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Corn as a model organism for fundamental and applied researches in phytobiology

The purpose. The survey of the literature on use of corn as model system for genetic researches. Results. History of corn as model organism, beginning from Gregor Mendel's classical investigations is presented. Advantages of corn as model plant are described. The information on parentage, domestication and spread of corn on the basis of modern molecular and archeological data is brought. The state of the art of researches on genetics and genonomy of corn is shown. Conclusions. Genetic regularities for the first time determined on corn, are tolerated on other cultures that promoted heightening of general level of genetic researches and selection studies for farm-production.

Key words: corn, model organism, genetics, genonomy.

Introduction. Zea mays ssp. Mays is one of the most important crops in the world, which provides multibillion dollar annual revenues (http: // faostat.fao.org). At the same time, with agronomic importance, corn is a model organism for conducting fundamental researches for almost a century. Among the cereals that contain other plant model species, such as rice (Oryza sativa), sorghum (Sorghum bicoior), wheat (Triticum spp.), Barley (Hordeum vulgare), corn is the most carefully studied genetic system . Some features of corn, including a large collection of mutants, large heterochromatic chromosomes, numerous nucopoietic diversity and genetic colonyarity among related herbs, position this species as the central genetic, cytogenetic and genomic research. As a model organism, maize is the subject of such far-reaching biological research as planting, genome evolution, developmental physiology, epigenetics, resistance to pests, heterosis, quantitative inheritance and comparative genomics [45, 49] . These and other studies are enhanced by the complete sequencing of the nuclear genome of corn [46]. The origin of corn. Decoding the genetic history of corn in the light of its enrichment is crucial for the understanding of its natural history [17]. In addition, corn is a model for studying the evolution of plant nuclear genomes [24]. Herb Zea mays L. ssp. Mays, corn belongs to the tribe Andropogoneae of the Gramineae family (Roasaye). Herbs arose 55-70 million years ago (mt), and then diversified. All major types of grain crops included in addition to almost 10,000 non-domesticated relatives. The divergence of the predecessors of the main grain crops has gone through the last 50 m (figure). Corn and rice went about 50 mt, and corn and sorghum - 9 mt [7]. Following the divergence from the genus Tripsacum, from the ancestral genus Zea there were 4 species present and at least 4 subspecies. The closest wild related species of domesticated (put out) cornucopia - teosint, perennial and perennial grasses of the genus Zea [23], include 4 species: Z. luxurians, Z. diploperennis, Z. perennis and Z. mays. The species Z. mays is composed of at least four subspecies (ssp. Mays, ssp. Mexicana, ssp. Parviglum, ssp. Huehuetenangensis). It is believed that the cornfield diverged from its ancestor toosinte 6000-9000 years ago [33]. The maize genome originated 4.8 m. Through a segmental alototraploidization of 2 genomes of the ancestors who themselves diverged from the fore-sorghum [50]. Although the genomes of cereals are differentiated by podidity and overall size, they have a relatively high degree of genetic collinearity and conservatism of sequences [6]. Much of the variation in size within the grain genomes is due to the duplication of the gel and the amplification of mobile elements [4]. Based on genetic studies of corn placement, molecular and archeological data, Z. mays spp. Parviglumis was identified as a direct ancestor and closest relative of the modern maize (Z mays spp. Mays) ', these 2 subtypes dispersed about 9000 years ago [38, 52]. There is a postulate of the only event of the dome, which has probably occurred in the central region of the Balsas River in southern Mexico. Subsequent diversification (maize) of corn was held in the Mexican highlands between the provinces of Oaxaca and Jalisco. Modern corn was then distributed in two principal directions: the northern route - from northwest Mexico, southwest to the eastern part of CIJJA and Canada; And the southern route - from the southwestern lowland of Mexico to

Guatemala, the Caribbean and South America [33]. On the territory of Eurasia, the first specimens and seeds of corn came to Spain after the return of X. Columbus from the second voyage to America in 1496. It then spread to Portugal, Italy, France, England, the countries of Southeastern Europe, Turkey, northern regions of Africa . In Ukraine, corn came from Bessarabia about 200 years ago [1].

