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Environmental Factors Affecting the Expression of Bilateral-Symmetrical Traits in Plants

Sergey Baranov, Igor Vinokurov and Lubov Fedorova

Abstract

In recent years, there has been a growing interest in the problem of asymmetry of bilateral traits in plants. Three types of bilateral asymmetry are found in the leaf blade, of interest to ecologists and evolutionists. A brief review of the methods used in testing bilateral asymmetry and developmental stability discusses their role in the development of homeostasis and ontogenesis. Intra- and interspecific differences are considered on the example of woody plants under the influence of factors influencing the expression of bilaterally symmetry. The influence of stress on the manifestation of asymmetric traits is considered. Apparently, the climate and topography of the area play a more important role, determining the plastic and fluctuating variability. The relationship of plasticity, evolutionary canalization, and development stability is considered on the example of woody and cultivated plants. Plasticity and fluctuation variability are in a relationship coordinated by climatic conditions, primarily lighting and temperature. This, in turn, determines the mechanisms of gene regulatory networks. Thus, phenogenetics, which studies the patterns and mechanisms of gene expression and ontogenesis, is based on the data from field botanical studies of plant shape and asymmetry. Epigenetic and population studies of phenotypic variations play a role in standardizing and finding suitable plant species and varieties.

Keywords: bilateral asymmetry, fluctuating variability, gene regulatory networks

1. Three types of bilateral asymmetry

One of the promising areas of monitoring for the environment is bioindication by determining the developmental stability (DS) of plants, including woody ones. Database on the developmental stability of different species of plants is to be complementing other data sets, such as chemical contamination of air, soil, and water.

Fluctuating asymmetry (FA) is a kind of asymmetry used to assess the stability of development, as the organism's ability to regulate its development on the phylogenetic level.

The concept of developmental noise was introduced by Worthington [1], developed and completed in the works of foreign and Russian scientists at the end of the 20th century [2–6]. This term originally meant the factors that lead to deviations

from bilateral symmetry, such as metabolic rate, the concentration of biochemical regulator molecules, diffusion of substances, temperature gradient, growth, and cell death.

Fluctuating asymmetry is most often referred to as the minor variation of morphological characters from perfect symmetry. FA is an expression of ontogenetic noise and, hence, the level of developmental stability. The value of FA is defined as a nondirectional minor deviation from the strict bilateral symmetry. At the same time, the value of fluctuating asymmetry means independence in phenotypic realization on the left and right lateral sides. Thus, currently FA is the only characteristic that allows studying the developmental stability in a morphogenetic aspect. Fluctuating asymmetry is a common phenomenon among the flora of higher plants (Embryophyta). FA is most frequently expressed in the leaf blade, since they are commonly bilaterally asymmetric. As can be seen from many sources, the large number of plastic (metric) traits and meristic (countable) traits promotes the robust FA testing. Integral index is an average means of FA some traits. This takes into account only the trait values that are not correlated with each other [7, 8].

Deviations from genetically predetermined rules are presented as a fact of random expression genotype under the influence of environmental impact. Based on the genetically determined reaction, fluctuating asymmetry is also considered as a deviation from the reaction norms. The fluctuating asymmetry has to be distinguished from phenodeviation having more genetic sense. Phenodeviant organisms may occur in combination of some genes, such as in high homozygosity. Sometimes they indicate the presence of certain specific actions breaks or simulates normal activity substance regulators—morphogens and hormones [9].

The relative magnitude of the FA is about 1% of the trait value [10]. Most approaches to the FA testing based on an evaluation of the variance differences between the left and right magnitudes in bilaterally symmetrical traits. The overcoming imperfection in methods of FA testing includes the standardizing of the size of the chosen traits, the sample size, and the number of traits selected for FA testing.

As a signal reflecting the environmental stress, FA is a typical attribute of the genetically determined norm of reaction of the organism. Two other types of asymmetry, the directional asymmetry and the antisymmetry, are implied as a genetic deviation from strict symmetry. The fluctuating asymmetry itself is related to nondirectional asymmetry. Some characteristics of three types of asymmetry are shown in **Table 1**.

