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REVIEW

Breeding strategies to consolidate canola among the main crops for biofuels

Bruno Galvêas Laviola · Erina Vitório Rodrigues · Adriano dos Santos · Larissa Pereira Ribeiro Teodoro · Leonardo Azevedo Peixoto · Paulo Eduardo Teodoro · Leonardo Lopes Bhering

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Abstract Canola is a product of traditional plant breeding techniques to remove from rapeseed the antinutritional components erucic acid. This crop proves to be a promising crop due to the diverse purposes of its oil, especially by its potential for biofuel production. This paper aimed to integrate the information available in the literature and report the most promising strategies for genetic and biotechnological progress in canola. Thus, we carried out a detailed review of the origin and uses of canola, its socioeconomic importance in the global and Brazilian aspects, tropicalization, with emphasis on genetic breeding. We demonstrate the main breeding strategies that can be used to increase your oil production. We propose here a breeding strategy for canola, in which some strategies previously mentioned are integrated. The purpose of this strategy is to enhance the selection and efficiency at the beginning of a breeding program. Among these, genome wide selection (GWS) is a suitable tool to help breeders to improve the efficiency selection in a canola breeding program increasing the selection accuracy or even reducing the cycle time. The proposed strategies must be analyzed for each situation, adjusting the GWS model to obtain highest selection accuracy.

Keywords *Brassica napus* L. · Plant breeding · Genome wide selection · Tropicalization

B. G. Laviola · A. dos Santos
Embrapa Agroenergia - Parque Estação Biológica, PqEB s/n, Asa Norte, Brasília, DF 70770-901, Brasil
e-mail: bruno.laviola@embrapa.br

A. dos Santos
e-mail: adriano.agro84@yahoo.com.br

E. V. Rodrigues
Universidade de Brasília - Campus Faculdade UnB Planaltina, Brasília –Vila Nossa Senhora de Fátima, Planaltina, DF 73345-010, Brasil
e-mail: erinavict@hotmail.com

L. P. R. Teodoro · P. E. Teodoro (✉)
Universidade Federal do Mato Grosso do Sul - Campus de Chapadão do Sul, Chapadão do Sul, Mato Grosso do Sul 79560-000, Brasil
e-mail: eduteodoro@hotmail.com

L. P. R. Teodoro
e-mail: larissa.uems@gmail.com

L. A. Peixoto · L. L. Bhering
Universidade Federal de Viçosa, Avenida Peter Henry Rolfs, s/n, Campus Universitário, Viçosa, MG 36570-900, Brasil
e-mail: leoazevedop@gmail.com

L. L. Bhering
e-mail: leonardo.bhering@ufv.br

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Introduction

Canola (*Brassica napus* L. var. oleifera) is an oleaginous crop of the Brassicaceae (Bergmann et al. 2013). Improved variety from rapeseed (*Brassica napus* L.), canola has developed into a major crop, with canola oil becoming one of the most important sources of vegetable oil in the world (Reddy 2017). Rapeseed/canola has been used for animal feed, fertilization for soil and oil production, which has been used for human consumption, lighting, industrial purposes and, more recently, for biofuel production (De Mori et al. 2014).

It is a product of traditional plant breeding techniques to remove from rapeseed the antinutritional components erucic acid, which is toxic to humans in high concentrations, and glucosinolates, which gives the oil an unpleasant flavor, making the product absolutely safe for human and animal consumption. Its oil should contain less than 2% erucic acid and the non-oil portion of the seed should have less than 30 mmol of glucosinolates (Milazzo et al. 2013).

The crop is the world's second largest oilseed producing crop (behind soybean) and is planted in many countries worldwide (Zhou et al. 2017). Its domestication as an oilseed crop can be considered recent, around 400–500 years ago (Prakash et al. 2011). Nevertheless, the breeding performed in different climatic conditions and for different morphotypes has resulted in strong population structure (Rahman 2013). Zhou et al. (2017) reported that regarding rapeseed germplasm worldwide, these can be differentiated into three ecotypes: winter, semi-winter, and spring, which result from long-term selection for low temperature vernalization and photoperiod sensitivity. Winter rapeseed with strict vernalization requirements is mainly distributed in Europe; semi-winter rapeseed with moderate cold tolerance and vernalization requirements is planted primarily in the Yangtze valley of south China (Sun 1946), and spring rapeseed with early flowering is mainly distributed in North America, Canada, and Australia.

Canola proves to be a promising crop due to the diverse purposes of its oil, especially by its potential for biofuel production. However, Reddy (2017) states that, unlike most major crops, which have been the subject of scientific research for hundreds of years, the advent of canola oil was in the 1970s, so canola production is still in its early stages of development, and there is still much to learn.

Recently, some researches with genetic breeding have been carried out with canola aiming at the development of more productive genotypes, mainly in tropical regions. These researches used from classical breeding techniques like diallel crossings (Grigolo et al. 2017) to molecular genetics for estimating genetic diversity between genotypes (Havlíčková et al. 2014; Guo et al. 2016), identifying QTLs for seed quality traits (Huang et al. 2016), and genomic prediction of testcross (Jan et al. 2016). This paper aimed to integrate the information available in the literature and report the most promising strategies for genetic and biotechnological progress in canola.

General aspects

Origin and uses

Canola is an improved cultivar from cross-breeding of four main Brassica oil-seed species, namely, rapeseed (*B. napus*), field mustard (*B. rapa*), Indian mustard (*B. juncea*), and Ethiopian mustard (*B. carinata*) (Yeboah et al. 2013). The genus *Brassica* comprises a large number of crops with different biological characteristics. This diversity is directly related to its domestication and ways to use (Becker et al. 1999).

The centers of origin and diversity of *Brassica napus*, according to the studies, is Central Asia and the Mediterranean. History suggests that rapeseed was already cultivated in India in 2000 BC and was introduced in China and Japan at the beginning of the Christian era (Canada 2013). Its adaptability to relatively low temperatures, requiring less than demanded by other oilseeds, allowed its cultivation in extreme temperature regions and expanded its cultivation in Europe since the thirteenth century.

Subsequently, there has been a diversification of oil use, after the discovery of its lubricating properties. During World War II, in the face of the shortage of oil owing to the blockade of European and Asian sources, the introduction of canola cultivation in Canada in 1942 was encouraged, from which oil was extracted primarily to supply steam engines on merchant and war ships (Robertson et al. 2002).

In the seventeenth century, the habit of fried foods with rapeseed oil was developed and the oil acquired

edible product status. However, research results conducted in the 1970s showed that erucic acid present in the oil caused health problems in humans, which led to the development of rapeseed cultivars with low levels of erucic acid. Continued improvement efforts led to the development of new cultivars with the added benefit of low levels of glucosinolates (Carlsson et al. 2007). In this way, breeders from the University of Manitoba, Canada, selected rapeseed plants with low erucic acid content in the oil and other plants with low glucosinolate content in the meal, which were crossed and resulted in the release of the first canola cultivar, "Tower", in 1974 (Canada 2013).

Different rapeseed varieties have been developed for different uses. For example, cultivars with a high-erucic acid content, called HEAR (high-erucic acid rapeseed), were developed to meet the industrial oils industry (De Mori et al. 2014). To distinguish rapeseed varieties, the *Western Canadian Oilseed Crusher Association* recorded as canola, initials of **Can**adian **O**il **L**ow **A**cid, cultivars that have less than 2% erucic acid in the oil and less than 30 µm glucosinolate per gram of dry seed matter (Thomas 2003).