The evolutionary relationship of maize with respect to grain crops and within the genus 2ea: a is a partial phylogenetic of cereals (AghaislorBIS is selected as an "outsider"); B - phylogeny of the genus eea [7, 49, 52]

Due to its exceptional genetic diversity, maize is highly adaptive and responsive to selective pressure. It is cultivated in both hemispheres of the Earth - from the tropics to zones of temperate climate, in a wide biogeographic range, which envisages enormous diversity in the soil, climate, duration of the day, altitude above sea level. The duration of the vegetation period and the quality of the light of the environment are the main determinants of geographical distribution, suitable for field cultivation of specific corn inbred lines. History of corn as a modeling organism. Corn is an organism of historical importance for all biologists. The history of corn as a model organism begins with the early studies of G. Mendel (1869 p.), Which used corn to confirm their well-known breeding experiments carried out earlier on Pisum peas [12, 43]. Like peas, corn is a large plant, so it is suitable for phenotypic analysis and has a significant advantage in the genetic analysis of morphological mutants. About C.O. years later, C. Correns and H. de Vries used corn in their xenium studies, namely, the dominant influence of father's pollen on the endosperm phenotype. The results of these studies supplemented and expanded the original genetic studies of G. Mendel and were an integral part of the redefinition of his extramural work. Although S. Correns and H. de Vries were among the pioneers of corn research, R. Emerson and E. East are considered to be founders of modern corn genetics. They developed the concept of epistatic and quantitative genetics [21, 22]. R. Emerson was the mentor for the first generation of corn geneticists (G. Beadle, S. Burnheham, M. Rhoades, V. McClintock), which made significant discoveries in corn genetics. Thus, G. Beadle discovered such an important biological phenomenon as genetic control of meiosis [3]. In studies L. Stadler found that X-rays lead to mutations [48]. In works by N. Creighton and V. McClintock, it has been shown that a genetic cross-overoverer is accompanied by physical crossovers between chromosomes [14]. M. Rhoades from the curve cytoplasmic inheritance of male sterility [42]. V. McClintock described and hinted at the mobile genetic elements [36], which was highly appreciated by the world community - the award of the Nobel Prize. Consequently, the conceptual studies of this group of scientists in genetics and cytology, made during the 20-30th years of the XXth century, provided the basis for the further use of cucumbers as a model genetic system. In subsequent years, such important biologic phenomena as paramutations [9, 13] were discovered, the presence of B-chromosomes [41] was established, and the use of A-B translocation for the geneization of localization was proved [44]. It should be noted that the corn dealt with theoretical aspects of such significant biologic phenomena as heterosis and cytoplasmic male sterility, thus creating a complex of methods for selection of hybrids [20, 28, 42, 47]. The laws, first discovered on cornflower, were transferred to other crops, which contributed to raising the overall level of both genetic research and breeding developments for agricultural production. Benefits of corn as a model plant. Corn is especially suitable for genetic analysis due to its one-way development of flowers. The division of the development of male and female flowers was important for the discovery of genes that control the definition of sex [11, 15]. In addition, the physical separation of male and female flowers greatly facilitates controlled pollination. Crossing corn is not only simple, but also highly productive: several hundred seeds can be obtained from one dusty pile. This allows separating corn from other grains as a beneficial genetic system, since genetic crossings in other grains require castration - a laborious procedure that gives one seed to a flower. Maize meiosis is synchronized in such a way that the relative size of developing birds correlates with the meiotic stasis of microsporosity. This useful function, combined with the relatively large physical size of corn chromosomes, made cornstarch a pioneer in cytogenetic plant studies [53]. Detection of maize meiotic mutants is relatively simple. In addition, chromosomal aberrations, in particular translocation and inversion, are used for chromosomal localization of genes [43]. For example, a waxy-labeled translocation has a linkage between this endospermic marker and each shoulder of 10 g of haploid chromosomes of corn, thereby facilitating the placement of genes on the shoulders of chromosomes [31]. Recent, more sophisticated approaches to cytogenetic analysis, such as the development of single-photon fluorescence in situ hybridization techniques (fluorescence in situ hybridization, FISH) and fiber-FISH, have revolutionized genomic corn research [27, 29, 54].

