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ON HOW WE CAN NON-CANONICALLY INCREASE HEREDITARY DROUGHT RESISTANCE IN PLANTS (BY AN EXAMPLE OF CEREALS)

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Abstract

Improvement of hereditary drought resistance in crops is recently being among the main objectives for food security of humanity because of global warming and the growing costs for bakery and forage grain. Analysis of complex properties of drought resistance in cereals (phenotyping) shows the limitations of a canonical genocentric approach and the approaches based on molecular genetics to solve the problem of significant hereditary improvement of drought resistance. The priority epigenetic approach that we propose is based on the theory of eco-genetic organization of quantitative traits (TEGOQT). In TEGOQT seven genetic-physiological systems (GPS) involved in harvest increasing, but not particular traits of productivity, are to be operated with. These GPS are attractions; micro-distribution of attractive plastic substances between grains and chaff in ear; adaptability to drought, cold, frost, heat, salt, etc; horizontal immunity; «payment» by dry biomass for a limitative factor of soil nutrition — N, P, K, etc; tolerance to plant density in phytocenosis; hereditary variability in duration of the phases of ontogenesis). In this paper we discuss drought adaptability as a part of GPS complex. It is shown that phenotyping evaluation is necessary to analyze drought tolerance, the complex property to which no less than 22 component characters contribute. This allows to construct a set of eco-genetic portraits (EGP) of parent plants at different types of drought simulated in an artificial climate control chamber. The EGP are histograms which reflect the values of all components of drought resistance for each parent thus allowing to select pairs complementary in the elements of the EGP. Based on a predictive EGP, it is possible to define, through mathematical models that reflect the contribution of each component to the resulting drought tolerance, the optimum combination of components for ensuring maximum positive additive effect, and thus to manage selection of the parents for hybridization in view to create new drought resistant varieties.

Keywords: crop cereals, drought resistance, phenotyping, eco-genetic portraits, management by selection of parental pairs

Evolution did not produce any plant that would prefer drought

(V.V. Kyznetsov, G.A. Dmitreieva)

*There are so many hungry people that God cannot appear to them
except in the form of bread*

(Korita Kent)

Every year, the Russian grain industry loses 5-7 billion rubles due to drought. In 2015, the damage amounted to 7.9 billion rubles. In Australia, in 2003, the wheat production reduced from 24 to 9 million tons, or by 62.5 %, because of drought [1]. For any plant, the direct effects of moisture deficiency (drought) are reduced cell turgor, stomata closing, suppressed growth, and a decreased yielding [2, p. 218]. There are various agrotechnical methods for combating drought: snow accumulation in fields by forest belts, fallows and watering

(from irrigation to sprinkling and drip irrigation), etc. However, the number of genetic breeding techniques is much greater, and they are cheaper than agricultural technologies, especially those used for irrigation or applied annually.

Is it possible to substantially increase hereditary drought resistance of cultivated cereals? For the answer, it is necessary, according to the Vavilov's law of homological series in hereditary variability, to seek for an increased drought resistance in wild relatives of traditional crops [3]. It is known that some cereals (*Gramineae*) overcome cultivated cereals in drought resistance. *Phleum phleoides* Wib., *Agrostis vulgaris* With., *Stipa capillata* L., *Lasiagrostis splendens* Kunth., *Poa bulbosa* L., *Festuca ovina* L., *F. sulcata* L., *Bromus inermis* Leyss., *B. sterilis* L., *Agropyrum cristatum* L., *Hordeum spontaneum* C. Koch. grow on dry soils where no cultivated cereals can exist [4]. Consequently, we can talk about the principle possibility of significantly increasing the drought resistance of traditional cereal crops. Wild varieties have increased this property over tens of thousands years by natural selection. Modern geneticists, physiologists and breeders should create new drought resistant varieties in the next decade.

