plants were grown under phytotron and field conditions. Every series was grown on the record plot with a sown area of 3 m^2. Seeds were treated by IP 11 and 29 MPa. IP was generated by an impact wave created by the detonation of a water resistant explosive and propagated in an aqueous medium, resulting in a volume compression of the seeds for 15–25 μs.

The pressure in the wave front was calculated by formulae for spot charge

$$P = 53{,}3 \cdot \left(\frac{Q^{\frac{1}{3}}}{R} \right)^{1{,}13}$$

where P is the pressure, MPa; Q is the weight of the explosive, kg; R is the distance between the center of the explosion and the seed surface, m [26].

The seeds were treated as follows (Fig. 1). Dry seeds (3) were placed in porolone cells (2), which were situated at the bottom of a stainless-steel container (1) filled with water (4). Beneath the water surface, we clamped a water-resistant explosive (5) with the weight of Q and at the distance from the seed surface equal to R using plank (6), and then the explosive was detonated by electric detonator (7). This technique of seed treatment is covered by a patent [27]. An individual cell contained up to 500 g of seeds, that is, more than 15000 individual seeds, and this amount represented one replication.

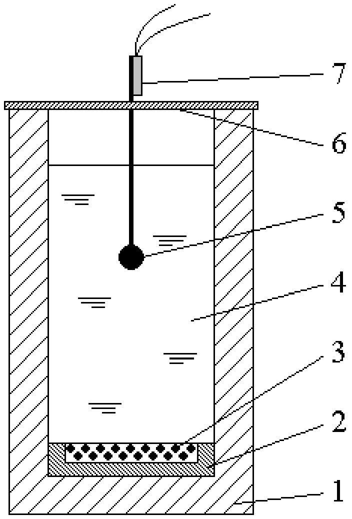

Fig. 1. Device for seed treatment

After such treatment, the seeds were kept for 24 h at room temperature, bringing them to an air-dry state. Control seeds were soaked in water for the same time used for soaking seeds during the IP treatment, and then air dried [28].

Treated seeds were germinated on filter paper at the temperature of 25℃ in a humid atmosphere. The numbers of germinated seeds at the age of 8 days were determined, and the results obtained were expressed as a percent of total number of seeds from four groups of 100 seeds.

Anatomic microscopic sections were prepared in hypocotyls as well as in leafstalks and peduncles and observed under a microscope with 600-times magnification (ocular 15x, object-glass 40x); the measurements were taken by eyepiece (ocular) micrometer. Each embodiment of the experiment was independently repeated for four times.

The dry weights of roots, stems, leaves and inflorescences were assessed after drying at 105℃. There were four replicates each of five plants.

The productivity of treated plants was compared to the control plants in four replicates (plots); the square of each plot was 1 m^2. We calculated the seeding rate taking into account the germination of seeds (*G*). The seeding rate was 200 plants per 1 m^2 (10 rows × 20 seeds in a row). The number of fruits per m^2 (*NF*) was calculated by formula:

$$NF = \frac{200 \cdot 100\%}{G}$$

The weight of 1,000 sowing fruits (*m*) was 32.1 g. The weight of fruits (*WF*), g/m^2 was calculated by formula:

$$WF = \frac{200 \cdot\ m\ \cdot 100\%}{G \cdot 1000}$$

The weight of sowing material, kg/10,000 m^2 was calculated as the proportion.

Plants were grown up using standard agricultural technology, which included application of fertilizers $N_{40}P_{60}K_{40}$, watering (depth drenching H = 0.4 m, 3 times, 0.05 m^3/m^2), hoeing, and weeding.

We used 25 plants per plot to assess the number of fruits per plant and weight of fruits, g/plant; so we used four replicates which contain 25 plants in each variant. The number of fruits per plant was determined on each sample plant. The four means were calculated from 25 plants. That means were used to calculate the resultant arithmetic mean and its error from four replicates. Fruits from each sample (25 plants) were combined, weighed, and the average fruit weight per plant was calculated from four groups of 25 plants to assess the weight of fruits, g/plant.

The yield, g/m^2 was assessed as a total weight of fruits from a plot (1 m^2, 200 plants). Fruits were combined and weighted. Resultant arithmetic mean and its error were calculated from four replicates for each variant. The yield, kg/ 10,000 m^2 was calculated proportionally.

Weight of 1,000 fruits was assessed using the International Seed Testing Association (ISTA) rules. Each sample from a plot (four samples in each variant) was mixed down to obtain an accurate working sample and then pure seeds were selected for weighing. Counting has been done with an electronic seed counter. There were two repetitions of 1,000 seeds that were weighted separately, each repetition with a precision of two decimals. The mean for a plot was calculated from those two repetitions. The arithmetic mean and standard error of mean was calculated from four means for a plot in each variant.

The arithmetic means, standard errors of means, and Student-t criteria were calculated, significance of means determined at P = 0.05.

3. RESULTS AND DISCUSSION

3.1 Dependence of Germination and Yield on the Value of IP

Primarily we revealed dependence of germination and yield on the value of IP (Fig. 1). Seed germinability after the treatment by IP 3 MPa, 5 MPa, 8 MPa, and 11 MPa was equal to the control one. The damage of seeds by IP 17-35 MPa led to the reduction of seed germinability on 22%-58% (Fig. 1). The mortality of seeds occurred during germination but not directly after the IP treatment, so any reactions promoted by the treatment developed in seeds. IP in the range of 11-29 MPa did not promote the acute lethality of seeds [29] determined by phosphorescence at room temperature [29]. So there was no elimination of unproductive individuals but IP stimulated physiological processes in seeds and plants, leading to increased yield [29]. Air-dry seeds are known [29] to be subdivided to three fractions using the application to individual seeds of room temperature phosphorescence. These fractions are strong seeds (fraction I) producing normal seedlings, weak seeds (fraction II) producing mainly abnormal seedlings, and dead seeds (fraction III). Weak seeds under different conditions can produce normal seedlings, back transition of weak seeds to "improved" seeds occurred [30]. Also that group of seeds can produce weak (abnormal) seedlings or miss plants. So weak seeds are the most sensitive to influences. That phenomenon allows to explain the slightly increase of germination after the treatment of pressure 11 MPa (Fig. 1).