The relation between the FA as a signal violating the DS and environmental stress of different nature, in spite of the large number of publications, is in the focus of scientific interest [11, 12].

According to Shmalgauzen's concept of stabilizing selection, the natural selection takes place even in a relatively stable and optimal ambient. It results in two

Sample characteristics	Fluctuating asymmetry	Directional asymmetry	Antisymmetry
R and L values	$R = L$	$R \neq L$	$R = L$
Kurtosis, γ in descriptive statistics (R-L)	$\gamma = 0-2$	$\gamma = 0-2$	$\gamma < 2$
Type of frequency distribution (R-L)	Normal	Not normal	Normal/not normal

Note: R and L, values of right and left metric bilaterally symmetric traits; γ , mean of kurtosis.

Table 1.
Typical features of the three types of asymmetry.

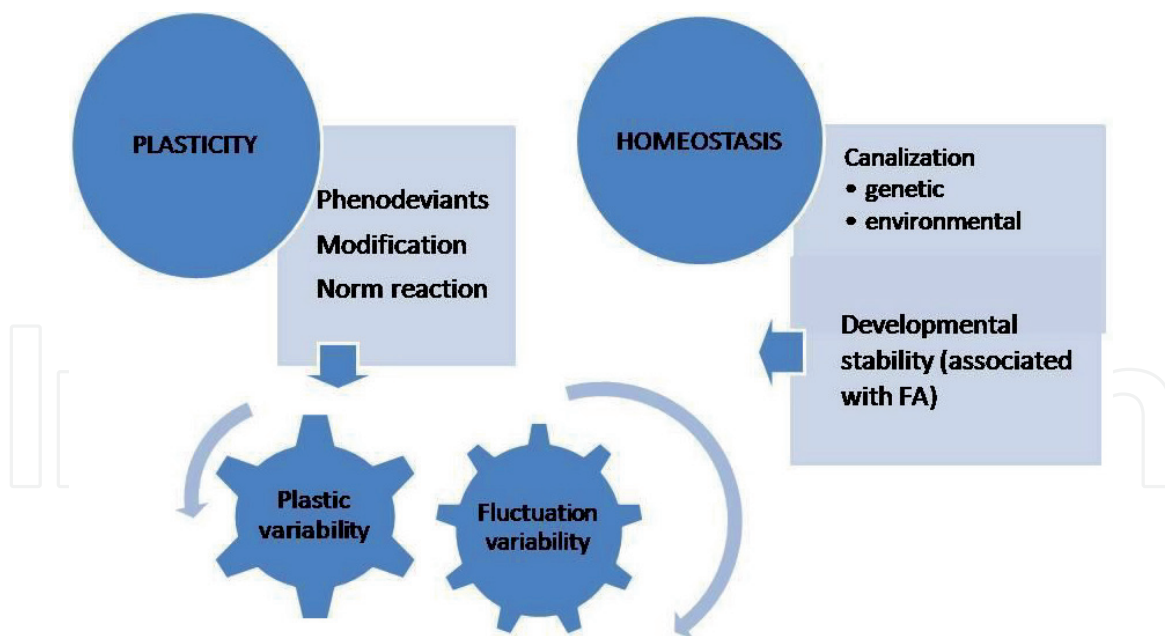


Figure 1.
Two types of phenotypic variability.

effects: in the elimination of mutants and recombinants and in the accumulation of mutations in a small population, which means the modification of the phenotype. By the term “canalization” Schmalhausen meant a tendency to achieve a certain genetically predetermined final state, different from the variability at the beginning of development [13]. Canalized selection addresses to the elimination of individuals that are susceptible to changing environmental factors. The term “ecological canalization,” as an attribute of development homeostasis, has the meaning of stabilizing phenotypic variability [14]. The term “ecological plasticity” explains rather adaptive processes and characterizes the increased variability. Such a dialectical opposition pretends to be a source of microlevel adaptation in the population [15]. Developmental noise is the term that characterizes FA as an environmental origin phenomenon. On the other hand, the stability of development mostly is a genetic phenomenon which may vary in homo-/heterozygosity and depends on stress-reducing physiological status of the organism.

