

APPLYING MENDELIAN RULES IN RAPESEED (*Brassica napus*) BREEDING

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Marjanović Jeromela A., A. Dimitrijević, S. Terzić, A. Mikić, J. Atlagic, D. Miladinović, M. Jankulovska, J. Savić, W. Friedt (2016): *Applying Mendelian rules in rapeseed (Brassica napus) breeding*.- Genetika, Vol 48, No.3, 1077 - 1086.

Rapeseed is one of the most important sources of edible oil, raw material for industry, as well as feed. The yield and quality of rapeseed have significantly been improved in recent decades as a result of intensive breeding and optimized production technology. The application of Mendel's rules in introducing monogenic traits has also contributed to success in rapeseed breeding. Rule 1, which refers to the uniformity of F₁ generation, is now the basis of widespread development of rapeseed hybrids. Rule 2, dealing with genetic segregation in the F₂ generation, is the basis for understanding the process of breeding lines. Rule 3, regarding the independent segregation of genes and traits, while exempting linked traits, is the basis of combining different desirable properties by selection. In the last few decades, the systematic use of Mendel's rules has contributed to the improvement of many properties of rapeseed, including tolerance to biotic and abiotic stress, yield and seed quality. Particular progress has been made in breeding for resistance to diseases, including the identification of molecular markers for marker-assisted selection. The next objective of rapeseed breeding is to create varieties with improved tolerance to environmental stress (e.g. frost, heat, and drought). Based on Mendel's rules, classical breeding methods and the latest developments in the field of molecular genetics and breeding, future progress is expected in the field of rapeseed breeding with an emphasis on polygenic, quantitative traits such as biomass, seed, and oil yield.

Keywords: applied genetics; *Brassica napus*; breeding; fatty acid composition; grain quality; grain yield; Mendelian traits; protein meal; rapeseed

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THE GREGOR MENDEL'S SESQUICENTENARY

The year 2016 marks the 150th anniversary of Gregor Johann Mendel's (1822-1884) study on heredity "Versuche über Pflanzen-hybriden" (MENDEL, 1866). Mendel's laws are fundamental for any type of genetic study which consequently led to naming Mendel the "father of genetics". Gregor Mendel examined approximately 28,000 plants of pea (*Pisum sativum* L.) in an eight-year long study in order to properly examine the inheritance of several different traits (HELLENS *et al.*, 2010; ELLIS, 2011). Mendel worked with this important grain legume crop because in the 19th century pea was considered to be a common model plant that had well-defined characteristics, fast proliferation and could be grown in a limited space. Additionally, pea is a self-pollinating species and thus is easy to maintain in numerous collections worldwide and rather grateful for genomic research (ELLIS and POYSER, 2002).

The application of Mendelian rules in introducing monogenic traits has greatly contributed to the enhancement of rapeseed (*Brassica napus* L.) breeding. The Rule 1, which refers to the uniformity of F₁ generation, is now the basis of widespread development of rapeseed hybrids. The Rule 2, dealing with genetic segregation in the F₂ generation, is essential for understanding the process of breeding lines. The Rule 3, regarding the independent segregation of genes and traits, while exempting linked traits, is a tool for combining different desirable properties by selection. In the last few decades, the systematic use of Mendelian rules has contributed to the improvement of many rapeseed properties, including tolerance to biotic and abiotic stress, yield and seed quality (ORDON and FRIEDT, 1998). A particular progress has been made in breeding for resistance to diseases, including the identification of molecular markers for marker-assisted selection. The next objective of rapeseed breeding is to develop varieties with improved tolerance to environmental stress (e.g. frost, heat, and drought). Based on the Mendelian rules, classical breeding methods and the latest developments in the field of molecular genetics and breeding, a progress is expected in rapeseed breeding with an emphasis on polygenic, quantitative traits such as biomass, seed, and oil yield (MARJANOVIĆ-JEROMELA *et al.*, 2012).

OVERVIEW OF RAPESEED BREEDING AND PRODUCTION

The selection of rapeseed was intensified after the World War II, while research on rapeseed in Serbia began in the mid-1970s. Today, rapeseed is the third most important oil crop in the world, after palm and soybean (*Glycine max* (L.) Merr.). It is expected that production of rapeseed will increase more than 7 times, making it the second most promising oil crop in the world (HARWOOD *et al.*, 2013).