As to the traditional genocentric paradigm, according to which genes determine productivity, adaptability and the genotypic variability of these characteristics, drought resistance is the trait to be studied by the Mendelian genetics. In case of a not clear segregation histogram, the analysis of diallel crosses according to Hayman [5] can be used, based on the same Mendelian genetics postulates. Hence, there is an aspiration to find a gene (polygenes) of drought resistance. The multi-component nature of drought resistance formed during phases of ontogenesis due both to gene differential activity and epigenetic effects (e.g. in hardening and induction by drought of the sleeping genes expression) is not usually considered. These change the hypothetically unambiguous path from the gene to the trait.

There are various types of drought [6], and each depends on many physiological and morphological features of plants. The main ones are the orthotropicity and depth of the root system [7-10]; a labile functionally active part of the root system (for example, a small number of deep roots, reaching the moist soil horizon, increases the moisture absorption by several times, whereas the bulk of the roots in the upper dry horizon practically do not work) [7]; the depth of tillering node, determined by the balance of hormones [11]; osmotic pressure in root hairs [12-14]; energy transport of soil solutions [15, 16]; energy consumed for enzymatic reactions [17]; the temperature limiting catalytic activity of nodal enzymes [17]; ATP synthesis [18]; membrane efficiency [19]; total surface area of the leaves as related to their volume and weight [20]; the thickness and density of the cuticle [11]; the number of stomata per leaf area unit and their size [21]; the osmotic mode of stomata opening and closing [21]; leaf pubescence (i.e. hair density, length, stiffness and light reflection) [11]; leaf ability to twist when drought [14]; vertically oriented leaves [14]; short and narrow leaves [11]; shift of the critical phase of ontogenesis under a typical stressor at a certain time [11]; the intensity of metabolic water production [14]; the structure of chloroplasts, optimal for droughts [14]; CO₂ assimilation per moisture loss [22]; energy expenditures for attraction [23]. The papers on the phenotyping (dissection) of the drought resistance trait into elementary components begin to appear [24].

Each of the components of drought resistance as a complex property cannot be determined by one or two Mendel genes. For example, let us consider the genetic determinism of the component "the osmotic pressure in root hairs". It is known [25] that the total number of genes expressed in human cells is about 24,000, of which about 11,000 are present in cells of any type. If this principle is valid for plants, it can be assumed that there is a pool of products of more than

10,000 genes in each cell of a root hair and each product contributes to the resultant osmotic pressure of hair cells, which allows extracting soil solution from the semi-dry substrate. By the traditional breeding methods (pair crosses and phenotypic selections), it is hardly possible to assemble 10,000 genes for the maximum osmotic activity. A smaller number of genes most likely determine the remaining components of drought resistance; however, geneticists have not found discrete histograms of Mendelian segregation for any of these 22 components. N.L. Udolskaya in 1936 showed [25] that drought tolerance of the variety varies in ontogenesis and depends on the combination of factors that cause drought. Drought resistant varieties can become drought sensitive when precipitation regime changes.

Productivity and yields are determined by genotype \times environment interaction (GEI) effects rather than by quantitative trait genes. GEIs are emergent properties of high organization levels (ontogenetic, population, phytocenotic) which are absent at the molecular level [26]. N.I. Vavilov wrote: "We will not be surprised if a thorough study of the heredity of quantitative traits leads to a fundamental revision of simplified Mendel's ideas" [27, p. 275]. The specific genes for productivity, yielding and yield homeostasis (plasticity of the variety), horizontal immunity, species immunity, drought, winter, heat and cold resistance, and so on have not been found, isolated, localized, cloned or sequenced [28]. Similarly, the processes responsible, for example, for consciousness, long before the transition to molecular level will disintegrate to ordinary occurring reactions [29].

Now, it is proposed to radically increase drought resistance with the help of transgenesis, by introducing Mendel genes into non-drought resistant plants. Sometimes, under a certain type of drought, such a gene can slightly increase the yield. Unfortunately, Mendel genes in plants are described very little (only 1-3 %). The products of the remaining 97 % of the genes are, firstly, almost unknown, and, secondly, they are in the most complex interactions with each other and with the constantly changing (even within 24 hours) external limiting factors. As a result, when the LIM factors change, these products alternately determine the components of drought resistance and the resulting manifestation of this property as a whole.