Among the various uses of canola, meal and oil stand out as the most profitable products of the crop. Canola meal, a solid coproduct from oil extraction, is used as a protein supplement in animal feed formulations, presenting 36 to 39% protein (Canada 2013). Thus, canola meal is an economical protein source for animals that do not have high levels of energy and lysine requirements. In the case of the price of canola meal, the ratio is approximately 75% of the price of soybean meal due to the food value (De Mori et al. 2014).

Canola oil has quality higher than other oilseeds, characterized by low content of saturated fatty acids (7%), high content of monounsaturated fatty acids (61%) and intermediate level of polyunsaturated fatty acids with a good balance between omega-6 and omega-3 acids (McDonald 2000). Such properties are important in immune system development functions and protective actions against coronary diseases (Mutalib et al. 1999; Lorgeril et al. 2001; Lin et al. 2013)

Owing to the reputation of being one of the best oils for human consumption, the use of canola oil for human consumption was over 90% until the 1990s (USDA 2018). From the year 2002, there was an increasing destination of canola oil for industrial processes, which accounted more than 30% of the total consumed from the 2008/2009 harvest (USDA 2018). Notably, this increased use of canola oil in industrial processes is owing to biofuel production in Europe, which is mostly carried out with canola oil (De Mori et al. 2014).

Declining crude oil resources, volatile petroleum markets, the quest for energy security, and the impact of petroleum fuel use on global climate change have spurred efforts to identify and develop alternative renewable energy sources (Kaufmann and Shiers 2008). Recent efforts have focused on the use of canola oil to produce biodiesel and canola is currently the third most important crop after soybean and maize for biodiesel production (Vasudevan and Briggs 2008). Several papers published in recent years (Babaki et al. 2015; Bergmann et al. 2013; Bradley et al. 2016; Chen and Chen 2011; Dizge and Keskinler 2008; Kumar and Sharma 2016; Lee et al. 2010; Milazzo et al. 2013) show that currently the use of canola oil has been focused on the biodiesel production.

Canola oil has been proven to be an excellent feedstock for biodiesel production (George et al. 2008). Canola biodiesel is one of the biofuels that have lower emissions for both the production and combustion stage compared to fossil fuels. Milazzo et al. (2013) reported that the fuel life cycle emissions from the production and use of biodiesel include the benefit of the biogenic emissions, being that canola biodiesel reduces the life cycle GHG emissions by 90.1% compared to fossil diesel (0.0015%). The EPA (2010) states that canola oil biodiesel pathway creates a 50% reduction in greenhouse gas emissions compared to conventional diesel fuel baseline. In a a study analyzing the life cycle on biodiesel production from canola oil, EPA (2010) found canola oil has high conversion efficiencies compared to biodiesel produced from soybean oil.

Another factor that contributes to the successful use of canola oil for biodiesel production is the property of biodiesel from oil canola to become gel only at an atmospheric temperature lower than biodiesel produced from other raw materials, making canola biodiesel the most suitable option for colder regions (Flach et al. 2011). In addition, the standards established by the European standard (DIN EN 14214) for biodiesel, in relation to iodine content and stability,

favor the use of canola oil and limit the use of soybean and palm oils (De Mori et al. 2014).

Socioeconomic importance

Canola in the word

Worldwide canola production is concentrated far from the equatorial line in areas with a dry climate and short growth seasons. In Europe, Ukraine, Russia and parts of China, winter varieties are cultivated, while spring varieties are grown mainly in parts of China, India, Canada and United States (De Mori et al. 2014). The production of canola grain in the world increased from just over 8 million tons in the 1970s to current 76.7 million tons in 2019/20 (USDA 2021), which reveals a recent and fast expansion of the crop.

The European Union are the world's largest producers of canola, a production in the last harvest (2020) at about 17 million tons, accounting for 21.2% of all canola oilseed production, as shown in Figure 1. Canada is the first largest producer, accounting for 19.49 million tons, in addition to be the largest grain exporter, responsible for exporting 10.5 million tons, which corresponds to about 61.3% of all canola oilseed exported (USDA 2021). European Union, Canada, China, India and Japan concentrate the production of rapeseed/canola oil in the world, accounting for over 80% of total production in the 2019/20 harvest. The world's largest consumers of rapeseed/canola are European Union, China, Canada, India and Japan (USDA 2021).

According to data from USDA (2021), the world production of canola oil in the 2019/20 harvest was about 28.08 million tons, with world consumption

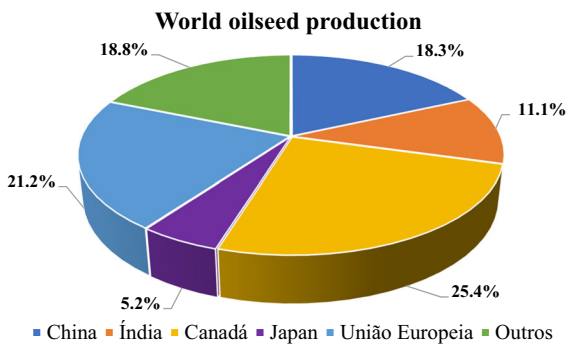


Fig. 1 World's major oilseed canola producers. *Source*: USDA (2021)

around 32.6 million tons. The largest producer of canola oil is the European Union with a production of around 32%, followed by China and Canada, which account for 21.51% and 15.79%, respectively, of all canola oil produced in the world. Canada is the largest exporter of canola oil, accounting for 58,6% of the word exports.

Word production of canola meal in the 2017/18 harvest according to USDA (2018) was around 39.45 million tons. Word consumption was approximately 39 million tons. The largest producer of canola meal is the European Union, with a production of 12.03 tones. Next is China, with a production of 9 million tons, but consuming everything it produces.

Canola in Brazil

In Brazil, canola started being cultivated in the 1970s in the southern region of the country as a rotation crop for wheat (Bergmann et al. 2013). Canola growing in Brazil has been in expansion since 2005, when Embrapa (Brazilian Agricultural Research Corporation) developed hybrid cultivars resistant to diseases caused by fungi (Tomm et al. 2009a, b, c). The evolution of canola area and yield in Brazil is shown in Figure 2. A growing expansion in the harvested area from 2005 extending to currently can be observed, consolidating the canola as an expanding crop in the country.

Canola crop in Brazil has been an option employed in crop rotation systems, mainly in the south of the country (Luz 2011). Its growing fits perfectly into the crop rotation system, along with soybean and preceding maize sowing. Already in the Southwest of Goiás and other states of the Brazilian Midwest, the crop is an alternative for diversification and income generation in the off-season. Only spring canola varieties of the species *Brassica napus* L. var. oleifera are cultivated (Tomm et al. 2009b), which does not require vernalization and has low sensitivity to photoperiod.