Rapeseed oil has low content of polyunsaturated fatty acids and is rich in highly desirable monounsaturated oleic acid. However, rapeseed oil of older cultivars was rich in nutritionally undesired erucic acid (35% - 50%). In addition to oil, de-oiled rapeseed cake is rich in protein and minerals; however, in the past it had high glucosinolate content. Erucic acid is considered toxic for humans, while glucosinolates that remain in the cake are harmful for animals and have negative effect on animal productivity. Therefore, one of the main goals for promoting rapeseed oil was to produce low erucic acid content genotypes (AGNIHOTORI *et al.*, 2007). The first spring cultivar with low erucic acid content/single low (Oro) was registered in 1968 in Canada. Apart from low erucic acid content, "00" varieties are distinguished by a low content of glucosinolates. The source of low glucosinolate content was discovered by Krzymanski in 1967 in rapeseed cultivar "Bronowski" (FINLAYSON *et al.*, 1973). This source is widely used in rapeseed breeding and creation of double low rapeseed genotypes.

In the 1970s, the Rapeseed Association of Canada wanted to re-brand rapeseed oil in order to convince the consumer that the newly created oil is healthier for consumption (RAKOW *et al.*, 2012). Therefore, they named double low rapeseed varieties canola. The origin of the word „canola“ comes from „Canadian oil, low acid“. The term "canola" refers to those varieties that meet specific standards for the level of erucic acid and glucosinolates, and in Serbia this type is designated as "type 00". `Tower` was the first registered canola variety worldwide in 2012, while `Banaćanka` was the first variety of rapeseed "00" type that was registered by the Institute of Field and Vegetable Crops in 1998 (MARJANOVIĆ JEROMELA *et al.*, 2008).

In Serbia, the rapeseed production has a long tradition and rapeseed was the main oil crop in the early 20th century. Several decades later, sunflower (*Helianthus annuus* L.) prevailed, making rapeseed the second most important oil crop in Serbia. In the mid-1980s *Phomopsis* devastated sunflower production which made rapeseed the main oil crop for several years, before *Phomopsis* tolerance genes were introduced into cultivated sunflower. The production of rapeseed in Serbia greatly varied in the last 65 years, even more than in the world (Figures 1 and 2).

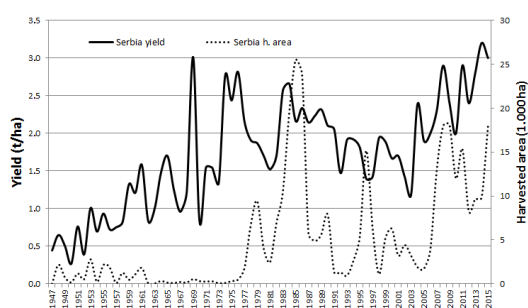


Figure 1. Improvements in rapeseed production in the last 68 years in Serbia

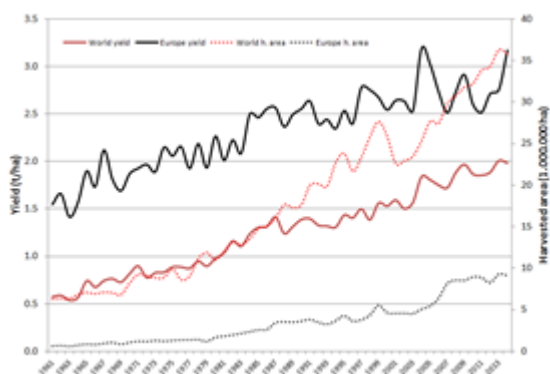


Figure 2. Improvements in rapeseed production in the last 50 years in the world

GOALS IN RAPESEED BREEDING

Today, there are several directions in rapeseed breeding. Two main ones are breeding for higher yield and better quality. Breeding objectives and tasks for rapeseed breeders in terms of improving quality could be divided in three main groups: (1) obtaining high oil yield and optimal fatty acid composition for different purposes, (2) obtaining optimal protein content, superior quality (amino acids), and (3) developing genotypes with varying content of different secondary compounds depending on the purpose of use (FRIEDT and SNOWDON, 2009; WITTKOP *et al.*, 2009).