In transgenesis, which currently allows transferring only Mendel genes, there are many weaknesses. The existing methods of plant transformation are effective enough, species- and variety-specific, lead to the random integration of foreign DNA into the recipient genome, impose limitations on the amount of information transferred, etc. The transfer of transgenes from one variety to another requires multiple return crosses and cannot be considered a genetically pure procedure, because in a random recombination, with the transfer of foreign DNA, different DNA fragments of the donor variety are transferred. Transgenes in commercial varieties are expressed constantly and, as a rule, in all plant organs and tissues (similar to cancer behavior when cells escape from the control of the whole organism and divide arbitrarily in any tissues). Effective integration of transgenes into a predefined region of the genome still remains problematic. Manipulating even a few independent traits and coordinating them into hundreds of varieties is an extremely difficult task for breeders [30].

Unfortunately, some geneticists consider such a complex property as drought resistance, which is due to different activity of the genes in ontogenesis, as a feature that is genetically controlled like the elementary Mendel's ones. No attention is paid to the variety specific characters, drought types and duration, the periods of plant sensitivity to drought and the ontogeny phase, in which various productivity elements are pre-formed, the number of which is reduced by the

effect of drought in the corresponding phase of the ontogeny [31]. D.A. Sabinin, the founder of the Russian scientific school of plant physiology, urged to study how various organs and yield components are initiated in ontogenesis.

Breeders and agronomists traditionally estimate drought resistance as a yield value, although there are varieties with the same dry plant weight (that is, in fact, with the same drought resistance), but with different GPS (genetic physiological systems) of attraction, which unequal activity of which results in different grain yield. That is, the grain yield cannot be a correct and strict estimate of drought resistance. Thus, firstly, it is necessary in every particular case to take into account the type of drought in connection with the phase of ontogenesis, in which it occurred, and characterize drought by the force of the action and duration. Secondly, "drought resistance", in our opinion, is biologically very indefinite (this term is used in physics), and it is more appropriate to use the notation "drought tolerance", "drought endurance" or "drought productivity" (the last concept seems to be the most adequate). The final strict quantitative measure of drought productivity should be a reduction in dry plant biomass as compared to that of analogues of the same variety grown in comfortable conditions. In this article, by drought resistance we will understand drought productivity.

Note that the drought productivity, as plant biomass per area of agrophytocenosis, is determined not only by elements of drought resistance, but also by the polygenes of competitiveness and tolerance to sowing density that is, this criterion is much less stringent than the dry biomass production of a single plant at drought.

Breeders test many varieties at different droughts, cross the most drought resistant ones, and in segregating generations, starting with F_2 , visually select the most productive individuals by the phenotype. In this case, each productivity trait has a phenotypic variability in the population, including ecological (modification), genotypic, genetic (additive) and epigenetic components of the variability that are not eye-visible. The genotypic variability for yield elements usually amounted to 10-20 %, while ecological one amounted to 80-90 % (if the plants are located at a sufficient distance from each other and do not interact). At the usual density for the nursery, additional noise appears, masking the unique genotypes necessary for the breeder such as genotypic, ecological (competitive) and ontogenetic ones [32]. P.P. Litun [33] on the model wheat populations tested the reliability of selection for phenotypes under drought and found out that of the 10,000 visually isolated plants, only one was genetically drought resistant.

Such a low efficiency of individual genotype identification by phenotype creates a significant obstacle to the inherent increase in drought resistance. The application of the principle of background traits [34] and a new method of genetic analysis of quantitative traits [35] radically solve the problems.