According to current data from the National Supply Company (Conab), the area of canola growing in the 2021 harvest was 35,000 ha, which is concentrated in the states of Rio Grande do Sul and Paraná, located in the southern region of the country. The state of Rio Grande do Sul is the largest national canola producer, with an area of 34,800 ha and a production of 31,400 tons, (Conab, Companhia nacional de abastecimento

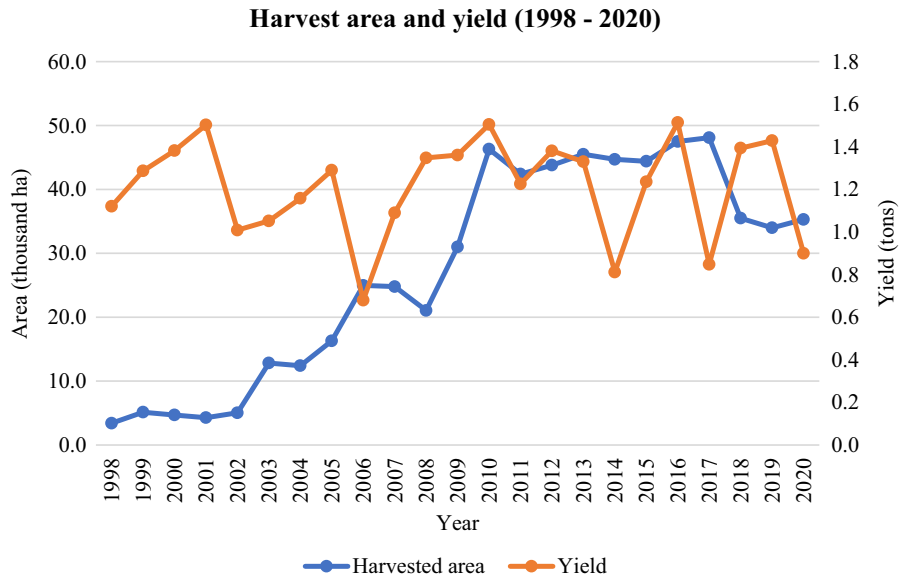


Fig. 2 Evolution of harvested area and yield of canola in Brazil from 1998 to 2020. *Source*: drawn up based on data from IBGE (2008) and Conab (2020)

2021). The average national yield in the 2020 harvest was 912 kg ha^{-1} (Conab, Companhia nacional de abastecimento 2021), which represented a decrease of 36% in relation to the previous harvest (2019), whose yield was 1429 kg ha^{-1}. Even so, canola yield in the country has changed little over the last 20 years, as seen in Figure 2, and it is still considered low when compared to the crop yield potential. According to (Tomm et al. 2009a), this comes from the difficulty of the farmers with little experience in canola growing to attend the particularities of this crop.

In a study conducted in a large number of farms in Canada, Robertson et al. (2002) concluded that the canola yield is more limited by failures to apply, modify and adjust production factors within cropping systems than by the soil and climate conditions. According to those authors, the genetic potential of hybrids used in Canada is 4500 kg ha^{-1}. This information indicates the great potential for improving yield in Brazil and wherever the efforts should be directed. Despite the great variation in grain yield in the most diverse growing conditions, the guaranteed marketing (liquidity) and the price (equivalent to soy) are the biggest incentives for the farmer in rapeseed cultivation.

Canola oil production in Brazil is mostly for the food market. However, it is considered as an alternative to soybean by the Brazilian government, which has encouraged canola crop expansion to other regions of the country (Bergmann et al. 2013). To increase the availability of oil and better use its regional resources, vegetable oil crops alternative to soybean are being considered. Canola oil can be an alternative to soybean oil because while the soybean oil content is 18–21% and oil yield is 560 kg ha^{-1}, canola oil content and yield is 34–40% and 570 kg ha^{-1}, respectively (MAPA 2017). Its oil composition meets the European specifications for biodiesel production with excellence, as well as being very healthy from a food point of view. The cultivation of this oleaginous tends to increase further in Brazil due to the demand for the product in the Brazilian and European markets as well as being a good economic option for the Brazilian farmer (Tomm et al. 2009a, b, c).

Canola tropicalization

Canola is grown in latitudes from 35° to 55°, in temperate climates and in systems that allow only one crop per year. Most canola produced in Europe is winter-type, sown in the fall, with the plants covered by snow during the winter, and harvested in the summer of the following year (Fuzaro et al. 2019; Tomm et al. 2009a, b, c). The optimal temperature for full development of the crop is about 20 °C, with extreme limits between 12 and 30 °C (Robertson et al. 2002). In Brazil, these thermal conditions are found predominantly in the southern region, during fall, winter and early spring, which corresponds to the

period of canola growing in these regions (Dalmago et al. 2010). On the other hand, several studies have been reported its potential for growing in warmer climates, known as "tropicalization" (Panozzo et al. 2014; Tomm et al. 2009a, b, c).

Canola growing in Brazil has been expanded from South region to the southwest of the states of Goiás, Minas Gerais and Mato Grosso do Sul, located in the Cerrado biome, which is leading to research for adapting the crop in this region. Even the northeastern region of the country, known for its high temperatures, besides being situated closer to the equator, has been the subject of research evaluating the canola performance. Tomm et al. (2008) evaluated the performance of canola genotypes in the northeastern state of Paraíba, Northeast Brazil, and they reported that the region may be promising for growing canola genotypes with low sensitivity to photoperiod.

The main strategy used in directing the efforts to tropicalize canola has been to prioritize the experimentation and the beginning of commercial cropping in areas with altitudes above 600 m, which have milder temperatures (Fuzaro et al. 2019; Tomm et al. 2008). It is seeking to offset the lower latitude of the new areas of experimentation and early canola growing, located ever closer to the equator, in relation to areas where farming is most widespread in Brazil. The results obtained in higher-altitude sites will indicate the potential of success in sites with lower altitude in regions of similar latitude, increasing safety in the crop expansion (Tomm et al. 2009a, b, c).

In order to promote the canola tropicalization, a joint effort of the Federal University of Uberlândia and Embrapa Wheat has been carried out aiming the expansion of the crop to new farming areas, such as the Cerrado (Nery-Silva et al. 2017). Wheat farming areas have been used as an indication of the greater probability of success in canola growing. Based on this strategy, coupled with the use of low-sensitivity to photoperiod hybrids, successful experiments in canola growing in Brazil already range from tropical regions, such as the state of Paraíba, to the temperate or subtropical conditions of South of Brazil.

Genetic breeding

Despite the great worldwide importance and socioeconomic potential of canola, we noteworthy that there is no genetic breeding program in Brazil to date. In the 1980s, a research institution developed open-pollinated varieties, such as PFB-2 generated by Embrapa Wheat (Tomm et al. 2009a, b, c). Canola seeds grown in Brazil are imported from major producing countries, which invest in germplasm development and manage the production and marketing of canola cultivars to the private institution.

In this context, Schnell (1982) suggests that in the implementation of a genetic breeding program the following steps should be taken into account: (1) searching appropriate initial variation; (2) establishing candidates for potential cultivars, and (3) selecting final cultivars via performance tests. However, allied to these steps we still mention the breeding objective, germplasm, breeding strategy, cultivar type. It is important to note that to achieve the objective of a canola breeding program quickly and efficiently, a combination of traditional methods with genetic engineering should be carried out, since the basis of plant breeding is the multidisciplinary science.

Genetic diversity

Genetic variability is the main tool for the success of any breeding program. It constitutes divergence in plants based on different traits. Thus, plant breeders focus their efforts on exploring and increasing genetic diversity among available genotypes, and hence on the development of high-yielding cultivars adapted to different edaphoclimatic conditions (Khan and Razi 2016).

The genus *Brassica* composes about 100 species that present variability among them. Cytogenetic relationships between rapeseed species were originally described by Nagaharu (1935). It was established that the three allotetraploid species, *B. napus*, *B. juncea* and *B. carinata*, are amphidiploids derived from diploid species *B. nigra. B. rapa,* and *B. oleraceae* (Paterson et al. 2006; Sabharwal et al. 2006). The *Brassica napus* species (2n=38 AACC) is a hybrid from the rapeseed species *B. oleraceae* and *B. rapa*, as shown in Figure 3.