Thus, developmental stability of the organism is a biological characteristic depending on both causes as developmental noise (from the environment) and genetic variability characterizing the stages of ontogenesis.

Developmental homeostasis includes two attributes: developmental stability (FA is indicator) and environmental canalization. Plasticity and homeostasis lead to both types of phenotypic variability—plastic and fluctuation (**Figure 1**).

Phenotypic plasticity can help plants to overcome negative effects of some factors, first of all, temperature variability, and allow them to rapidly adjust traits to adverse conditions. The genetic variation could provide potential for adaptive evolution in response to changing climate variability [16].

2. Gene expression regulation

Expression of gene regulators of plant development is controlled by a number of internal and external factors. The internal factors affecting their activity include hormones, sucrose, and some mineral elements, and the external factors include temperature and light. In the regulation of differentiation and development, an

important role is played by genes that contain promoters sensitive and specific to phytohormones and to such environmental factors as light and temperature. Currently, key genes have been identified that control embryogenesis, aging, and photomorphogenesis; regulate the functioning of the apical, lateral, and floral meristem; and are responsible for the formation of the root, leaves, and blood vessels. The expression of the genes regulating the development of flowers is best studied. Currently, based on the currently available genetic information, mathematical apparatus, and computer programs, key genes have been identified [17–19]. It has become possible to build so-called genetic regulatory networks (gene regulatory network, GRN), which allow to evaluate the whole range of interactions between different regulatory genes in the process of cell differentiation and the formation of plant organs. Original elements of these networks are capable of controlling several processes at different stages of development. Therefore, mutations affecting different parts of the same regulatory gene may differ in their phenotypic expression [20–22].

The MYB family (myeloblastosis) of transcription factors (TF) is known, which includes about 200 proteins that control such processes as root development, leaf patterning, trichome formation, cell cycle, circadian rhythms, and phytochrome signal transmission. A transcription factor (or sequence-specific DNA-binding factor) is a protein that controls the rate of transcription of genetic information from DNA to messenger RNA, by binding to a specific DNA sequence. The function of transcription factors is to regulate the on and off of genes for their expression in the right cell at the right time and in the right amount throughout cell and body life. Groups of TFs function in a coordinated fashion to direct cell division, cell growth, and cell death throughout life, cell migration, and organization during embryonic development and intermittently in response to signals from outside the cell, such as hormones [23].

A coactivator is a protein that works with transcription factors to increase the rate of gene transcription, whereas a corepressor is a protein that works with transcription factors to decrease the rate of gene transcription. Some of the transcription factors (AS1, AS2) are proteins responded for asymmetry in leaves.

Polycomb group proteins are important repressors of numerous genes in higher eukaryotes. In *Arabidopsis*, like heterochromatin protein 1 (LHP1), also known as TERMINAL FLOWER 2, was proposed as a subunit of polycomb repressive complex [24].

The theory of gene regulatory network dynamics can be represented in **Figure 2**:

The elementary units of the GRN are the genetic element G . It includes the pair (g, p) , consisting of the g (gene) and the target (final) product synthesized p . The activity of the genetic element G is characterized by the rate of synthesis V of the target product p and the rate of its degradation/dissipation D . The target product

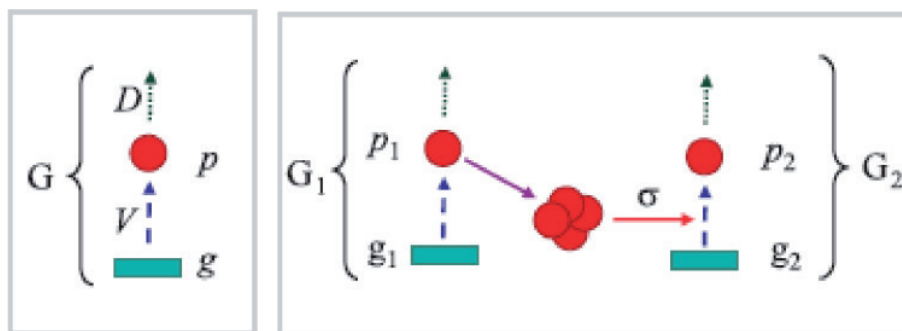


Figure 2.