Unfortunately, drought-induced expression of the so-called sleeping genes, like the inducible genes of heat and cold shock proteins [1], has not been adequately studied. The plant response to water deficiency through the synthesis of abscisic acid (ABA), which closes the stomata to reduce water loss, is known [20]. In case of water deficiency, the synthesis of low molecular weight osmotically active substances (mono- and oligosaccharides, as well as amino acid, primarily proline), betaine, polyhydric alcohols and various stress proteins (osmotin, dehydrin) is activated. Proline is of particular importance; its content increases sharply in drought [36, 37]. The *RD29* (responsive to dehydration) genes, for example, are activated in osmotic shock, cooling, water deficiency and by ABA treatment; that is, the genes that are expressed in response to different stressors are known [24].

For a simplified analysis, of all 12 ontogenetic phases in cereals, we sin-

gle out tillering as one of those determining final productivity. In this phase, the drought has a significant effect on the grain number per ear, so it is important to create tolerant varieties for the climatic zones where drought occurred during the onset of this phase (i.e. the most of the grain zones of Siberia). A quantitative measure of drought resistance in tillering (by analogy with the overall resultant drought resistance) is the reduction in the grain number in the ear in a drought-affected plant, compared to the same index for a plant of the same variety under comfortable conditions. The second phase, which we will consider, is grain filling. Saratov type drought, having the greatest impact on this phase, could be estimated by wrinkled grain ratio.

Thus, there are two serious obstacles to the inherent increase in drought resistance: the complexity of the combinatorics of the best polygenes in one class and the very low efficiency of reliable visual identification of genotypes by phenotypes. The second problem is practically removed by the innovative technology of selection, which unlike all existing ones is built on the principles of background traits [34] and “orthogonal” (multidirectional) identification [23]. According to this technology, the productivity traits [35] are not used to visually identify plants that possess the breeder's desired property. They serve as coordinates in which the contributions of genetic and physiological systems are multidirectional. It allows to eliminate interferences that reduce effectiveness of visual identification of genotypes in the field, and help to unerringly identify individual positive hereditary deviations in any of the seven GPS, including the adaptive system, which manifestation at drought leads to drought resistance.

In this paper, we present the development of the formalized approach to selection according to the GPS data, with the example of a hereditary increase in drought resistance in cultivated cereals. We believe that the management of this process should not be carried out at the molecular level (DNA and Mendel genes), but at the level of setting and forming each of the 22 components of the resulting drought resistance and estimating for each component its additive fraction of variance in a specific varieties set. After detection of the genotypes bearing additive polygenes with the maximum contribution to each component of drought resistance, one should try to combine these polygenes by diallelic crosses of 22 varieties with the additive genes, of which the maximum contribution to drought resistance of at least one component is characteristic. To solve this problem, it is proposed to use the model of a quantitative productivity indicator, replacing the traditional model of Ronald Aylmer Fisher [32] for plants. The model proposed by us is formalized in the corresponding algorithms and programs [38].

A success in the selection of wheat indicates that this culture has a very significant additive (genetic) variance [11]. That is why the optimal approach to increasing hereditary drought resistance is the use of ecological genetics methods of quantitative characteristics (one of the branches of epigenetics of quantitative properties) [39]. With its help, it is possible to estimate the additive variance for each of the 22 components of drought resistance and combine the most valuable additive shifts.

Developing our model [38, 40, 41], we proceed from the fact that the plants have the following seven GPS, controlling which breeders achieve an ecogenetic increase in yield. The first is the system of photosynthetic product attraction from stems and leaves to the ear (cereals), capitulum (sunflower), cob (corn), fruit and berries. The second is micro distribution of plastic substances between the grain and the chaff in the ear, the kernel and husk in sunflower, etc. The third one is adaptability (determines the general adaptability to the local conditions of the zone, field and year, as well as adaptability to a certain limiting

factor at a provocative conditions, for example, drought, cold, heat, salinity, soil pH, etc.). The fourth system is horizontal immunity; the fifth one is the dry weight gain per a small dose of soil nutrients (nitrogen, phosphorus, potassium, etc.); the sixth one is tolerance to sowing density; the seventh one is genetic variability of the duration of ontogeny phases. For breeders, the most important types of abiotic adaptability are drought resistance, cold resistance, frost resistance, winter hardiness, heat resistance, tolerance to saline and acidic soils, to lodging and seed germination in ear.