Changes in plant productivity (Fig. 2) were represented the curved line with 2 maxims corresponded to IP 11 MPa and 29 MPa. Changes in the yield after the treatment of IP 3-8 MPa were not revealed. The best variant for practice is 11 MPa. Seed germinability after that IP treatments was equal to the control variant, and productivity increased. These, in theoretical terms, other variants are interesting to appreciate the dependence of growth and development of plants on the treatment.

Hence there were at least two types of responses. The first type was an adaptive response (Fig. 2, A) – hormesis, which provides the basis for accommodation to the environment [31]. The second type was damage of seeds (Fig. 1, D) and the stimulation of physiological processes in plants. In the intermediate group changes of plant productivity were instable over a long period (Fig. 2, I). This effect indicated the transient to stress [32]. So we used for further experiments two contrast variants, 11 and 29 MPa.

The main result from Fig. 2 indicates the best germination rate at IP 11 MPa and a significant decrease at higher IP. However, increase of fruit weight is the lowest at 11 MPa, but it significantly increases with higher IP. Details of sowing and yield are shown in Table 1.

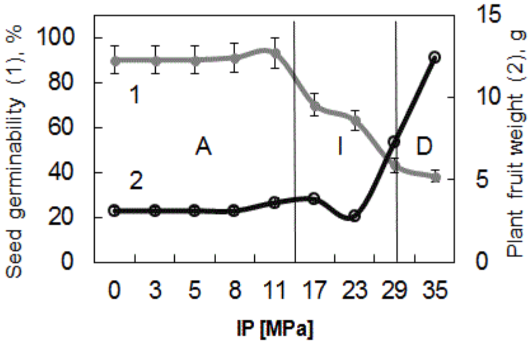

Fig. 2. Seed germinability (1, left axes) and plant productivity (2, right axes) of buckwheat after treatment of seeds by IP

A - adaptive response; I - instable period; D - damage of seeds M±m; n=4

Due to the changes of germination we calculated the weight of sowing material which was taken for 1 m^2. The weight of 1,000 fruits (32.1 g), number of plants (200 plants per 1 m^2 were grown), and germination (Fig. 2) were taken into account. So the number of fruits was some more than 200, it was 223 in control variant, and more, up to 518 at 35 MPa (Table 1, line 1). The weight of sowing material per 10,000 m^2 increased on 54.7-95.2 kg (at 26 and 35 MPa correspondingly, Table 1, line 2). It is an additional cost to get great harvest.

Indeed, the yield (Table 1, line 6) which depended on the weight of matured fruits, g / plant (Table 1, line 4) increased significantly due to the number of matured fruits per plant (Table 1, line 3). Weight of 1,000 fruits (Table 1, line 5) changed but its contribution was insignificant.

So agricultural profit can be chose from two contrast variants. The first variant is 11 MPa. The germination did not change (Fig. 2), but the increase of yield is about 17% (approximately 1 ton from hectare, Table 1, line 6). The cost of additional yield is (7,160 – 6,120)·50 = 52,000 rubles per 10,000 m^2. There is no additional cost and risk in this variant, but the profit is less than in the following variant.

We cannot recommend using IP 17-23 MPa in agriculture, because the germination decreases, and yield is instable. Those pressures are interesting in theoretical studies, because they perform a transitional phase in the dose-depended reaction of plants.

The second remarkable variant is 29 MPa. The germination decreased (Fig. 2), so there is additional cost, 77 kg of sowing material per 1 hectar (Table 1, line 2), it is double seeding rate. The cost of additional sowing material is (77·50) = 3,850 rubles per 10,000 m^2. Besides, if germination rate decreases more than 50% at 29 MPa, crop homogeneity was strongly deleted. Crops can be irregular; it is a sufficient flaw of the method. The use of seedling technology allows eliminating the lack, but it is not used for buckwheat plants. Application of IP treatment of tomato and cucumber plants which were cultivated by seedling technology in greenhouses was approved, recognized and recommended for the wide use [33,34]. That variant is interesting in theoretical researches as an approach to study the physiological processes of plants under stress. Application of IP 29 MPa is risk, but the 2.3-fold increase of yield is tempting. It can provide the greater resulting profit (more than 8 ton from hectare, Table 1, line 6). So the research of germination process is the main point of the following investigation.

If we use IP 26-35 MPa the agricultural profit can be more than at 29 MPa, but the germination and resistance of plants are instable due to high intensity of physiological processes directed to yield. So unfavorable ecological conditions such as drought, high or low temperature can influence the plants and promote the death of plants.

The choice depends on economic and agricultural opportunities. The negotiated price of treatment must allow using that method in practice.