This genre has a long history regarding taxonomy and evolution, and many studies have focused on elucidating how its genome was modified over its evolutionary process, because so far there is still ambiguity. Thus, Thakur et al. (2018) mention that it is essential to carry out genetic dissection between

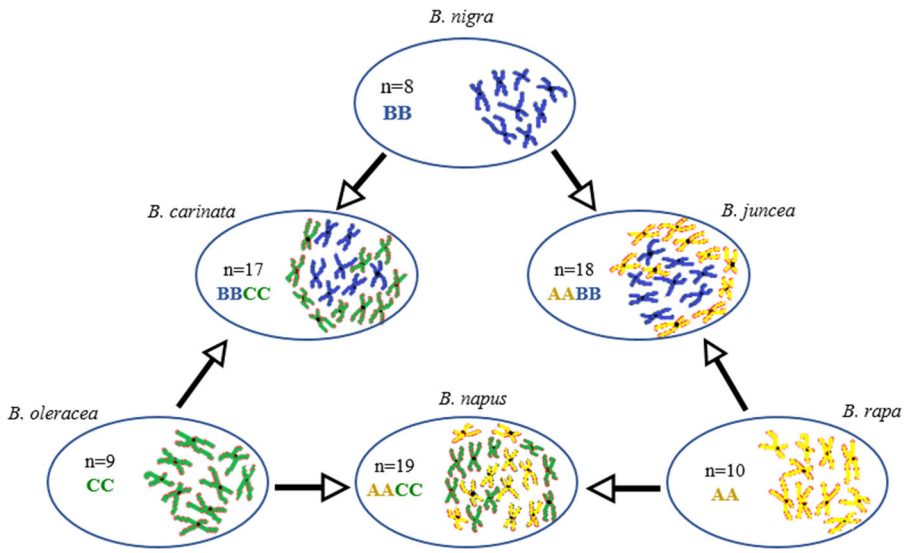


Fig. 3 Scheme representative of the cytogenetics of the Brassicaceae, n: basic chromosome number; AA: *Brassica rapa* genome; BB: *Brassica nigra* genome; CC: *Brassica oleraceae* genome

diploid and amphidiploid species, and with advances in biotechnology, genetic diversity studies and phylogenetic analyses in canola breeding programs have been carried out.

The formation and evolution of allotetraploid species affected by different phylogenetic relationships between diploid species (Li and Wang 2017). Song and Osborn (1992) analyzed the genomic DNA of canola parents and suggested that interspecific hybridization occurred in different places, involving more than one morphological type. Thus, it is unlikely that the *B. napus* species combine all parent variants, so it is important to consider germplasm from different geographic regions to introgress genetic diversity (Rahman 2013).

Although there was such evidence, uncertainty remained as to the nature, direction and geographical location of the initial hybridization of *B. napus* species. However, only by using molecular markers, Allender and King (2010) they clarified the origin of this species through the approach that provides basic evidence for possible polyphyletic origins of the species. This information is elucidated by using molecular markers that allow detailed information very useful for breeding programs.

From this perspective, several studies have been carried out using Restriction fragment length polymorphism (RFLP) (Riaz et al. 2001), Simple Sequence Repeats (SSR) (Guo et al. 2016), Amplified fragment length polymorphism (AFLP) (Eckes et al. 2017), and Random Amplified Polymorphic DNA (RAPD) (Qiao et al. 2016) in order to investigate the level of genetic diversity in canola germplasm. Already the use of SNPs for genome-wide association studies to identify allelic variation of elite genotypes for oil content in canola seeds (Liu et al. 2016).

Given the importance of genetic diversity analysis to assist breeders in choosing potential genotypes that will make up crossbreeding blocks, Havlíčková et al. (2014) evaluated genetic diversity in a canola collection using SSRs, ISSRs and AFLPs markers. The three types of markers differed in the observed polymorphism, and the largest genetic distance was found by ISSRs. Genetic distance detection facilitates parental selection, which is based on greater diversity, increasing efficiency in the development of lines and hybrids.

Moreover, considering that canola is a predominantly self-pollinating plant, but presenting an cross-pollination rate over 20% (Grigolo et al. 2017). There is sufficient genetic variability available within the species. However, to search for new desired genes or gene complex, it is necessary to resort to interspecific crosses or even intraspecific crosses (Gupta and Pratap 2007).

Canola breeding strategies

Although the diversity and quantity of genotypes is immense, the availability of canola cultivars suitable to

Brazilian conditions is restricted. Experiments and commercial crops have shown that canola has potential to contribute to the expansion of Brazilian agribusiness, as it is suitable as an off-season crop in grain production systems in low latitude regions, i.e., the so-called "tropicalization" of canola (Tomm et al. 2008; Panozzo et al. 2014). However, to date, there are no breeding programs for canola. Thus, it is important to highlight some strategies of genetic breeding of this crop in order to provide information to the scientific community, since it is the third largest oilseed in the world.

Genetic diversity and particularities of the canola reproductive system, an self-pollinating plant with an cross-pollination rate higher than 20% (Grigolo et al. 2017), allow the application of several breeding strategies for developing lines, as well as exploring hybrid heterosis. Among the strategies for cultivar selection, the fastest is the introduction and evaluation of cultivars in new regions, which allows validating the cultivation of already improved genotypes. As these genotypes have already gone through the selection process, it becomes possible to skip some steps of conventional breeding.

However, in order to obtain short, medium and long-term gains for several agribusiness traits of interest, it is essential to implement breeding programs with all their steps (Borém et al. 2017). In this respect genetic breeding from the rapeseed some conventional strategies were used as bulk and pedigree methods, and use of double-haploids combined with other techniques.

Pedigree method

In this method, as many F_1 plants as possible are grown to obtain F_2 seeds, restricting to a minimum of 5 to 10 F_1 plants, subsequently F_2 plants are carried out under representative cultivation conditions, using larger plant spacing to facilitate individual evaluation. For a better understanding, the steps of applying the pedigree method for *Brassica napus* breeding were described as shown in Figure 4.

Step 1 Initially, progenies that will constitute the breeding population should be obtained. The use of partial or complete diallel crossings are an option to obtain F_1 plants. The largest number of these plants should be grown to obtain the F_2 plants.

Step 2 The size of the F_2 population depends, among others, on the number of F_3 families that the breeder can handle and the breeding objectives. It can range from 2000 to 10,000 well-spaced plants to facilitate evaluations. We suggest a ratio between F_2 individuals and F_3 families between 10:1 and 100:1. The ratio will be greater the more the parents differ from each other. At this stage the breeder should not select too many plants when it is not possible to work with many F_3 families.

Step 3 The progenies F_3 from each selected F_2 plant are sown in individual rows. Each row must have a sufficient number of plants, usually around 30. This number will also depend on the amount of seed that F_2 plants yield on average. Selection between and within F_3 lines is practiced. Normally, the total number of plants selected is not higher than the cultivated rows.

Step 4 The selected F_4 progenies from each F_3 plant are grown similarly to Step 3, in which the progenies of plants from the same row are sown side by side (family), but the selection between rows is emphasized. Plants with the best performance in each of the rows are selected.