Quantitative geneticists, physiologists and breeders can ignore the complexity of combining multiple genes and their products that affect GPS, and consider only seven GPS (instead of 120,000 genes in soft wheat) as sufficiently indivisible units that are able to combine with each other, gathering in an ideal future variety. Of course, these systems are not 100 % additive, and there are certain interactions between them that do not greatly hamper the historical trend of selective yield increase. This is confirmed by winter wheat varieties for Kuban and Moscow regions with more than 100 c/ha yield which were successfully selected without genetic engineering, genomics, proteomics and metabolomics.

Let us define the formalized form of the criteria for drought resistance of grains in accordance with the verbal definitions formulated above.

For total drought resistance (during grain filling)

$$J_{\Sigma}(T) = \frac{x_{dr}(T) - \Delta_{dr}(T)}{x_{dr}(T)} \cdot 100 \%, \quad (1)$$

and for the partial drought resistance (during tillering)

$$J_k(T_k) = \frac{n_k(T_k) - \delta_k(T_k)}{n_k(T_k)} \cdot 100 \%, \quad (2)$$

where $x_{dr}(T)$ is plant dry weight at filling T phase onset for favorable conditions, Δ_{dr} is the dry weight loss due to drought, $n_k(T_k)$ is the grain number per ear for favorable conditions at tillering, $\delta_k(T_k)$ is the loss of the grain number because of drought.

When predicting drought resistance criteria, we need the following mathematical models: for the structure “moisture—dry matter”

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} b \\ 0 \end{bmatrix} u(t) + \begin{bmatrix} c_{11} & c_{12} & c_{13} \\ 0 & c_{22} & c_{23} \end{bmatrix} \begin{bmatrix} f_1(t) \\ f_2(t) \\ f_3(t) \end{bmatrix} + \begin{bmatrix} \xi_1(t) \\ \xi_2(t) \end{bmatrix}, \quad (3)$$

$$t \in (0, T);$$

for grain number per ear

$$n_k = b_1 f_1 + b_2 f_2 + b_3 f_3 + \zeta_k, \quad (4)$$

where x_1 is plant dry weight, x_2 is the green plant biomass, u is soil available nitrogen; f_1 is PAR as a factor of biomass productivity, f_2 is air temperature as a factor of biomass productivity, f_3 is soil moisture as a factor of biomass productivity; ξ_1 , ξ_2 are random perturbations reflecting uncertainty of the model; a_{11} , a_{22} are parameters of the dynamic model (3); n_k is the grain number per ear at tillering; b_1 , b_2 , b_3 are parameters of the model (4); ζ_k is simulation error.

The models (3) and (4) characterize one of the initial varieties used as a parent to produce a new drought resistant generation. The other parents described in the same way will have other parameters. It is necessary to find due combination of drought resistance elements in final variety. In the second (seg-

regating) generation, pairwise combinations of the best plus additive shifts begin to occur. The information-algorithmic basis of these problems is the concept of “ecogenetic portrait” (EGP) [42]. It is a combination of positive shifts in each of the seven GPS (or components within a single GPS, for example, drought resistance components) which are desirable to combine.

Model (3) describes plant state under favorable conditions. Their violation, like GPS effects, leads to disturbances and the appearance of environmental and genetic variances in plants. However, the above 22 physiological and morphological components indicate the possibility of further deepening the proposed EGP-based approach. After all, each of the seven EGP is characterized by its own number of state components, and most of them can be measured in artificial climate chambers. Let us describe the 22 components that determine drought resistance, as related to all GPS. To do this, we denote these states by the vector $Z = (22 \times 1)$ for all seven EGP, according to their numbering:

$$\begin{aligned} Z &= (z_1 0), \\ Z_2^T &= (0 0), \\ Z_3^T &= (z_1 z_2 z_3 z_4 z_5 z_6 z_7 z_8 z_9 z_{10} z_{11} z_{12} z_{13} z_{14} z_{15} z_{16} z_{17} z_{18} z_{19} z_{20} z_{21} z_{22}), \\ Z_4^T &= (0 0 0 z_4 z_5 z_6 z_7 z_8 z_9 z_{10} 0 0 z_{13} 0 0 0 0 0 0 z_{21} 0), \\ Z_5^T &= (0 0), \\ Z_6^T &= (0 z_2 0 0 0 0 0 0 z_{10} 0 0 z_{13} 0 0 0 0 0 0 z_{21} z_{22}), \\ Z_7^T &= (z_1 z_2 z_3 z_4 z_5 z_6 z_7 z_8 z_9 z_{10} 0 0 z_{13} 0 0 0 0 z_{18} 0 0 z_{21} z_{22}), \end{aligned}$$

where T is the transposition index of the vector and matrix.

As it can be seen from the state vectors structure characterizing drought resistance, the contributions of the EGP to this selection feature are very different. In fact, it is advisable to take into account the contributions of the following EGP, while leaving the most significant states:

$$\begin{aligned} Z_3^T &= (0 0 0 z_4 0 0 0 z_8 0 0 z_{11} 0 0 0 0 0 0 0 0 z_{21} 0), \\ Z_6^T &= (0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 z_{21} 0), \\ Z_7^T &= (0 0 0 z_4 0 0 0 z_8 0 0 0 0 0 0 0 0 0 0 0 z_{21} 0), \end{aligned}$$

(provides drought resistance at tillering when grain number per ear is formed);

$$\begin{aligned} Z_3^T &= (z_1 z_2 0 z_4 0 0 0 z_8 0 0 0 0 0 0 0 0 0 0 z_{18} 0 0 0), \\ Z_6^T &= (z_1 z_2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0), \\ Z_7^T &= (z_1 z_2 0 z_4 z_5 0 0 z_8 0 0 0 0 0 0 0 0 0 z_{18} 0 0 0), \end{aligned}$$

(provides drought resistance at grain filling when 1000 grain weight to one grain weight ratio is formed)

These GPS affect the structure and parameters of the models (3), (4). Strictly speaking, the location and extent of such influence could be identified in the artificial climate chambers. However, when considering general principles of breeding formalization, we confine to the following hypothesis of influence (for mathematical expectation in time scale:

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} a_{11}(Z_3) & a_{12} \\ a_{21} & a_{22}(Z_3) \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} b(Z_6) \\ 0 \end{bmatrix} u(t) + \begin{bmatrix} c_{11}(Z_6) & c_{12}(Z_3) & c_{13}(Z_3) \\ 0 & c_{22}(Z_3) & c_{23}(Z_6) \end{bmatrix} \begin{bmatrix} f_1(t) + \delta f_1(t) \\ f_2(t) + \delta f_2(t) \\ f_3(t) + \delta f_3(t) \end{bmatrix}, \quad (5)$$

$$t \in (0, T(Z_7));$$

$$n_k = b_1(Z_6)(f_1 + \delta f_1) + b_2(Z_3)(f_2 + \delta f_2) + b_3(Z_3)(f_3 + \delta f_3). \quad (6)$$

The considered GPS models influence the overall dynamics of plant biomass accumulation, plant response to fertilizers, light, thermal and water regimes, and also determine the growing season duration.

We convert the models (5), (6) in a more compact and convenient form, where all the variables and parameters are grouped into corresponding vectors and matrices:

$$\dot{X} = A(Z_3)X(t) + b(Z_6)u(t) + C(Z_3, Z_6)(F(t) + DF(t)), \quad (7)$$

$$t \in [t_0; T(Z_7)];$$

$$n_k = B^T(Z_3, Z_6)(F_k + \Delta F_k), \quad (8)$$

The hypothesis of such GPS effect will be incomplete without the parametric approximations of the parametric perturbations introduced by GPS:

$$A(Z_3) = A_0 + P^T \Delta Z_3, \quad (9)$$

$$b(Z_6) = b_0 + D^T \Delta Z_6, \quad (10)$$

$$C(Z_3, Z_6) = C_0 + G \Delta Z_3 + Q \Delta Z_6, \quad (11)$$

$$B(Z_3, Z_6) = B_0 + V^T \Delta Z_3 + W^T \Delta Z_6, \quad (12)$$

$$T(Z_7) = T \pm dT. \quad (13)$$

Thus, we can model the state of plants for favorable conditions (3), (4), taking into account environmental disturbances and genetic and physiological effects (7)-(12). Based on the simulation results, it is possible to predict the criteria of drought resistance (1), (2). However, such a simulation is possible only when specifying EGP taking into account the state vectors that characterize drought resistance and are the result of GPS effects. Now EGP is a normalized response of the parameters characterizing drought resistance to a disturbed environment, and is formed by three main GPS, the adaptability, tolerance to thickening and genetic variability on the ontogenetic periods.

Now let us formalize this. At first, we combine the criteria of drought resistance (1), (2) in the general criterion, which will facilitate classification and selection of parents:

$$J = J_\Sigma + gJ_k, \quad (14)$$

where g is a weighting factor serving as an additional independent variable (argument) in optimization of general selection problem. Crossing plants, we do not know in advance which genotypes and in what quantity we will receive in a new generation. We can only indicate their difference Ω_g , for which the region of the general criterion of drought resistance [14] is divided into N intervals:

$$\Omega_n = \frac{J}{N} * n, n = 1, N - 1. \quad (15)$$

Then the EGP will be a combination of the components of GPS vectors $\Delta\varphi_g [\Delta Z_3, \Delta Z_6, \Delta Z_7 | \Omega_g]$, which ensures that the criterion of drought resistance falls in the region Ω_g .

Since all these components can be estimated quantitatively in the artificial climate chambers, the EGP formation becomes one of the tasks of preliminary identification of the initial varieties of parental pairs. Let us consider the algorithm of the optimum selection of parental pairs for a hereditary increase in drought resistance. A criterion for the breeding result when crossing (an increased drought resistance), and the typical dynamics of all limiting factors for the place of cultivation of the future variety are at breeder's disposal. In addition, the breeder has an initial base variety or a hybrid which drought resistance must be improved, as well as a data bank for the potential parents in accordance with the above mathemati-

cal models through which the result of increased drought resistance can be predicted for the given dynamics of environmental conditions and the technology used. The base variety itself was previously created by the selection methods, and besides the mathematical model, the breeder has its EGP, obtained in preliminary tests in artificial climate chambers. Using the rapid assessment principle of the additives of GPS [43], which should be confirmed in experiments in artificial climate chambers, we select parents' EGP reflecting all the indicators taken into account, and obtain the predicted EGP of the best transgressions in the F_2 generation, i.e. $\Delta\varphi_g [\Delta Z_3, \Delta Z_6, \Delta Z_7 | \Omega_g]$, after input of which into the mathematical model of "dry—wet biomass", it is possible to predict the expected increase in drought resistance J . Comparing it with the required value of J^* , we can decide to stop the process or move to the next possible variant of crossing. By sequentially sorting out the available for cross-breeding options, one is identified that provides the greatest approximation to the required drought resistance J^* .

We understand that we are at the initial stage of the selection process formalization. The simple model of drought resistance components presented in this paper is the initial approach to constructing a complex mathematical model of evolution from the 22 parameters that have been considered, which determine the complex drought resistance property. In particular, the central problem is the identification of drought resistance models in artificial climate chambers, since these models are intended to reveal the possibilities of our proposed theory of ecological and genetic organization of the quantitative trait in the population, an important element of which is the idea of seven GPS and the availability of components within each GPS. The proposed theory replaced the general model of R. Fisher and was adapted for plants. If a breeder knows the contributions of each of the seven GPS to the crop at a typical dynamics of LIM factors, this gives him a tool to control the formation of EGP in real time during the growing season, which makes it possible to transform the selection process from the passive expectation of a probable result to a controlled selection technology.