Researches demonstrated that IP 3-11 MPa did not influenced germination of seeds of buckwheat sufficiently, but it increased of yield of plants on 17% (at 11 MPa). That effect is hormesis – common stimulation of growth. IP 11 MPa can be recommended for agriculture practice due to its safety and efficiency. The instable period of dose dependence with fluctuations of physiological processes was at IP 17-23 MPa, it corresponded to transition zone between two different types of reaction. IP 29-35 MPa promoted decrease of germination of seeds of buckwheat, but the yield increased 2.3-fold. That variant is interesting for researches, but it can be used in agriculture only for seedling technology due to decimation of crops. We conclude that doze dependence of germination and yield on the value of IP is irregular, and there is transition zone, so reactions of buckwheat plants on IP 11 MPa and 29 MPa fundamentally differ.

3.2 Distribution of Photosynthates and Development of Vascular System

So IP changed the productivity of buckwheat plants. Productivity is an integrative process; it is known to depend on the combination of assimilation, distribution and dissimilation of photosynthates. The cause of changes in productivity after the treatment of IP lays in the accumulation of photosyntates in leaves (source) and re-distribution into fruits (sink). Those processes are characterized at the total level by dry weight of leaves, stem and roots. The next objective is to assess the distribution of photosynthates which influence the yield. The distribution of nutrients is realized by vascular system. The size and amount of vascular elements is one of the indicators of transportation of photosyntates. Another objective is to search development of vascular system, and sink-source dynamics.

IP 11 and 29 MPa was changed as contrasting variants for the research.

The total dry weight of seedlings (Fig. 3, Germination) reduced by a third in treated seedlings compared to control ones due to a deceleration in growth. Even so, a part of leaves taken by the total weight was equal in tests. Also a part of stems in treated plants was higher than in control ones.

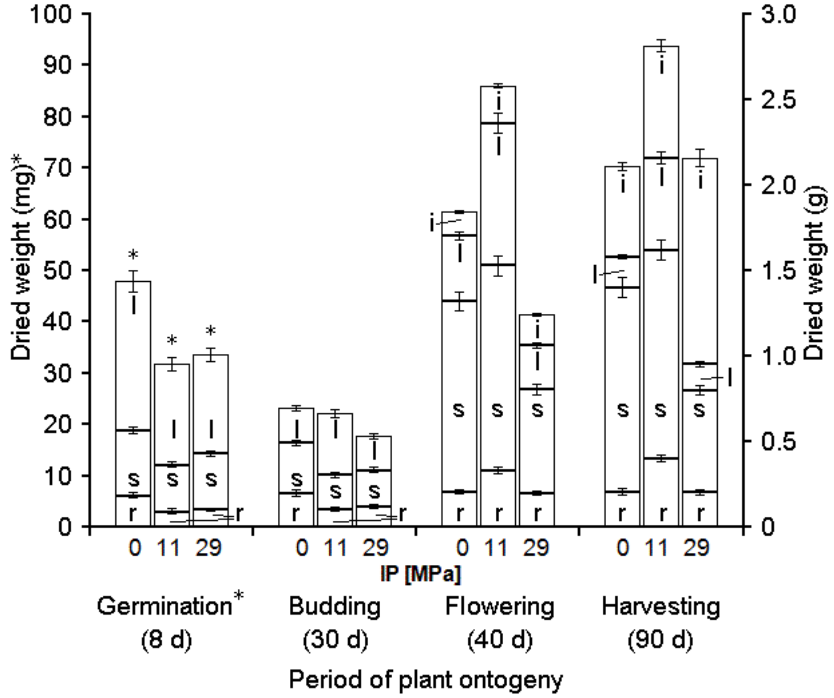

Fig. 3. Dry substance accumulation in buckwheat plants treated by IP

Left vertical axis displays dried weight, mg of roots (r), stems (s), and leaves (l) of seedlings in Germination phase (8 days).*

Right vertical axis displays dried weight, g of roots (r), stems (s), leaves (l), and inflorescences (i) of plants in Budding (30 days), Flowering (40 days), and Harvesting (90 days) phases. M±m; n=4

The foundation of plant productivity potential after the IP treatment is laid at early phases of plant ontogenesis when germinal organs originate from meristems [35]. The inhibition of vegetative growth of seedlings activates plant development. The accumulation and distribution of organic substances makes an important contribution to plant productivity during the next phases of ontogeny.

The next stage of ontogenesis is budding (30 days). The dry weights of plants (Fig. 3) corresponded to control after treatment by IP 11 MPa, and decreased at plants treated by IP 29 MPa as compared to control ones. Plants treated by IP 11 MPa had the biggest weight of leaves, so they formed assimilation potential. Plants treated by IP 29 MPa had stem and roots with smaller weight than control plants. The weight of leaves in that variant was more than in control one. Stem can accumulate and redistribute photosynthates, so it functions as an intermediate sink and source of photosynthates. It is now accepted that the transport phloem, linking major sources and sinks, is leaky, and this leakage can be considerable. Hence for phloem transport to function over the long distances observed, a large fraction of this unloaded photosynthate must be reloaded. A fraction of this unloaded solute is used to maintain tissues, as well as being stored. Also, pathway unloading/reloading acts as a short-term buffer to source and sink changes [36]. The accumulation of nutrients in the stem is a factor of resistance. Described features confirm the idea about hormesis in plants treated by IP 11 MPa and stress reaction in plants treated by IP 29 MPa. The first group of plants forms assimilation apparatus and vegetation organs, but the second group, in opposite, uses an economic and efficient utilization of nutrients.

Growth is supplied by water and photosynthates. Vascular system plays the main role in that process. The plant vascular system, composed of the xylem and phloem, is important for the transport of water, mineral nutrients, and photosynthate throughout the plant body. The xylem vessels and phloem sieve tubes of the plant vascular system connect above- and below-ground organs, allowing vascular plants to draw from two distinct resource pools. In contrast, the phloem allows for the bidirectional movement of photosynthate and other macromolecules throughout the plant, from areas of synthesis or excess (source) to areas of use (sink) such as storage tissues or zones of active growth. The vasculature is also the primary means by which developmental and stress signals move from one organ to another [37].