Single-seeded fruit - a large corn grain has become the object of hundreds of genetic analyzes of morphological and biochemical characteristics of the grain, including the development of the embryo, accumulation of stock proteins and starch in the endosperm, directions of biosynthesis of certain substances [19, 3O, 36, 45] . Corn is a very "obedient" system for genetics and genomics of development. The relatively large size of corn organs, such as primordia (leaves) and root apical meristem, is particularly suitable for laser microdisection, which allows isolating individual cells, tissues or organs from thin sections of fixed plant tissues immobilized on the glass. The RNA isolated from such specimens is suitable for use in expression analysis such as quantitative real-time PCR, qRT-PCR, hybridization of microchips, and massive paralellal sequencing (massive parallel) RNA sequencing, RNA-Seq). As a cross-species, maize has an exceptionally high level of genotype diversity. The frequency of the nucleotide polymorphism that is observed when comparing the genomes of any two modern inbred lines of corn rootworm is equivalent to the diversity of sequences between chimpanzees and humans [10]. Since this nucleotide diversity is crucial for the successful placement of maize, it continues to be used in modern breeding programs. For example, the natural heterozygosity of the maize genome is used in associative mapping strategies, in which correlations between phenotypic and genetic varieties are identified in the analysis of complex natural populations [10]. In these studies, candidate genes have been identified, associated with complex features, particularly during flowering [51], starch biosynthesis [56], carotenoid content in grain [26], which the breeder can manipulate for agronomic and nutritional improvement of varieties Corn The Maize Genetics Collaboration Center (MGCSC) (USA) is the main source of maize mutants used in research. As a free service for the "corn" community, MGCSC receives, maintains and distributes seed stocks at the international level, provides information on all known allelic and cytological variants of corn. The MGCSC collection contains over 100,000 pedigrees, several hundreds of genetic mutants and alleles, samples of chromosomal aberrations and aneuploidy, a collection of inbred-specific ethyl methane sulfonate (EMS) mutants, a large collection of well-characterized transonic elements, which Is a distinctive feature of corn genetic research. Genetics and genomics of corn. Various resources and tools for genetic analysis of maize are readily available to the scientific community. Although hundreds of corn inbred lines are described, the B73, My 7 and W22 are widely used in laboratory studies. The B73 line is selected as the reference nucleic genome for sequencing, which is completed in 2009 [46]. It is widely used in most of SI1IA, it has high yields, is the most popular inbred line in the main research laboratories. Consequently, the B73 is the source of most expressed expressions (expressed sequence tag, EST), and the predominant collection of bacterial artificial chromosomes (BAC) libraries [5]. Due to the considerable synness among the genomes of cereals, comparative studies provide a powerful tool for detecting genes and analyzing the evolution of the genome [16]. This significant collinearity of the genetic order and the orientation between corn, sorghum, rice, rice, barley is often used to circumvent experimental barriers. The genus of maize has an average size (2.5x109 bp) compared to many kin, such as rice (0.4x109 bp), sorghum (0.75x109 bp), barley (6.0x109 P.n.) and wheat (17x109 p.n.) [40]. As the first genome of grasses that is completely secreted [25], rice is widely used in the annotation of the genomic sequence of maize. Comprehensive, standardized nomenclature of corn genes was developed in the late 90's of the XX century. Guiding principles for the naming of nuclear, organelin and gene products, allelic and non-causal agents, transposon-induced mutations, chromosomal alterations, and molecular genetic markers of loci are available on the site. Databases on maize genome and genetics Genome and Genetics Database (http: // www. Maizegdb.org/maize_ nomenclature.php).