Step 5 The procedure for selecting the best lines and within lines will be repeated in subsequent generations until the desired uniformity is achieved. The top rows will be subjected to comparative yield trials to be carried out at various sites over three or four crop seasons. This procedure allows an evaluation of genotype x environment interaction. The parents and other cultivars traditionally cultivated in each area or region are included in the trials.

At the end of the process, the best lines originated new improved cultivars, each line giving rise to one cultivar. In some cases, when superior lines are similar for important agronomic traits, their seeds may be mixed to form a new cultivar, provided this procedure does not compromise the uniformity required by farmers and consumers.

Bulk method

Step 1 In this method, sowing is carried out in a sufficiently large area of approximately 6000 plants or more, according to the amount of F_2 seeds available (Figure 5). Sowing density is the same as for commercial plantations, as selection will not be performed with the rigor of the pedigree method. Sowing in larger spacing should be avoided due to the

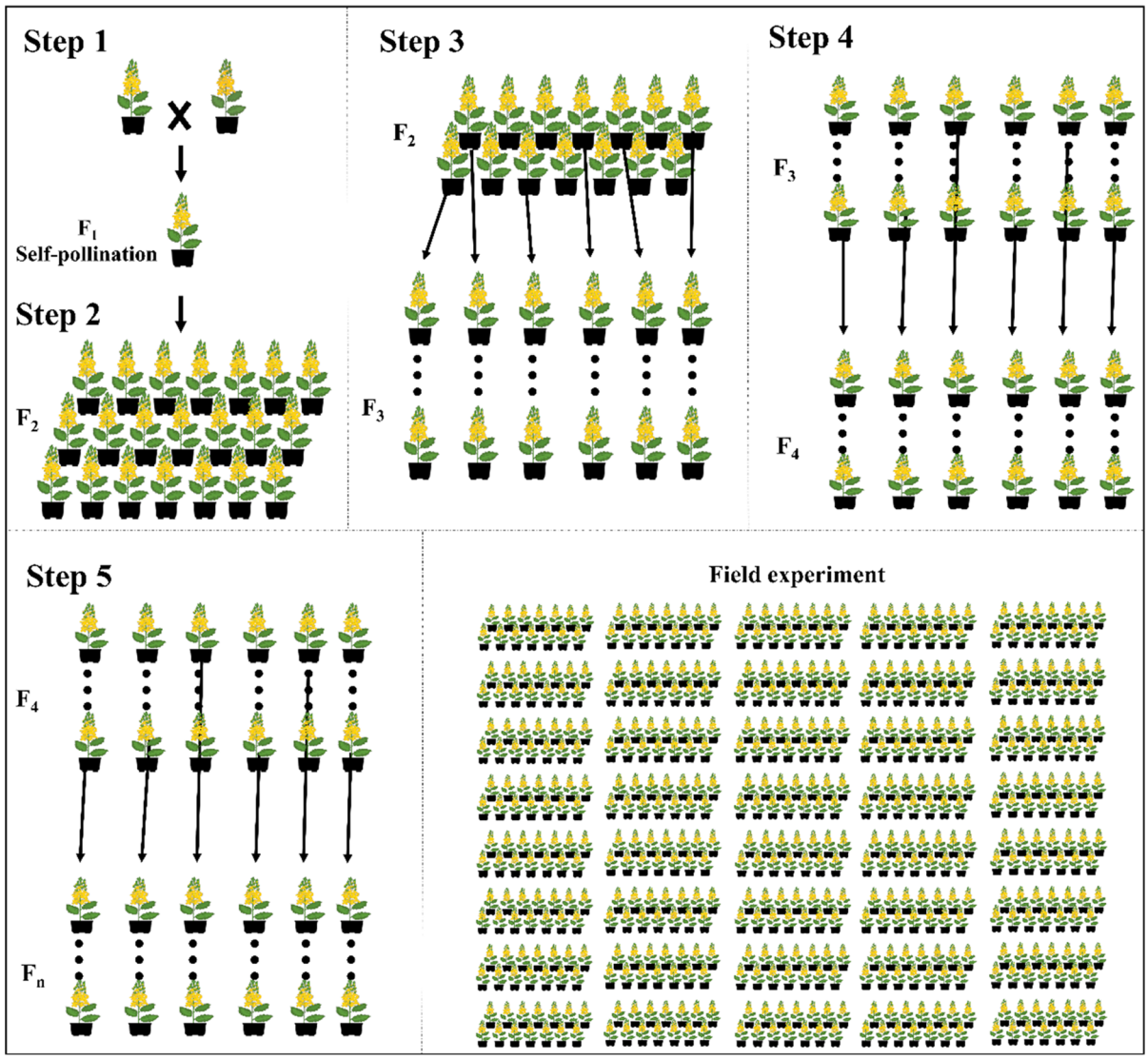


Fig. 4 Diagram of the pedigree method steps applied to *Brassica napus* breeding

tendency of heterozygous genotypes to be more vigorous and to exert greater competition with homozygotes, producing larger numbers of offspring in this condition.

Step 2 The seeds of all selected plants are harvested in bulk to produce the next generation, proceeding in the same way until the desired uniformity in the population is achieved. In the first generations we seek to select for high heritability traits, such as plant size and architecture, and vegetative cycle.

Step 3 From F_5 generation or more advanced generations, individual plants are selected and their progenies are evaluated in trials, initially preliminary and later advanced, increasing the number of sites and replicates in the experiments for selecting the best lines. From there the procedures are similar to those already described for the pedigree method.

Recurrent selection

Recurrent selection is a population breeding method that aims to increase the concentration of favorable alleles, conserving the genetic variability of the population. Populations improved by recurrent