To implement the proposed simplified scheme, it is necessary, firstly, to perform identification of the mathematical model of plant state dynamics during vegetation (based on this model, the forecast for increasing drought resistance and determining the criteria for selecting parental pairs are determined) at the initial experimental stage in the artificial climate chambers; secondly, to determine the action of all seven GPS and to compare their parameters with the dynamic model based on the results of vegetation; thirdly, to build EGP for initial varieties used as potential parents for subsequent crosses and obtaining the desired variety by the results of vegetation; fourthly, after receiving the F_2 generation, to determine the model of interaction of the parents' EGP, which should be used to form the predicted (required) EGP for a future variety.

Thus, the analysis of the problem of a significant increase in cereals drought resistant both regionally and globally shows that its solution is hardly possible on the basis of classical (Mendelian) and molecular genetics, or modern transgenic methods, in view of the extreme complexity of organizing the multi-component drought resistance, which includes, as a minimum, 22 components. Each of them is formed according to the ontogenesis phases (against the background of the differential activity of genes) and is affected during the vegetation by different types of drought of different duration and intensity. The optimal solution to the problem lies in the application of the recently emerged new direction of genetics, the ecological genetics of quantitative traits (one of the branches of epigenetic). In artificial climate chambers for drought types of a particular breeding zone, at phases critical for the formation of each productivity component, it is necessary to estimate its genotypic and genetic (additive) variability in the set of

varieties of the initial collection created for breeding in the relevant zone, or in world collections, for example, in the collection of VIR (N. I. Vavilov All-Russian Institute of Plant Genetic Resources, St. Petersburg). Next, we must select varieties that carry at least one maximum additive positive shift for at least one component of drought resistance. Then, the selected 22 varieties (there may be less of them if there are varieties bearing two additive positive shifts or more) should be crossed diallelly. Then, in F_2 , the individuals with several positive shifts should be identified and selected. Then they will be crossed again, and finally, the genotype will be selected, which will include 22 (this is the desired maximum) positive additive shifts. It will be a new variety with increased drought resistance, close to the maximum possible.

The structural analysis of the problem of increasing drought resistance in plants has become for us the basis for the further development of the methodological foundations of selection for increasing productivity and yield using the theory of eco-genetic organization of quantitative traits (TEGOQT) [44]. The introduction of measured contributions of the components of the resulting drought resistance into the model allows the construction of EGP of parental pairs when studying drought resistance structure in artificial climate chambers. In addition, it is possible to select parental pairs with complementary contributions from all seven GPS, creating the EGP of each potential parent, and, based on mathematical models reflecting the contributions of each of the seven GPS, to predict yield increase through controlled selection of parental pairs.

Note that in recent years' works on the physiological mechanisms of plant drought resistance [45-47], promising scenarios of phenotyping [48, 49], the study of the inheritance of drought resistance and the relationship of the phenotype to the genotype [50-52], genomics [53] and phenomics [54], the researchers do not yet attempt to approach the phenotyping of this complex adaptive property from the positions of the ecogenetic organization of the seven GPS and EGP for the selection of parental pairs and the management of the selection process on the basis of innovative phytotron technologies.

So, the original phenotyping proposed dissects the complex characteristics of "productivity" and "yield" not into the component traits of the crop structure as in traditional breeding (ear length, ear weight, grain weight per spikelet and per ear, the 1000 grain weight, etc.), but into the contributions of each of the seven genetic and physiological systems (GPS) by which breeders increase yields, most often not having information on the contributions to the yield of each GPS from the used parent variety. Because of this, in traditional breeding, a new variety in the field requires a huge effort and time (P.P. Luk'yanenko and B.I. Sandukhadze created the best domestic varieties for about 30 years). One of the seven GPS (adaptability) is divided into drought, cold, winter, salt resistance, resistance to acidic soils, etc. This paper presents the first attempt of phenotyping such a complex property as drought resistance, which is determined by at least 22 elements, and gives recommendations on the development of innovative phytotron technologies that can quickly and effectively improve the hereditary drought resistance in new varieties of cereals.

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