Genetic elements and regulatory relationships of the GRN (on Kolchanov et al., 2013). G , G_1 , and G_2 are genetic elements, σ is the regulatory element, V is the synthesis of the target product, and D is the degradation/dissipation of the target product.

can be either a RNA molecule or a protein. If a change in the concentration of the product p_1 decreases/increases the rate of change in the concentration of the product p_2 , there is a regulatory (oriented) relationship $\sigma = \sigma(G_1, G_2)$ between the genetic elements G_1 and G_2 .

3. Epigenetics as a new branch of genetics

3.1 Interspecific differences in the response to the environmental conditions

The different genotypes differed in their sensitivity to developmental noise. The heritable component of FA can thus be understood as a genetically modulated expression of variation that is itself entirely nongenetic [25, 26].

Epigenetics studies the stable changes in the level of gene expression that are not related to changes in the nucleotide sequence in DNA. For the first time, the term “epigenetics” was introduced by the embryologist and geneticist Conrad Waddington to describe changes in gene expression observed during the course of development. Epistatic interaction is reduced to the suppressor effect of one gene on another. Dominant epistasis explains the influence of the gene as the dominant allele.

The epigenetic status of the organism is determined by the nature and level of DNA methylation, posttranslational modifications of histones, the presence of histone isoforms, and the nature of chromatin stack in [27, 28]. The most well-described epigenetic mechanism of regulation is DNA methylation. Epigenetic variability is the variability of the population response rate, which leads to the realization of discrete states of morphological structures. In the era of postindustrial society, epigenetic variation becomes of particular interest. We can outline the next key aspects of experimental and field epigenetics studies. They are:

- a. Frequency analysis of phenes as minor aberrations of morphogenesis
- b. Spatial correlation of the level of phenetic differences between pairs of impact and control population on a continuous part of the areal
- c. The use of methods of multidimensional ordination of phenetic compositions
- d. Epigenetic landscape of a population
- e. Comparison of dispersions of general asymmetry, fluctuating asymmetry, and directional asymmetry, characterizing manifestations of developmental destabilization at both individual and group levels

There are two genetic regulatory networks that play the main role in the manifestation of fluctuation and plastic variation. It is known that the heterogeneity of the sample value of metric or counting traits in a population, i.e., dispersion in heterogeneity, plays a key role in the magnitude of the revealed variability. The regulatory mechanisms of the epigenetic processes in the genome and at the cell level are the following: DNA methylation, histone code (posttranslational modifications of histones that occur by methylation, acetylation, phosphorylation, glycosylation, and ubiquity of histones), and followed by proteolysis [29, 30].

Genetic architecture and associations with fitness and with compensatory growth are studied under various stressful situations. Patterns in FAs play an important role in both DI and canalization of development. Their common origin and role in micro- and macroevolutionary processes are assumed [31, 32].

Phenogenetic variability is within the individual variability of the structure of antimers and metamers (homologue parts of plants). Asymmetry refers to the stochastic morphogenesis, i.e., random formation. The negative correlation between developmental instability and individual genetic diversity was obtained in flower petals within three *Opuntia echios* populations that suggest a buffer effect of heterozygosity on developmental instability [33].

The study showed that deletions do not affect the asymmetry of the *Drosophila* wing, but the development of canalization in a period of time changes. Consequently, genetic deletions have an impact on the canalization of the development of traits, but not on the stability of the development [34, 35]. Genetic assimilation is the subsequent genetic fixing of the new trait in the population. Some recent experimental and theoretical works have established a quantitative basis for these classic concepts of Waddington [36].