High intensity of physiological processes depends on the water abundance. The xylem provides an avenue for the unidirectional transport of water and soluble nutrients from roots to aerial tissues that is driven by the transpiration stream [38]. Xylem sap contains mineral nutrients, peptides, proteins, and hormones [37,38]. Despite the reduced part of roots (Fig. 3), the number of conductive bundles in the stem (Fig. 4A) of treated plants was more than in the control variant on 18-28% at 30 days. Due to increase of overall amount of vessels on 40-53% in the plants treated by IP 11 and 29 MPa as compared to control one the overall areas of vessels (Fig. 4 B) were shown to grow by 1.4- or 2.1-fold, respectively.

Phloem sap appears to be highly complex, containing a diverse set of molecules such as sugars, lipids, amino acids, peptides, proteins, coding and non-coding RNAs, small molecules, mineral nutrients, and phytohormones [38]. The area of the phloem of a bundle and the overall area of the phloem (Fig. 4 A) are good indexes of organic nutrient transport process after IP treatment having decreased by 36-37% and 26-114% respectively compared to control plants. It was a cause of the root growth inhibition (Fig. 3).

Development of conductive tissues in the leafstalks at 30 days (Fig. 4C) occurred simultaneously with the increase of the leaf dry weight (Fig. 3). The number of xylem vessels, their diameter and the overall area of vessels increased on 24-33%, 45-34%, and 2.6-2.3-fold, respectively after treatment by IP 11 and 29 MPa. The development of xylem in the leafstalk provided the leaf parenchyma with water and minerals in treated plants better than in control ones. The overall area of phloem of the leafstalks increased by 22-26% in treated plants in comparison with the control variant. Also the weight of leaves increased after treatment with IP (Fig. 3). At the same time the efflux of water in the leaf made the loading of phloem easier.

The increased development of conductive tissues promoted the development of “sink-source” systems in plants. Acceleration of out-flow of photosynthates from leaves (Fig. 4 C) resulted in growth, as evidenced by an increase in dry weight of the plants treated by IP compared to control ones, if the activity of "sink" was rather high. While the size of phloem in the lower part of the stem of treated plants decreased, the forming flowers were possibly a more active "sink" than the roots.

Plants are known to develop intensively and accumulate dry substance in a flowering phase (40 days). The stem grows quickly to raise flowers for better pollination. Indeed, the weight of stem increased 3.7-, 6.0-, and 2.8-fold in control, 11- and 29-MPa variants respectively at 40 days compared to 30 days (Fig. 3). Later, when the fruits will mature, the stem will supply them with its stored organic substances. The dry weight of leaves increased 2.2-fold in plants after the treatment with 11 MPa (Fig. 3) as compared to control ones.

At 40 days, in the lower parts of the stems the overall area of vessels increased on 48% in variant 11 MPa compared to control one due to a greater diameter of vessels. The overall area of vessels increased on 92% in variant 29 MPa due to the number of vessels (Fig. 4 B).

Vessel diameter is one of the most informative xylem traits. It determines xylem area-specific conductivity [39]. The safety versus efficiency paradigm provides the context for interpreting trends in vessel diameter. Hydraulic conductivity per xylem cross sectional area may be used as a proxy for transport efficiency. Transport safety impacts the ability of plants to cope with drought, frost, and certain pests and pathogens. Transport safety is most commonly defined as the ability to maintain cohesive water columns and to prevent a phase transition of liquid water to gas [39].

The area of phloem at the stem grew on 24% in plants treated with IP 11 MPa, and did not change in plants treated by 29 MPa IP as compared to the control plants (Fig. 4 A). The dry weight of inflorescences increased 1.6-1.3-fold after the treatment with 11 and 29 MPa respectively (Fig. 3). The overall area of phloem and xylem of leafstalk increased in treated plant as compared to control ones (Fig 4 C). That was a good precondition for effective photosynthesis and transport of photosynthates from leaves.

The harvesting of buckwheat plants was performed at 90 days. The accumulation of nutrients was completed now, but their redistribution in plant tissues continued [40,41]. Fig. 3 (90 days) demonstrated that the total dry weight increased 1.3-fold in plants treated by IP 11 MPa and corresponded to control ones in plants treated by IP 29 MPa. Treated plants differed from control ones in the distribution of dry substance. The weight of root and leaves increased 2-3-fold after treatment with 11 MPa compared to control ones. The dry weight of stem in plants treated by IP 11 MPa corresponded to control, but the weight of inflorescences increased 22.6%. The ratio inflorescence weight: total weight was equal in control and 11 MPa variants (0.25 and 0.23 respectively). So hormesis in that variant was realized as an overall improvement of growth. Plants treated by IP 29 MPa did not differ from control ones in the dry weight of root, but the weight of stem and leaves decreased 50% and 27% respectively compared to control ones. The dry weight of inflorescences in plants treated by IP 29 MPa increased 2.26-fold as compared with the control variant. The ratio inflorescence weight: total weight was 0.56. Hence plants treated by IP 29 MPa were inclined to move photosynthates into inflorescences instead of remaining them in stems and leaves.

The number of bundles, the overall number and area of vessels (Fig. 4) in the lower parts of the stems increased by a third in plants treated by IP 29 MPa compared to the control ones. These plants continued to flower at 90 days, so the tendency to everbearing was obvious.