The beginning of any breeding program involves establishing and examining an extensive rapeseed collection that contains as much variation as possible. At the Institute of Field and Vegetable Crops, the only Serbian research institute dealing with rapeseed breeding, so far 11 varieties and 20 lines of spring type, and 56 varieties and 980 lines of winter type rapeseed have been developed. All the varieties and lines have been tested for 23 agronomic and qualitative properties, as well as resistance to stress (MARJANOVIĆ JEROMELA *et al.*, 2014). In addition, diversity of the chosen rapeseed genotypes from our vast collection was assessed by use of RAPD markers (MARJANOVIĆ JEROMELA *et al.*, 2009). Molecular markers were used to identify variability within the collection since the genetic diversity of rapeseed is narrow. The reason for narrow genetic diversity in *B. napus* lies in its origin. Namely, *B. napus* most likely originates from a few interspecific hybridizations between *B. rapa* and *B. oleracea* (IÑIGUEZ LUY and FEDERICO, 2011). In addition, further rapeseed breeding only contributed to additional narrowing of rapeseed genetic diversity, especially in light of breeding for low erucic acid and seed glucosinolate content (BUS *et al.*, 2011; DELOURME *et al.*, 2013; WU *et al.*, 2014).

By analysing oil and protein variability, we discovered great variability in both traits and identified genotypes with desirable traits that could be used for breeding and development of new rapeseed varieties and lines.

Breeding for oil quality is difficult due to the fact that it is a polygenic trait and it is highly environmentally dependant. Breeding for oil composition is relatively easier than breeding for oil quantity, since it is controlled by a smaller number of genes and is less environmentally dependant than oil content. What is difficult is finding source of altered oil composition (MARJANOVIĆ JEROMELA *et al.*, 2011; JANKULOVSKA *et al.*, 2014).

COMBINED RAPESEED BREEDING ('CROSSING – MENDEL' MODEL)

Mendel's rules are especially applicable in breeding for monogenic traits such as white flower character (HUANG *et al.*, 2014), genic male sterility (GMS) (WANG *et al.*, 2007) or traits introduced by interspecific breeding such as clubroot resistance (DIEDERICHSEN *et al.*, 2009), cabbage aphid resistance (QUAZI, 1988), pollen fertility - *Rfp* gene (YANG *et al.*, 1996), etc.

In rapeseed breeding, the initial step is choosing proper parental lines and crossing them in order to obtain F₁ and F₂ progeny. F₂ is the genetically most diverse progeny population and allows breeders to create new gene combinations. Further breeding involves use of pedigree, SSD or some other method. After 6 progeny generations, selected newly created lines are tested in several locations for several years in order to analyse their genetic stability and adaptability.

Discovery and introduction of *cms* and *Rf* genes in *B. napus* lines enabled creation of rapeseed hybrids. There are several *cms* systems, however Ogu-INRA system is the most commonly used in rapeseed hybrid breeding. The Ogura *cms* was discovered in Japanese radish

(OGURA, 1968), and later introduced in *B. napus*. Similarly, fertility restorer gene, *Rfo*, that is used in creation of restorer lines was discovered and introduced from radish (HEYN, 1976).

In 1994, the first rapeseed hybrid `Synergy` was registered. For the creation of rapeseed hybrids breeders need to create sterile mother + maintainer (*Ms* Pool) and restorer line (*Rf* Pool). These lines are crossed and general and special combined abilities are examined.

Developing stable *cms* and *Rf* lines is challenging due to OGURA (1968) and consequently, there is a need to detect undesirable plants efficiently. One way is to use cytogenetic analysis by examination of stamens for pollen presence and by rating pollen viability (ATLAGIC *et al.*, 2010) (Figure 3). Another is molecular approach. Several markers have been used in detection of *cms* and *Rfo* gene (SIGAREVA and EARLE, 1997; IWABUCHIET *et al.*, 1999; PRIMARD-BRISSET *et al.*, 2005; HU *et al.*, 2008; DIMITRIJEVIĆ *et al.*, 2015a; 2015b).