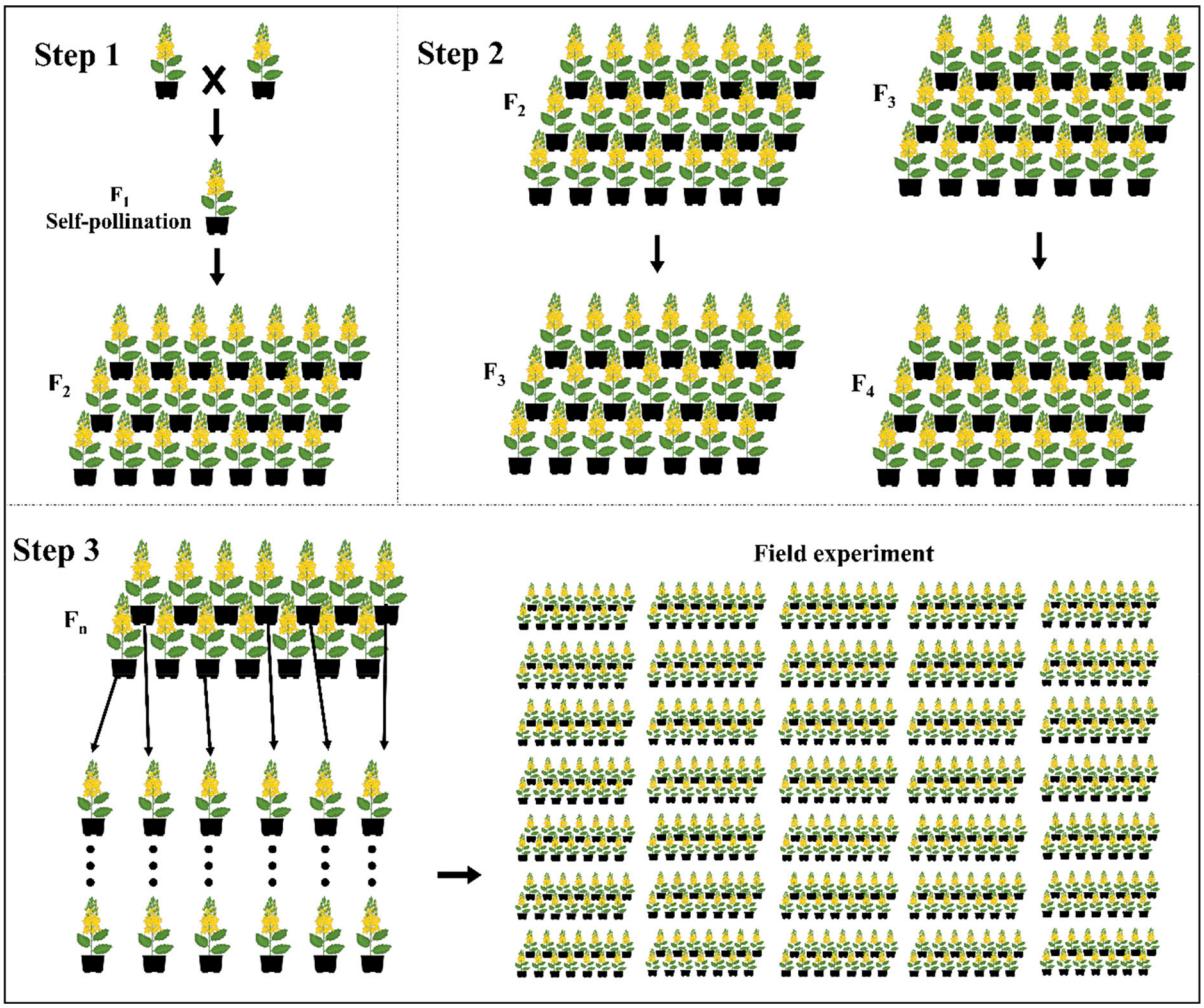


Fig. 5 Diagram of the bulk method steps applied to *Brassica napus* breeding

selection can be used directly as open-pollinated cultivars or to obtain inbred lines used in hybrid production.

Recurrent selection in $S_{0:1}$ progeny *Step 1* In this method, from 1000 to 10,000 plants of the base population are self-pollinated and each plant will be harvested individually, generating the $S_{0:1}$ progeny, as shown in Figure 6.

Step 2 Part of the seeds from $S_{0:1}$ progeny will be stored (remaining seeds) and the other part of the seeds will be used in experiments with replicates and at least in two sites for phenotypic selection.

Step 3 With the result of Step 2, 200 top plants will be selected based on phenotypic trait. Remaining seeds from these 200 selected $S_{0:1}$ plants are mixed and sown together for recombination in isolated field. Thus, the improved population and the first cycle of intrapopulation recurrent selection are obtained.

Reciprocal recurrent selection in full-sib progeny *Step 1* The stage begins with the formation of the base populations, which should be emphasized. These populations should present desirable alleles for the largest number of traits of interest, as well as the need to be as divergent as possible, making it possible to associate high mean and level of genetic variability, which are indispensable conditions for successful selection. The crossing between winter and spring Brassica may be a good option for the formation of the base populations (Figure 7).

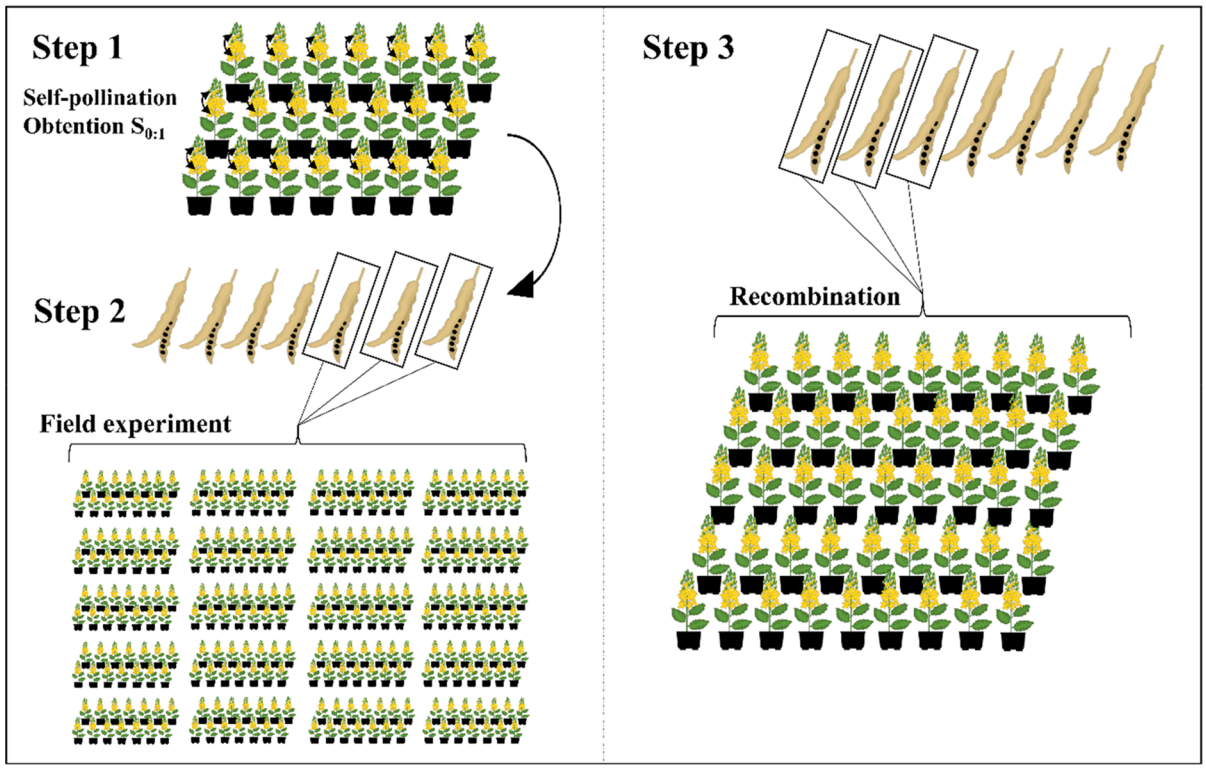


Fig. 6 Diagram of the intrapopulation recurrent selection steps in $S_{0:1}$ progenies applied to *Brassica napus* breeding

Step 2 Approximately 300 plants from population "A" are relocated in pairs with 300 plants from population "B". Crossings between populations "A" and "B" are performed, as well as reciprocal crossings, then obtaining full-sib families. However, 50% of siliques are used to obtain seeds from self-pollination. In this way, full-sib families and self-pollinated families will be obtained. Seeds from self-pollination should be stored.

Step 3 The 300 full-sib families are evaluated in experiments with replicates and at least two sites for phenotypic selection.

Step 4 Based on the result from Step 3, the top plants from each population are selected. Afterwards, equal amounts of the remaining seeds (seeds from self-pollination) from the selected plants are mixed in equal proportions. The composite mixture of the remaining seeds from each population is separately sowed in the field in isolation, thus recombining the plants within the populations. In this way, the first recurring selection cycle is completed.

Future strategy for *Brassica napus* breeding

We propose here a breeding strategy for *Brassica napus* in which some strategies previously mentioned are integrated. The purpose of this strategy is to enhance the selection and efficiency at the beginning of a breeding program.