The area of phloem increased (Fig. 4 A) to 60-33% in the lower parts of stems of treated plants compared to control. This implied both the transport of substances in the phloem acripetally and basipetally. Firstly, plants inclined to everbear stored nutrients in the root. Secondly, the root redistributed them to the ripening fruits, most probably because the total dry weight of the treated plants did not differ from the control, but their productivity increased. This is evidence of the redistribution of nutrients in the plants.

In the leafstalk (Fig. 4C) the overall area of vessels increased 1.2-1.9-fold in plants treated by IP compared to the control due to the number of vessels. The area of phloem increased by 22-27% respectively in plants treated by IP 11 and 29 MPa treated plants compared to the control ones. The water flow promoted the formation of phloem current in the leaf, which favoured the distribution of photosynthates to the "sink".

In the peduncles (Fig. 4C) of the plants treated by IP the number of vessels also increased by

60%, resulting in an increase in the overall area of vessels by 16-52% in 11 and 29 MPa variants compared to control ones. The increase in the area of phloem by 1.4-2.6-fold (Fig. 4C) in the peduncles of plants treated by IP was critically important in the nutrition of fruits and in the increase of productivity (Figs. 2, 3). While on buckwheat inflorescences ripe and ripening fruits as well as flowers are found together, they are "competitors" for nutrients. Often the buckwheat plant forms too many fruits, but only a small portion of them (4-6%) can ripen due to deficiencies. So an increase in activity of the conductive tissues resulted in the productivity.

The activation of plant growth and development conduced to the increase of flowers and provide favorable conditions for the supply of forming fruits with photosynthates. The formation of assimilating surface and the supply of nutrients to the fruits seem to be essential for fruit formation.

Results of our tests showed that the growth of seedlings treated by IP 11 and 29 MPa was decreased; the accumulation of dry substance was slower than in control variant. Probably, heterotrophic growth of seedling when it uses spare nutrients of endosperm was inhibited, but the growth of leaves starts to increase. Autotrophic nutrition promoted the growth of leaves and accumulation of dry substance in different parts of plants treated by IP 11 MPa in budding and flowering phases. Accumulation of dry substance was decreased in plants treated by IP 29 MPa as compared to control variant in budding and flowering phases. In harvesting phase, total dry weight of plants treated by IP 11 MPa increased, but ratios of the weight of its parts corresponded to control. Development of xylem and phloem in common corresponded to control variant, but the size and amount of elements mostly increased. So the distribution of photosynthates did not differ fundamentally. On the contrary, plants treated by IP 29 MPa had low weight of stem and leaves and poor conductive phloem in the stem, but they formed more fruits due to 2-fold increase of phloem in the bundle.

The commonly accepted concept (but it is not single) is concept of ecological strategies of Ramenskij-Grime [42-44]. It is the major generalization in plant physiology and ecology. Differences between plants lay on the rate of their growth. The growth of plans depends on the changes in environment. So there were identified two factor gradients, broadly categorized as disturbance and stress, which limit plant biomass. Stresses include factors such as the availability of water, nutrients, and light, along with growth-inhibiting influences like temperature and toxins. Conversely, disturbance encompasses herbivory, pathogens, anthropogenic interactions, fire, wind, etc. Emerging from high and low combinations of stress and disturbance are three life strategies commonly used to categorize plants based on environment: (1) C-competitors, (2) S-stress tolerators, and (3) R-ruderals [42-44].

Each life strategy varies in trade-offs of resource allocation to seed production, leaf morphology, leaf longevity, relative growth rate, and other factors, which can be summarized as allocation to (1) growth, (2) reproduction, and (3) maintenance. Competitors are primarily composed of species with high relative growth rate, short leaf-life, relatively low seed production, and high allocation to leaf construction. Stress-tolerators, found in high stress, low disturbance habitats, allocate resources to maintenance and defenses, such as anti-herbivory. Species are often evergreen with small, long-lived leaves or needles, slow resource turnover, and low plasticity and relative growth rate. Due to high stress conditions, vegetative growth and reproduction are reduced. Ruderals, inhabiting low stress, high disturbance regimes, allocate resources mainly to seed reproduction and are often annuals or short-lived perennials. Common characteristics of ruderal species include high relative growth rate, short-lived leaves, and short statured plants with minimal lateral expansion [42-44].

Plants of named groups differ in the intensity of photosynthesis; competitors have the maximal value, ruderals have intermediate quantity, and stress-tolerators have the lowest value. Then competitors and ruderals use more photosynthates for respiration and growth, but stress-tolerators growth and dissimilate slowly. Distribution of assimilates differs in plants. Competitors and ruderals form more leaves than stress-tolerators; they accumulate substance in the stem, flowers and fruits. Stress-tolerators develop their roots and organs for vegetative reproduction [45].

Traits of the distribution of assimilates is connected with the activities of vascular system which directs the flow of assimilates from source