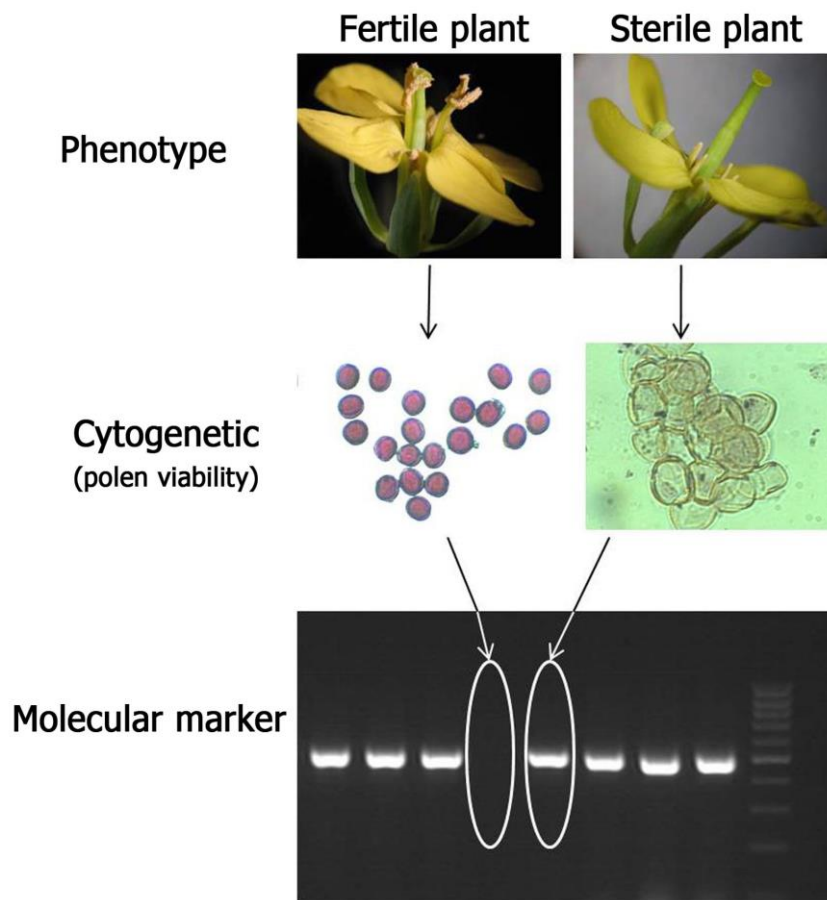


Figure 3. Discrimination between fertile and sterile rapeseed genotypes based on their phenotype and cytogenetic and molecular profiles

BREEDING FOR ROOT TRAITS

Rapeseed is the most productive oil crop on poor soils. This is exactly why special attention is paid to analysing rapeseed root morphology. Such a trait is nitrogen deficiency. STAHL (2015) analysed variation in rapeseed root morphology and identified the most desirable genotypes.

Further improvements in rapeseed will definitely occur by breeding for different root traits. However, all root traits are polygenic and therefore difficult to breed for.

ACHIEVEMENTS IN EUROPEAN RAPESEED PRODUCTION DURING THE LAST FIFTY YEARS

Breeding enabled significant increase in rapeseed yield in the last 40 years. This increase reached 40 dt/ha, i.e. it almost doubled since 1974. At the beginning of the 21st century, rapeseed hybrids started to be more widely used in rapeseed production, which further increased yield. In 2015, Institute of Field and Vegetable Crops registered its first rapeseed hybrid `NS Ras` (Figure 4).