4. Plasticity and developmental stability

The genes responsible for plasticity, as well as environment and developmental stability, are closely related. Consider the next example. There are five metric traits in leaf blade of small-leaf linden (*Tilia cordata*). When some traits of a leaf blade (measured distances between the veins) have a high plasticity, other ones expose instability of development with an increased FA value. FA is measured as $FA = L - R / (L + R)$ in absolute value, where L and R are means of the left and right values of the bilaterally symmetrical trait. Plastic variability is measured as $PL = 1 - x/X$, where x and X are means of the smallest and largest values of trait size. The reason for the deviation was the ecological factors of the location of the populations and the climatic features of the vegetative season. As a whole, the plastic variability correlates to fluctuation variability. The more PL (i.e., trait size), the more FA. On the other hand, the correlation is small. Moreover there is an effect of conjugacy within one sample when the trait expressed the high index of plastic variability and another one expressed a high value of fluctuation variability (**Figure 3**).

The correlation is changeable and sometime can be negative. For example, in other sites, correlation r between FA in fourth trait and PL in fourth trait was -0.69 ($p < 0.05$; 2014).

Both types of variability, fluctuating and plastic, showed a conjugative effect. The correlative dependency deserves the focusing study. The level and character of expression of two type phenotypic variability depend on some factors. For plants the temperature presumably is a dominant factor. For example, the cold and humid vegetative season in 2017 played a main role.

The impact of climate especially noticeable among species. Two close species of linden (*Tilia cordata* and *Tilia platyphyllos*) were studied in one ecosystem. 2017 showed an increase in the plastic dimensions of leaf blades of the broad-leaved linden to the conditions of the Central Russian plain, which is attributed by the authors to one of the stress response phases, with increasing plastic variability of dimensional traits of leaf plates. We attribute this fact to the phenotypic deviation caused by low temperatures of air (**Figure 4**).

Increased fluctuating asymmetry was associated with the small size of the leaf blades. The growing plate, as is known, develops in pulsating mode, in the right/left side, and has a high asymmetry. Some signs, as we have seen, have shown a negative correlation between FA and PL, and this relationship is of interest to phenogenetics [37].

In cultivated plants (wheat), a decrease in the stability of development occurred at elevated doses of fertilizer. It is assumed that this is a logical process, as a