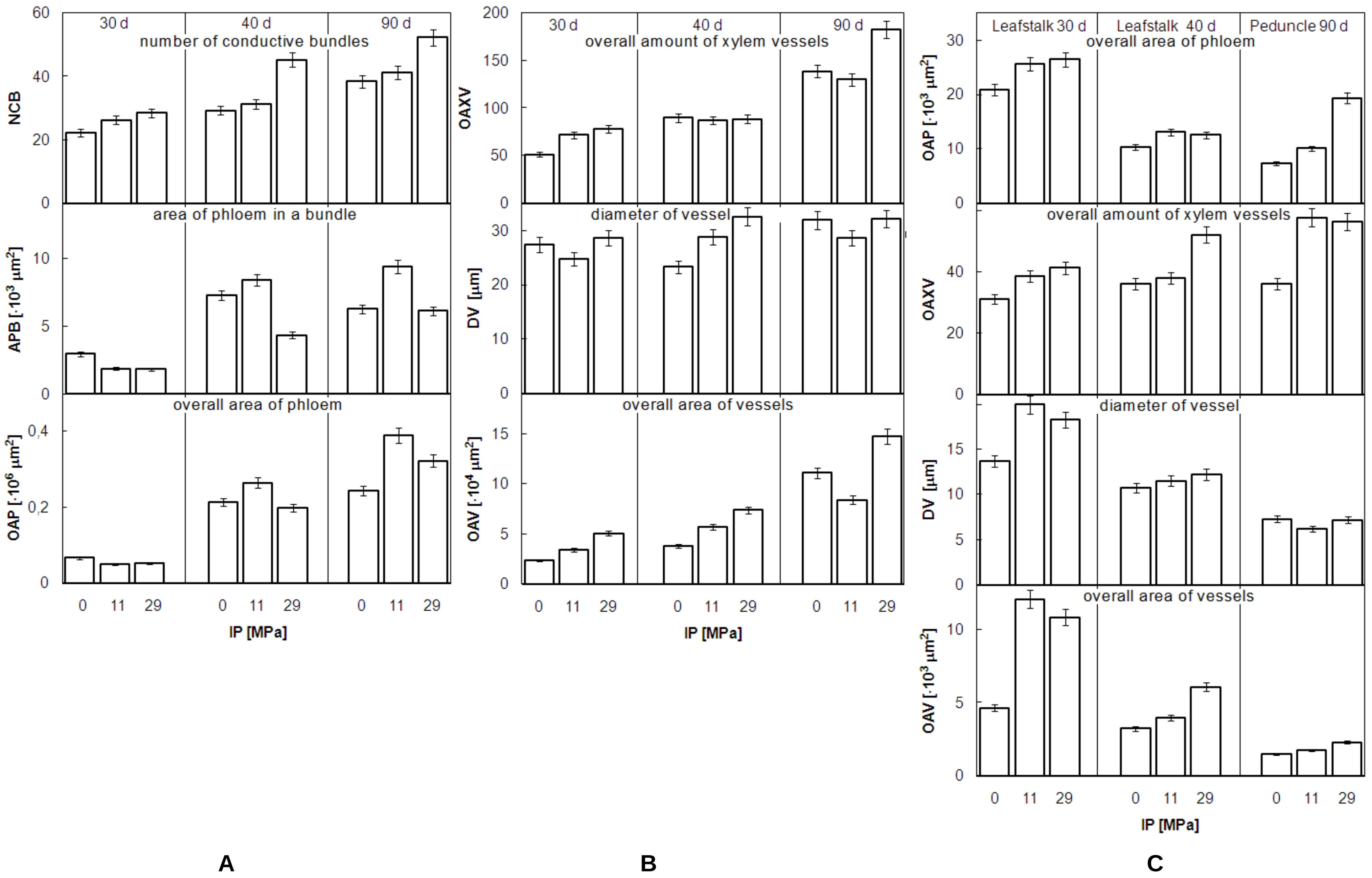

Fig. 4. Development of conductive tissues in the lower part of stem (hypocotyl), leafstalk and peduncle in the buckwheat plants treated by IP

M±m; n=4; NCB - number of conductive bundles; APB -area of phloem in a bundle, µm^2; OAP - overall area of phloem, 10^6 µm^2 (A), 10^3 µm^2 (C); OAXV - overall amount of xylem vessels; DV - diameter of vessel, µm; OAV - overall area of vessels, 10^4 µm^2 (B), 10^3 µm^2 (C).

Table 1. Seed germinability and parameters of yield of buckwheat after treatment of seeds by IP

Variant		Control	11 MPa	17 MPa	23 MPa	26 MPa	29 MPa	35 MPa
					Sowing			
1	Number of sowing fruits per m^2	223	219	285	380	394	463	518
2	Weight of sowing material, kg/10,000 m^2	71.7	70.2	91.5	122.1	126.4	148.6	166.3
					Yield			
3	Number of matured fruits per plant	109.9±6.8	130.8± 5.1*	134.6± 5.3*	104.9± 2.7	195.5± 7.4*	300.1± 8.5*	409.6± 9.2*
4	Weight of matured fruits, g / plant	3.069± 0.030	3.567± 0.196*	3.796± 0.125*	2.786± 0.064*	5.518± 0.460*	7.331± 0.317*	12.323 ± 0.289*
5	Weight of 1,000 fruits	27.78± 0.02	27.53± 0.02*	28.28± 0.03*	26.69± 0.02*	28.25± 0.02	24.43± 0.02*	30.22± 0.02*
6	Yield, kg / 10,000 m^2 (calculated)	6,120	7,160	7,630	5,550	10,970	14,380	21,320

M±m; n=4; P = 0.05

to sink due to "request" of attracting parts. The main sinks in competitors are meristems which form vegetative organs, the main sinks in ruderals are flowers and fruits, and the main sinks in stress-tolerators are reserving tissues and organs of vegetative reproduction.

If the stress in plants is evolutionary formed reaction, plants can change their physiological processes after the influence of different disturbing factors in accordance to ecological strategies. So reaction of plants treated by IP 11 MPa concludes mainly in increase of vegetative growth. Those plants were shown to have water stress and low temperature resistance [46]. So they are similar to competitors by the complex of traits. Conversely, plants treated by IP 29 MPa grow slowly, but forms many fruits like stress-tolerators.

4. CONCLUSION

IP promotes the appearance of three zones, which are in the dose-response relationship: stimulation (hormesis), transition and stress.