For research, a collection of genetic mutants of corn is widely used [37]. In the last decade, hi-tech programs of mutagenesis have been launched. For example, the Maize Tilling (Targeting Induced Local Lésions IN Genomes) project is a reverse genetic approach that uses gene-directed screening of an EMS-mutagenized inbred population [55]. Another project involves the use of the Activator (Ac) transponder element system! Dissociation (Ds) in the strategy of target, regional mutagenesis, whose purpose is to saturate specific chromosomal regions adjacent to the mapped Acids of transposons, to create new insertion mutations in the genes closely linked to existing transposons [2]. After identifying the new AclDs, the insertion mutations generate a molecular tag (shortcut) that is used to build target genes. Events of inaccurate deletions / insertions of transposons can create "footprint" alleles that contribute to the evolution of the genome [2]. The system of transposition elements of Mutator (MI) has become a popular method for the mutagenesis of seeded geneticists of maize. In particular, in the Maize-Targeted Mutagenesis (MTM) project, a strategy of reverse genetics based on polymerase chain reaction (PCR) was used to reveal gene-specific insertions of transposons in a population of about 44,000 plants enriched with mobilized Me elements, And the strategy of epigenetic silence, we killer, which eliminates the new transposition of the posterity [34]. The system of stationary mutagenesis is used in the strategy of direct and reverse genetics of UniformMu, in which the active We transitions are introgressive into the W22 inbred line, and the insertion mutations are identified by the technology of massive parallel sequencing (35). The use of various types of molecular markers on recombinant inbred lines (RILs) by crossing B73xMo17 [32] significantly increased the resolution of the corn genetic map. A population of 5,000 RILs from cross-breeding of the B73 line with 25 inbred lines from different embryonic maize plasmas, which encompassed most of the natural variability of apple available in Zea mays spp. Mays, and is a powerful tool for detecting genes that respond to complex signs [10, 57]. Positional cloning becomes the most powerful means for identifying genes in maize and proccess, which is greatly enhanced through genomic sequencing [8]. In 1991, for the purpose of collecting, storing and maintaining data on corn genetics, a database of maize genome was developed by the Department of Agriculture - the US Department of Agriculture Agricultural Research Service (USDA-ARS) - Bread genome database (MaizeDB) [39]. MaizeDB is one of the first biological databases that exists on-line (in dialog mode). Another "corn" Zea mays database (ZmDB) database [18] has been created, which contains information about microchips, EST clones, transposition inserts, GSS gene sequences (Genome Survey Sequence), proteins. In 2001, p. USDA-ARS initiated the integration of the MaizeDB and ZmDB databases in the Maize Genetics and Genomics Database, MaizeGDB. So, in 2003 p. A single database with modern web design and protocols (http: Wwww.maizegdb.org) has been created. MaizeGDB has become an indispensable tool for researching corn geneticists around the world.

Conclusions

Corn is a classic model object for studying the genetics of coloring, isoenzymes, mobile dispersed elements, chlorophyll mutations, biochemical composition of grain, signs of sex, cytoplasmic and meiotic mutations, crossings, various translocations. Corn is one of the most convenient genetic objects. A separate arrangement of male and female inflorescences allows cross-pollination and self-pollination to be done quickly and easily. Female inflorescence gives you the right amount of seeds for statistical evaluation of the results. Genetic studies of maize, established on the verge of the XIX and XX centuries, contributed not only to the radical improvement of this culture, but also became the basis for the development of theoretical and applied genetics of plants. Outstanding achievements in the biological science of the XX century. - Creation and introduction of hybrid maize in production - an example of fruitful purposeful genetic research. Corn is not only an object of intense genetic research, but also a model on which important genetic patterns are developed and used in breeding practice, in particular such significant discovery of biological science as heterosis and cytoplasmic male sterility. The regularities that were first detected in maize were transferred to other crops, which contributed to raising the overall level of both genetic research and breeding development for agricultural production.

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