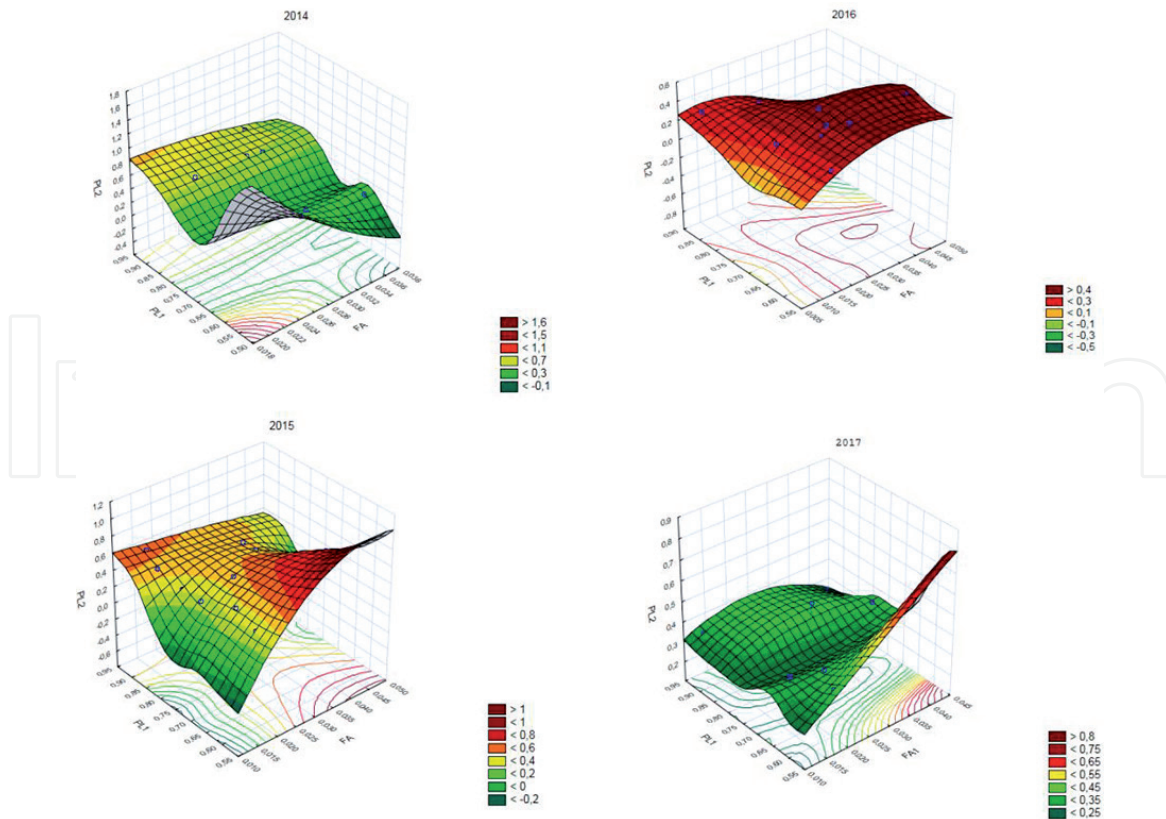


Figure 3. Surface plots for correlation between the magnitude of plastic variability (PL, two traits, PL1 and PL2) and fluctuation variability (FA, one trait), *Tilia cordata*, 2014–2017, Moscow region, Russia ($n = 100$). 2016 year—Person’s $r = 0.73$ ($p < 0.05$). Other year’s r is not statistically significant.

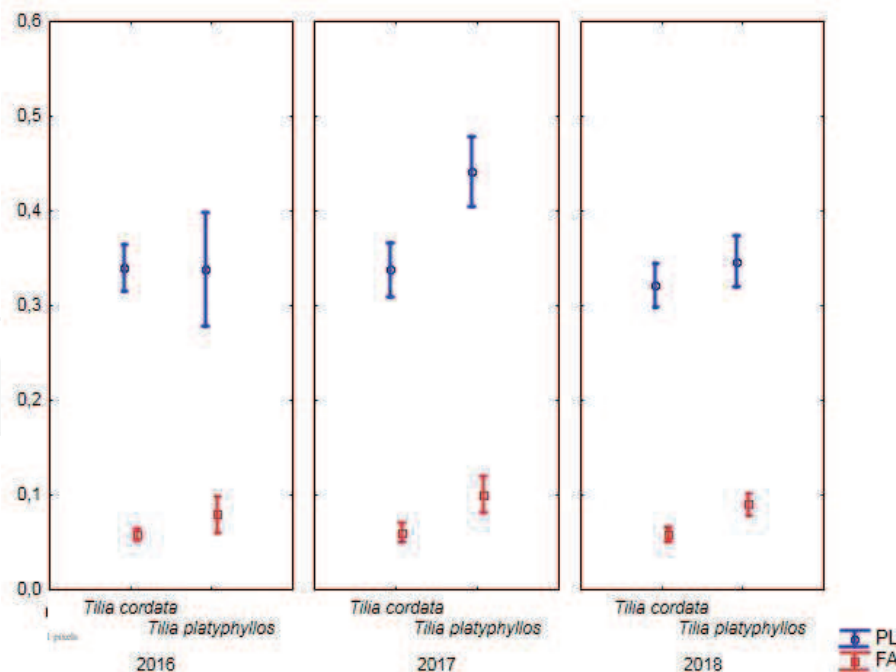


Figure 4. Plot of means two types of variability PL (plasticity) and FA (fluctuating asymmetry) (both $p < 0.05$) and conf. Intervals (95%) for two species of *Tilia* (2016–2018).

response to high doses of fertilizer and excessive amplification of the vegetative and generative phases of plant development.