IP did not influence the germinability of seeds in the range of 3-11 MPa, IP 17-23 MPa retarded germination, but did not bring about acute seed death. IP 29-35 MPa induced the death of some of seeds, and seed germinability reduced on 22%-57%.

Changes in the yield after the treatment of IP 3-8 MPa were not revealed. The yield was grown up to 17% after IP 11 MPa. This variant is recommended for agricultural use. Variability of yield after IP 17-23 MPa denotes the transition state. IP 29 MPa decreases the germination by half, but it would be tempting to get the 2.3-fold increase of yield. Application of high pressures is interesting as theoretical approach to plant productivity in stress.

The weight of vegetative organs and fruits as well as the size and amount of conductive elements increased at IP 11 MPa, but their dynamics and the sink-source dynamics corresponded to control variant in common. That reaction could be formed as ecological strategy of competitors which allows persisting in low disturbance environments, and rapidly monopolizing resource capture. IP 29 MPa promoted the change of sink-source dynamics. The ratio of fruits and vegetative organs changed as compared to control variant, the part of fruits increased twice (about a quarter in control and a half at IP 29 MPa). The area of phloem in the stem was equal to control, and it increased in the leafstalk and peduncle. Such an extreme reactions reminded the ecological strategy of stress-tolerators found in high stress. The phenomenon of the significant increase of yield under stress aims to ensure the survival of a population in common but not only one individual.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Toyota M, Gilroy S. Gravitropism and mechanical signaling in plants. American Journal of Botany. 2013;100(1): 111-125.
2. Puijalon S, Bouma TJ, Douady CJ, et al. Plant resistance to mechanical stress: Evidence of an avoidance-tolerance trade-off. New Phytologist. 2011;191(4):1141-1149.
3. Hoson T, Wakabayashi K. Role of the plant cell wall in gravity resistance. Phytochemistry. 2015;112(1):84-90.
4. Felix G, Regenass M, Boller T. Sensing of osmotic pressure changes in tomato cells. Plant Physiology. 2000;11:1169-1180.
5. Trewavas A. Signal perception and transduction. Bio- chemistry and Molecular Biology of Plants. B.B. Buchanan, W. Gruissem and R.L. Jones, eds. Rockville, USA: Amer. Society of Plant Physiologists. 2000;18:930-936.
6. Fensom DS, Tompson RG, Caldwell CD. Tandem moving pressure wave mechanism for phloem translocation. Fisiologia Rastenii (Moscow). 1994;41: 138-145 (Russian Journal of Plant Physiology, Engl. transl.).
7. Meitern A, Õunapuu-Pikas E, Sellin A. Circadian patterns of xylem sap properties and their covariation with plant hydraulic traits in hybrid aspen. Journal of Plant Physiology. 2017;213:148-156.
8. Afreen F, Zobayed SMA, Armstrong J, Armstrong W. Pressure gradients along whole culms and leaf sheaths, and other aspects of humidity-induced gas transport in *Phragmites australis*. Journal of Experimental Botany. 2007;58:1651-1662.
9. Pfeffer V. Druch und Arbeitsleistung durch wachsende pflanzen. Leipzig; 1893.
10. Zhou Y, Coventry DR, Denton MD. Soil surface pressure reduces post-emergent shoot growth in wheat. Plant and Soil. 2017;413(1-2):127-144.
11. Tardieu F. Growth and functioning of roots and of root systems subjected to soil compaction – towards a system with multiple signaling. Soil Tillage Research. 1994;30:217-243.
12. Croser C, Bengough AG, Pritchard J. The effect of mechanical impedance on root growth in pea (*Pisum sativum). 2*. Cell expansion and wall rheology during recovery. Physiologia Plantarum. 2000; 109:150–159.
13. Bizet F, A. Bengough G, Hummell, Bogeat-Triboulot M-B, Dupuy LX. 3D deformation field in growing plant roots reveals both mechanical and biological responses to axial mechanical forces. Journal of Experimental Botany. 2016;67(19):5605-5614.
14. Mirabet V, Das P, Boudaoud A, Hamant O. The role of mechanical forces in plant morphogenesis. Annual Review of Plant Biology. 2011;62:365-385.
15. Dumais J, Steele CR. New evidence for the role of mechanical forces in the shoot apical meristems. Journal of Plant Growth Regulation. 2000;19:7-18.
16. Kwiatkowska D. Structural integration at the shoot apical meristem: Models, measurements and experiments. American Journal of Botany. 2004;91: 1277-1293.
17. Nakayama N, Smith RS, Mandel T, et al. Mechanical regulation of auxin-mediated growth. Current Biology. 2012;22(16): 1468-1476.
18. Lysak VI, Kuzmin SV. Explosive welding of metal layered composite materials. BE Paton, ed. Kiev (Ukraine); 2003.
19. Woo S-H, Roy SK, Kwon SJ, et al. Concepts, prospects, and potentiality in buckwheat (*Fagopyrum esculentum* Moench). In Zhou M, Kreft I, Woo S-H, Chrungoo N, Wieslander G, editors. Molecular Breeding and Nutritional Aspects of Buckwheat: A Research Perspective. Elsevier. 2016;21–49.
20. Campbell CG. Buckwheat. *Fagopyrum esculentum* Moench. Promoting the conservation and use of underutilized and neglected crops. Institute of Plant Genetics and Crop Plant Research, Gatersleben / International Plant Genetic Resources Institute. Rome (Italy); 1997.
21. Alekseeva ES, Pausheva ZP. Genetika, selekcija i semenovodstvo grechihi (Genetics, selection and seed production of buckwheat). Kiev (Ukraine): Vyscha shkola; 1988.
22. Li S; Zhang QH. Advances in the development of functional foods from buckwheat. Food Science and Nutrition. 2001;41(6):451-464.
23. Bobkov S. Biochemical and technological properties of buckwheat grains In Zhou M, Kreft I, Woo S-H, Chrungoo N, Wieslander G, editors. Molecular breeding and nutritional aspects of buckwheat: A

research perspective. Elsevier. 2016;423–440.