Step 1 About 600 to 700 seeds from each $F_{1:2}$ families obtained will be sown in single plots (rows). Individual plant selection will be based on the traits of interest, along with resistance to lodging and disease. The top rows in $F_{2:3}$ generation will be selected for the next evaluation cycle. A total of 500 $F_{2:3}$ plants will be selected from all families and will be grown to generate the $F_{3:4}$ population. From five to ten plants per row in the generation ($F_{2:3}$) will be self-pollinated, and the remaining plants from each row will be harvested in bulk (Figure 8).

Step 2 The seeds from $F_{3:4}$ plants self-pollinated in the previous year will be grown as individual rows and advanced for the $F_{4:5}$ generation. In this phase, early generation tests will be carried out on 500 $F_{3:4}$ rows in

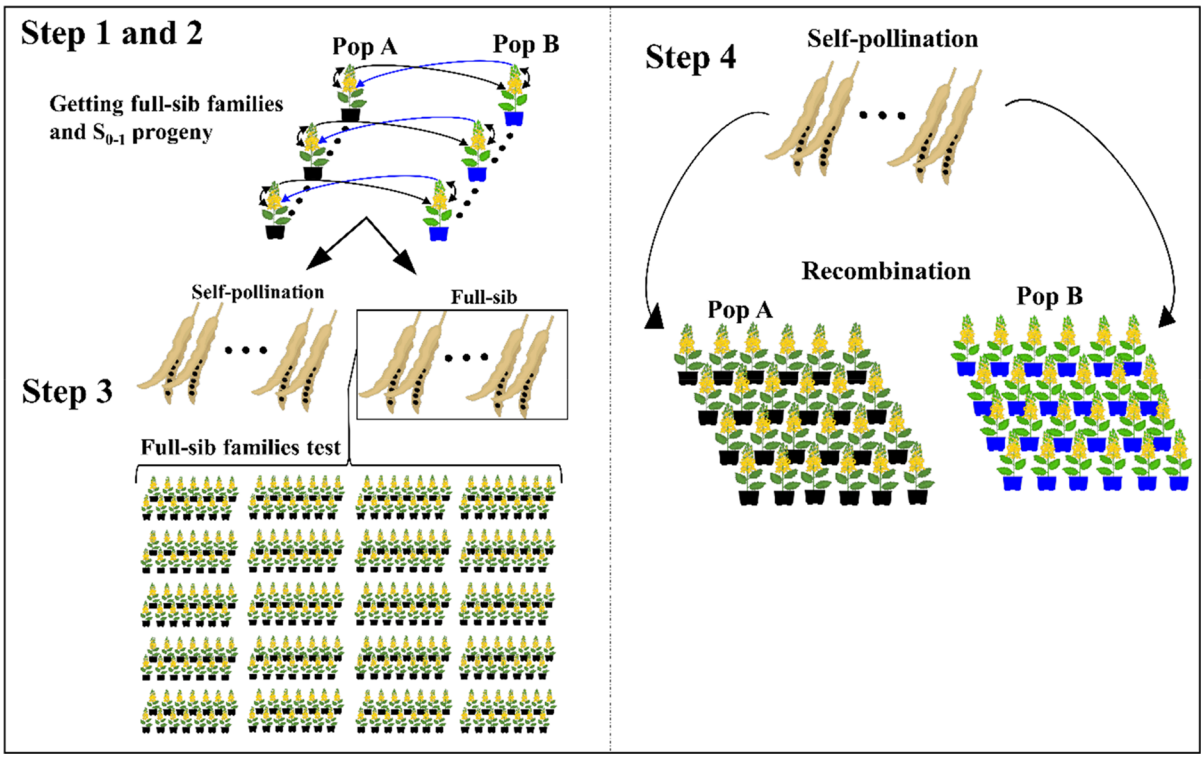


Fig. 7 Diagram of the reciprocal recurrent selection steps in full-sib families applied to *Brassica napus* breeding.

1.5 x 4 m plots. The traits to be evaluated will be based on the traits of interest, along with fatty acid composition, lodging and disease resistance. About 150 (25%) of the rows ($F_{4:5}$ seeds) should be selected from the trials.

Step 3 The 150 rows selected in the third year will be grown in individual rows. Three to five plants per row will be self-pollinated and advanced for the $F_{5:6}$ generation and the rest of the plants in each row will be harvested in bulk. The $F_{5:6}$ seeds from self-pollinated plants will be grown in individual rows and advanced to $F_{6:7}$ generation. The $F_{5:6}$ seeds harvested in bulk will be used for performing the preliminary yield trial to be carried out at three sites in single lattice. Thirty lines (30%) will be selected based on superior performance on the key traits evaluated.

Step 4 The 30 selected lines will be advanced to the next generation. Four to five plants per row should be self-pollinated and harvested individually (generation $F_{7:8}$). The self-pollinated $F_{7:8}$ plants will be advanced to the $F_{8:9}$ generation. An advanced performance trial will be carried out at four to five sites with three replicates. Data on grain yield, oil content, fatty acid composition, flowering, maturity, lodging, cycle and other agronomic traits should be collected. The rows with superior performance will be registered as new cultivars adapted to the region.

Although the canola cycle is short, the use of conventional breeding can take, on average, eight years for cultivar development. In view of the great worldwide expression of canola crop, as well as the advance in biotechnological tools, it is essential to implement techniques that combine speed and efficiency in the development of lines and/or hybrids, such as the use of genomic selection.

Strategies to use genome wide selection into traditional canola breeding

Molecular markers have been used since 80's when the first type of molecular marker called RFLP was developed (Langer and Maixner 2004). After that several types of marker were developed such as RAPD (Grattapaglia and Sederoff 1994), AFLP (Soldati et al. 2013), and SSR (Wenzl et al. 2006). These molecular markers were important to apply the first strategy to