The gene regulatory network (AS1, AS2?) responds to temperature in the phase of the development of meristem. We conclude that stress factor of chemical

pollution plays a secondary role. This confirms the fact of chemical load in site where fluctuating asymmetry was highest in 2017 and chemical pollution was less statistically significant. The mismatch between two types of variability in traits meant an absence of any correlation of FA-PL on some dimensional bilateral traits.

Proposed conclusion seems to be consensual, since in the literature on this issue there is a contradictory opinion on reciprocal effect of FA and PL [38, 39]. In other words, the traits were characterized by conjugation of two types of variability. The predominance of one type of variability is compensating by the weakness of other type of variability. For example, the weak fluctuation variability of trait No. 2 was compensated by its high plastic variability.

Thus the modularity of gene regulatory network associates with external factors. Based on the response to selection on the plasticity of a character, we concluded that plasticity is most likely due to epistasis. These models make some predictions with regard to correlations among trait plastic variety, developmental noise, and developmental instability. Modularity structure may enhance the adaptability and robustness of biological systems to perturbations [40, 41].

5. Methods of geometric morphometrics

The geometric morphometrics method allows to determine the value of the fluctuating asymmetry in combination of features and characteristics of the form of leaf blade and to test the presence directional asymmetry and antisymmetry. The degrees of freedom df were 14–18 times the number of degrees of freedom in the trivial two-factor analysis of variance with a high statistical significance ($p \leq 10^{-6}$) and an economy in the processing time and in the volume of the samples.

Methods of geometric morphometrics showed epistasis contributed ca. 20% of the variation in FA of size and 19% of the variation in FA of shape. This