24. Ikeda K, Ikeda S. Factors important for structural properties and quality of buckwheat products. In Zhou M, Kreft I, Woo S-H, Chrungoo N, Wieslander G, editors. Molecular Breeding and Nutritional Aspects of Buckwheat: A Research Perspective. Elsevier. 2016;193–202.
25. Zeller FJ Buckwheat (Fagopyrum esculentum Moench): Utilization, genetics, breeding (Übersichtsarbeiten buchweizen (Fagopyrum esculentum Moench): Nutzung, Genetik, Züchtung). Bodenkultur. 2001;52(3):259-276.
26. Pikhtovnikov RV, Zav'yalova VI. *Shtampovka listovogo materiala vzryvom* (Stamping of sheet material by explosion). Moscow (Russia); 1964.
27. Atroshchenko ES, Khryanin VN, Atroshchenko EE, et al. Method of presowing treatment of crop seeds. Patent RU 2083073 C1 6A01 C $^{1}/_{00}$ A01 G $^{7}/_{04}$. Byull. Izobretenii. 1997;19.
28. Nefedeva EE, Mazei NG, Khryanin VN. Changes in the hormonal balance in germinating seeds after an impulse-pressure treatment. Russian Journal of Plant Physiology. 2005;52(1):127-130.
29. Nefed'eva E, Veselova T, Veselovskii V, Lysak V. Influence of pulse pressure on seed quality and yield of buckwheat (*Fagopyrum esculentum Moench.*). European Journal of Molecular Biotechnology. 2013;1:12-27.
30. Veselova TV, Veselovsky VA, Obroucheva NV. Unexpected aftereffects of low dose γ-irradiation on quality of individual dry pea seeds. International Journal of Biochemistry and Biophysics. 2017;5(1):9-18.
31. Hormesis: A Revolution in Biology, Toxicology and Medicine. Ed: MP Mattson, EJ Calabrese. New York: Spinger; 2010.
32. Veselovskii VA, Veselova TV, Chernavskii DS. Plant stress: A biophysical approach. Fiziologia Rastenii (Moscow). 1993;40: 553-557 (Russian Journal of Plant Physiology, Engl. Transl.).
33. Nefedieva EE. The effect of impulse pressure on the crop productivity and physiological characteristics of some tomato (*Lycopersicon esculentum*) hybrids. Greenwich Journal of Science and Technology. 2002;3(1):51-59.
34. Nefedieva EE. Effect of impulse pressure on the crop productivity and germinating power of cucumber (*Cucumis sativus*) plants. Greenwich Journal of Science and Technology. 2003;4(1):25-30.
35. Nefedieva EE, Khryanin, VN. The arteffect of impulse pressure on the phytohormone content and some morphological characteristics of buckwheat plants. Russian Journal of Plant Physiology. 1999; 2:194-200.
36. Minchin PEH, Lacointe A. Consequences of phloem pathway unloading/reloading on equilibrium flows between source and sink: A modelling approach. Functional Plant Biology. 2017;44(5):507-514.
37. Carella P, Wilson DC, Kempthorne CJ, Cameron RK. Vascular sap proteomics: Providing insight into long-distance signaling during stress. Frontiers in Plant Science. 2016;7:651.
38. Lucas WJ, Liu CM. The plant vascular system I: From resource allocation, inter-organ communication and defense, to evolution of the monocot cambium. Journal of Integrative Plant Biology. 2017;59(5): 290-291.
39. Hacke UG, Spicer R, Schreiber SG, Plavcová L. An ecophysiological and developmental perspective on variation in vessel diameter. Plant Cell and Environment. 2017;40(6):831-845.
40. Van Bel AJE, Gamalei YV. Ecophysiology of phloem loading in source leaves. Plant Cell and Environment. 1992;15:265-270.
41. Van Bel AJE, Helariutta Y, Thompson GA, Ton J, Dinant S, Ding B, Patrick JW. Phloem: The integrative avenue for resource distribution, signaling, and defense. Frontiers in Plant Science. 2013; 4:471.
42. Ramenskij LG. O principial'nyh ustanovkah, osnovnyh ponjatijah i terminah proizvodstvennoj tipologii zemel', geobotaniki i jekologii (The fundamental units, basic concepts and terms of production typology of land geobotany and ecology). Sov. botanika (Soviet Botany). 1935;4:25-42.
43. Grime JR. Plant strategies and vegetation processes. Chichester, Brisbane, Toronto: S. Willey and Sons; 1972.
44. Grime JR. Vegetation classification by reference to strategies. Nature. 1974;250: 25-42.
45. P'yankov VI, Yashkov MYu, Lamanov AA. Transport and partitioning of assimilates and the structure of source-sink relations in wild plant species of middle Ural.

Russian Journal of Plant Physiology. 1998; 45(4):491-499.

46. Shilenkov AV, Mazej NG, Nefed'eva EE, Khrjanin VN. Dejstvie impul'snogo davlenija i ponizhennyh temperatur na soderzhanie prolina v prorastajushhih semenah grechihi (Effect of pulse pressure and low temperature on the contents of proline in germinating seeds of buckwheat) Sel'skohozjajstvennaja biologija (Agricultural biology). 2008;5:70-77.

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