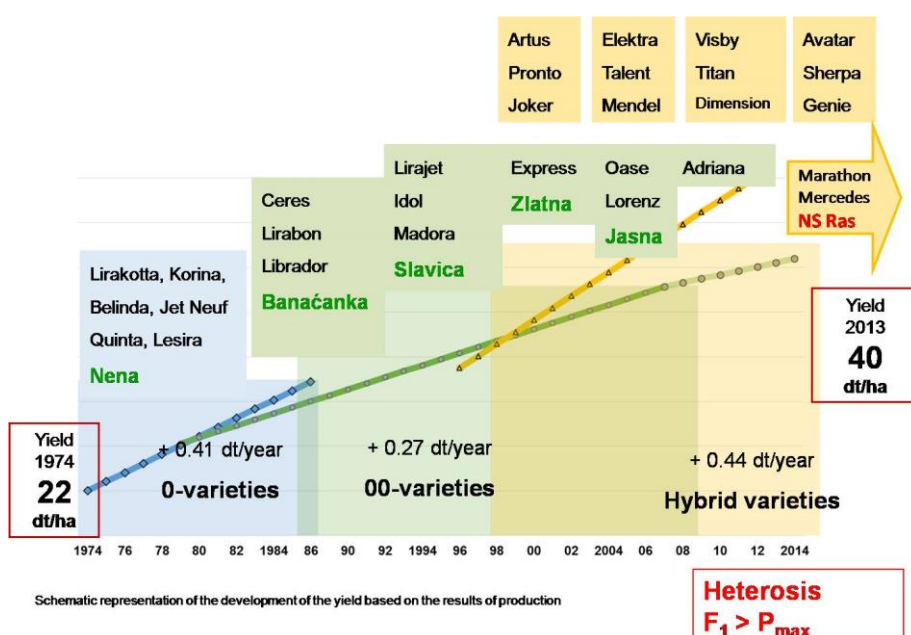


Figure 4. Improvements in rapeseed production in the last 40 years in Europe. Sources: Justus Liebig University Giessen, Rapool-Ring GmbH, Institute of Field and Vegetable Crops Novi Sad

FUTURE CHALLENGES

Future challenges for rapeseed breeders are numerous. It is important to further increase yield, improve quality and create stable genotypes which will be able to face future environmental challenges. The breeding goals could be divided into 5 categories:

1. Increased oil content (+50%)
2. Modified fatty acid composition in commercial varieties for different purposes
3. Improving seed protein content and amino acid composition
4. Improving the quality of meal (nutrients and anti-nutritional factors)
5. Use of different methods to improve yield under adverse conditions (abiotic and biotic stress)

An integrative approach should be taken in order to achieve the goals and tasks put before rapeseed breeders. It takes a joint effort made by breeders, phytopathologists, entomologists, chemists, and molecular biologists to meet today's market demands.

In 2014, the rapeseed genome sequence was published (CHALHOUB *et al.*, 2014). This was a result of a joint effort of more than 30 research institutes coordinated by scientists at INRA and CEA-Genoscope and associating CNRS and the University of Evry. The insight into *B. napus* genome will give molecular breeders ability to further analyse rapeseed at the molecular level and to develop high density markers in genome assisted selection.

CONCLUSIONS

Gregor Mendel's results are the basis for understanding the inheritance of different traits. Hereditary "factors" (genes) explain the phenotype. Factors appear in two basic forms (alleles) which can be combined to provide new phenotypes. Mendel's rules are the basis for development of methods in breeding from varieties to hybrids and systematic use of Mendel's rules has led to crop improvement. Today's varieties are superior in terms of stress resistance, they have higher yield, and are of superior quality.

Received May 09th, 2016

Accepted October 18th, 2016

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PRIMENA MENDELOVIH PRAVILA U OPLEMENJIVANJU ULJANE REPICE
(*Brassica napus*)

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Izvod

Uljana repica je jedan od najznačajnih izvora jestivog ulja, sirovina za industriju, kao i hrana za domaće životinje. Kao rezultat intenzivnog oplemenjivačkog rada i optimizovane tehnologije proizvodnje, prinos i kvalitet uljane repice su značajno poboljšani poslednjih decenija. Uspesima u oplemenjivanju uljane repice je doprinela i primena Mendelovih pravila u unošenju osobina koje se nasleđuju monogenski. Pravilo 1, koje se odnosi na uniformnost F₁ generacije, je osnova danas široko rasprostranjenog oplemenjivanja hibrida uljane repice. Pravilo 2 o razdvajanju gena u F₂ generaciji je osnova za razumevanje procesa oplemenjivanja linija. Pravilo 3 o nezavisnom kombinovanju osobina i gena, pri čemu se izuzimaju vezane osobine, je osnova kombinacionog oplemenjivanja različitih poželjnih svojstava. Primenom Mendelovih pravila su u prethodnim decenijama poboljšana mnoga svojstva uljane repice: tolerantnost na biotički i abiotički stres, prinos, kao i kvalitet semena. Poseban napredak je ostvaren u oplemenjivanju na otpornost prema bolestima i identifikovani molekularni markeri za primenu u marker asistiranoj selekciji. Naredni cilj u oplemenjivanju uljane repice je stvaranje sorti sa poboljšanom tolerantnošću na stresne uslove spoljašnje sredine (npr. mraz, visoke temperature, suša). Počevši od Mendelovih pravila kao osnove, kombinovanjem klasičnog oplemenjivanja i najnovijih dostignuća iz oblasti molekularne genetike i oplemenjivanja, očekuje se napredak u oplemenjivanju svojstva uljane repice koja se nasleđuju poligenski, odnosno kvantitativna svojstva kao što su habitus i prinos semena i ulja.

Primljeno 09. V. 2016.

Odobreno 18. X. 2016.