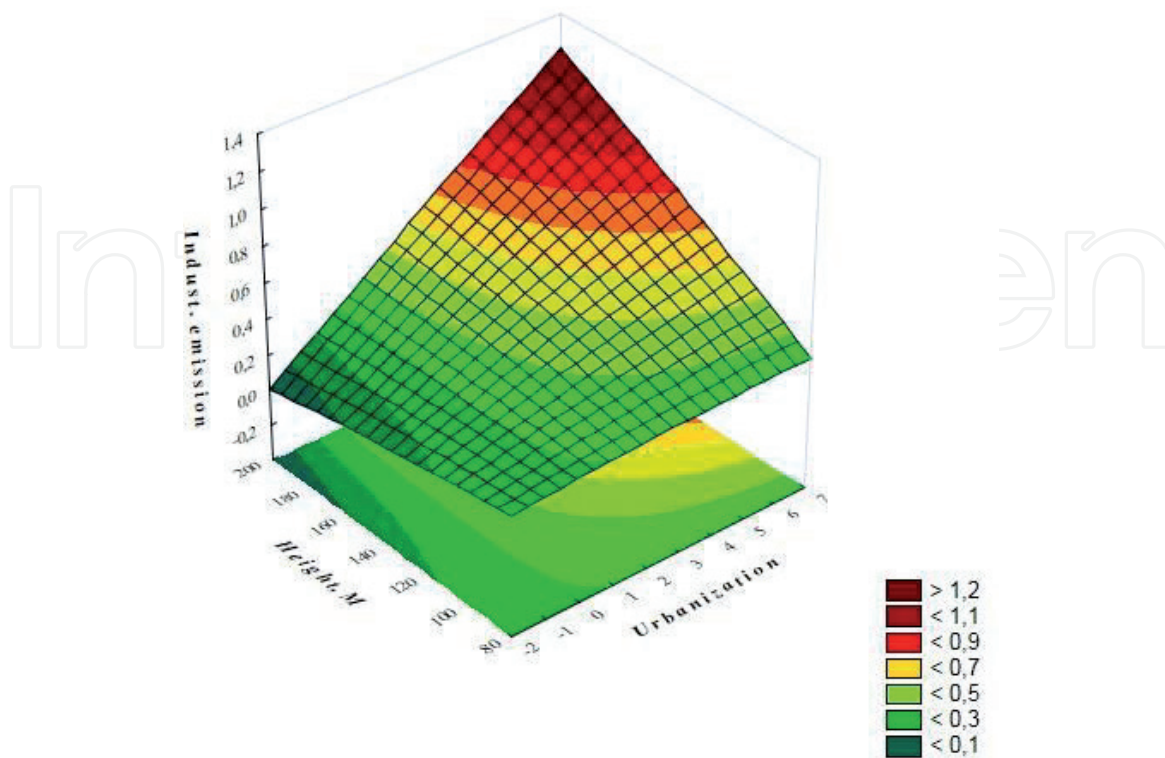


Figure 5. Response surface of the desirability function depending on three factors (industrial emission, level of relief, and degree of urbanization) ($n = 75$).

Factor	<i>Acer platanoides</i>	<i>Tilia cordata</i>	<i>Betula pendula</i>	<i>Quercus robur</i>
Height	++++	+++++	+	+
Industrial emission	+++	+	++	+
Urbanization level	+	+	+	+
Vehicle emission	+++	+++++	+	++

Note: + - $p < 0.05$; ++ - $p < 0.01$ +++ - $p < 0.001$; ++++ - $p < 0.0001$; +++++ - $p < 0.00001$.

Table 2.
 Factors influenced the developmental instability.

contribution was characteristic for the FA depending on the size of the studied traits of the mice [31]. Genetic screens in the model plant *Arabidopsis* have been particularly rewarding, identifying more than 130 epigenetic regulators. The diversity of epigenetic pathways in plants is remarkable, presumably contributing to the phenotypic plasticity of plant postembryonic development and the ability to survive and reproduce [42, 43]. Relief is an important factor determining plastic and fluctuation variability. The study of this factor using the example of birch (*Betula pendula*) showed that, together with other factors, such as the level of urbanization (on the graph in arbitrary units) and industrial emissions, an increase in the height of the relief reduces the stability of development (**Figure 5**).

The described interaction of three factors reflected a synergistic stress effect that influenced the stability of development. Differences in the range of reactions to the effect of each of the factors made it possible to compile a comparative scale for four plant species using the statistical significance p of the FA index, obtained by methods of geometric morphometrics (**Table 2**).

An autorepressor is a genetic element that provides, by a negative feedback mechanism, the regulation of expression of a gene encoding an autorepressor protein. Plastic and fluctuation variability are encoded by two genes. The mismatch between them occurs under stress, when regulatory proteins do not work on the principle of negative feedback. The regulatory gene network AS and AC2 seems to be a component of a wider regulatory network of plant development. Autorepressor appears as part of the GRN AS1 or AS2. Stress factors are simultaneously adaptive and destabilizing factors that temporarily disrupt the homeostasis of the development of the individual and the entire population.

6. Conclusion

This phenogenetic study contributes to the development of the epigenetic theory of gene networks. Bilateral asymmetry, reflecting phenotypic variation, is a convenient phenomenon for studying environmental dependencies in the frame of study of GRN and the direction of evolution.

Recently, there has been an increasing interest in system design information support for the storage and processing of phenotypic data and their integration with genomic information. To solve the problem of collection, integration, storage, and statistical processing of information about wheat plants, there are a number of computer systems, for example, WheatPGE (wheat-phenotype-genotype and environment).

The system stores various relationships describing the characteristics of an individual plant and allows you to uniquely establish the relationship between genotypic and phenotypic characteristics of plants as well as environmental parameters. The

database is constantly being improved. Data on developmental stability and plate shape is one of the components of such a database. Application of the system will automate the receipt data on the relationship of genotype, phenotype, and environment in plants, including wheat, thereby contributing to the effective creation of new varieties of wheat with the economically important traits. As a whole the study of environmental factors affecting the manifestation of bilaterally symmetrical traits in plants is part of the research, in the framework of the study of the subtle mechanisms of GRN that are important for the ecology and evolution of plants.

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