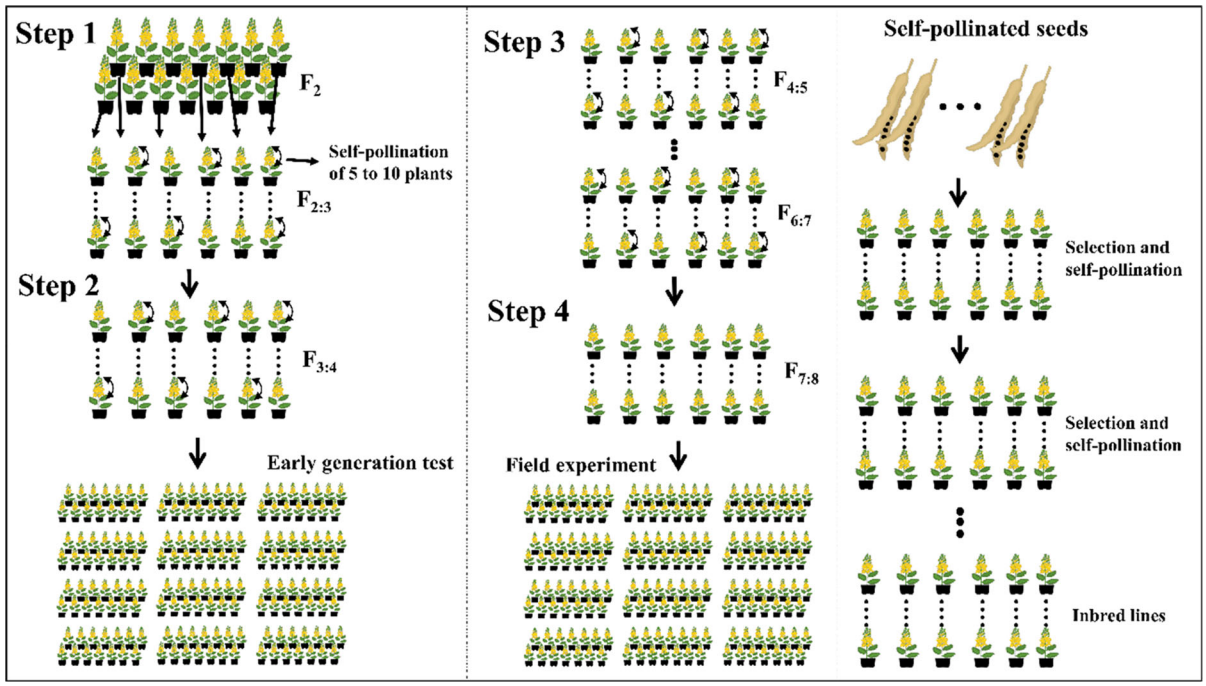


Fig. 8 Diagram of the breeding method steps applied to *Brassica napus* proposed by the authors

use molecular markers in plant breeding named molecular marker assisted selection (MAS) (Ashraf et al. 2012). Several researches were developed applying MAS in canola (Huang et al. 2016; Karim et al. 2016). Despite the importance of this method to select superior plants for traits controlled by few genes, it is not efficient to select plants for quantitative traits (Bernardo and Yu 2007; Arruda et al. 2016).

The advance of molecular markers with the development of SNPs (Baird et al. 2008; Marrano et al. 2017) and DArTs (Von Mark et al. 2013; Sardos et al. 2016) and also the development of many platforms (Poland et al. 2012; Jarquín et al. 2014) has become genome wide selection (GWS) a suitable strategy to increase the gain per time unit in the traditional breeding programs (Heffner et al. 2009; Jannink et al. 2010). The Genome-Wide Selection aims to estimate the genetic estimated breeding value (GEBV) based on markers information (Meuwissen et al. 2001). For the GEBV estimation, two main steps are important: the first step consists in the estimation of the markers effects using the training population (a population which all individuals are phenotyped and genotyped); the second step consists of the GEBV estimation using the validation population (population genotyped but no phenotyped) based on the markers effects estimated in the training population. The Genome-Wide Selection has been successfully used for several crops such as eucalyptus (Denis and Bouvet 2013), soybean (Zhang et al. 2016), jatropha (Peixoto et al. 2017a, b), and maize (Crossa et al. 2010). In addition, there are several researches evaluating the applicability of GWS in canola (Jan et al. 2016; Qian et al. 2014; Wei et al. 2017; Werner et al. 2018; Zou et al. 2019). Therefore, in this section we aimed to show opportunities, challenges and applicability of GWS in canola breeding.

The Genome-Wide Selection can be applied in many steps trough the traditional canola breeding. The strategy to apply GWS depends on the type of population (half-sib family, full-sib family, or endogamy family) or breeding methods (recurrent selection or reciprocal recurrent selection) that the breeder is working.

The application of GWS into a recurrent selection program was reported in maize (Mayor and Bernardo 2009; Massman et al. 2013). Based on these researches five steps are need to apply GWS in a recurrent selection as described below and also can be seen in the Figure 9:

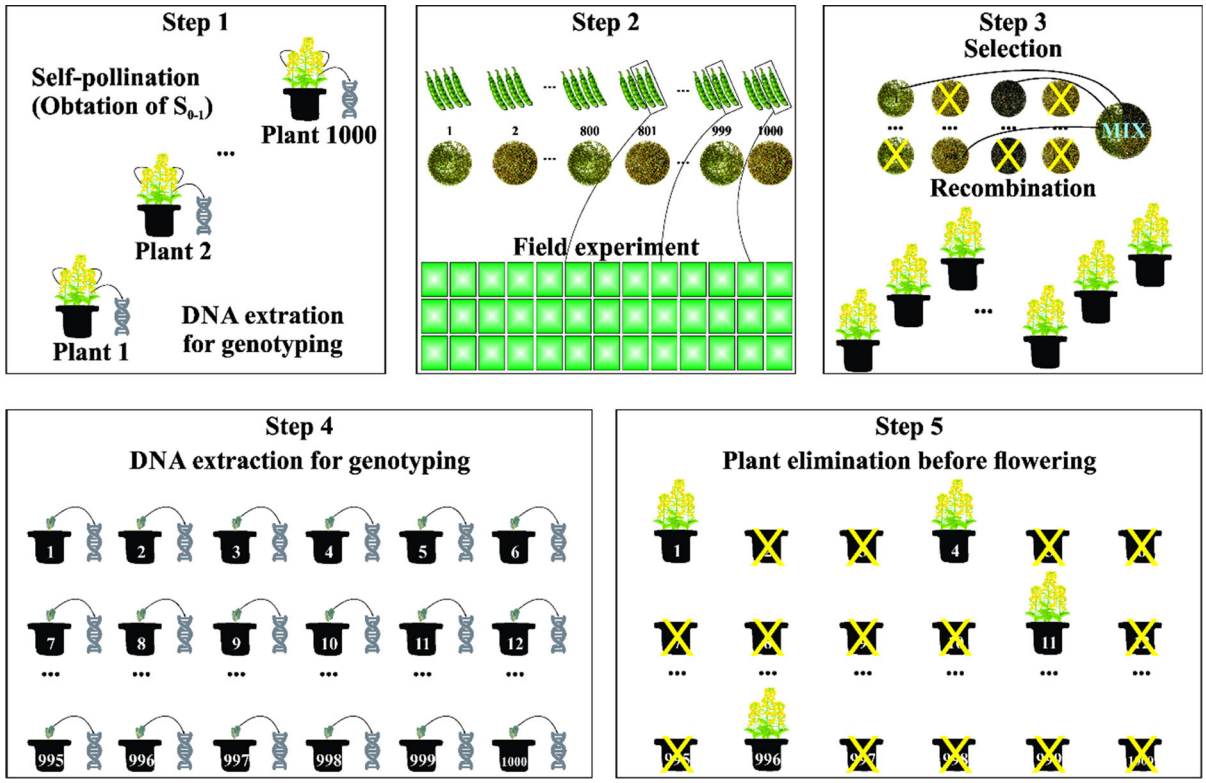


Fig. 9 Scheme of the application of Genome Wide Selection in a canola intrapopulation recurrent selection. Steps 1 through 3 represents one cycle with phenotyping of S_{0-1} progeny. Steps 4 and 5 represents the second cycle without phenotyping, i.e., plants were selected based on their GEBV estimated using the GWS models adjusted in Step 2

Step 1 Seedling of the base population—S_0, which 1000 plants are genotyped. These plants will be self-pollinated, and each plant will be harvested individually generating the S_{0-1} progeny;

Step 2 Two hundreds plants that were genotyped in the first step will be planted and all interested traits will be measured. Part of the seeds of these 200 plants will be stored. The markers effects will be estimated based on the phenotypic traits evaluated over these 200 plants and their genotypes (Training population). After that the GEBV for the 1000 plants will be estimated based on their markers and the markers effects estimated in the training population;

Step 3 Fifty superior plants will be selected based on their GEBV. Seeds from these 50 plants $S_{0:1}$ are mixed and plant together for recombination. Seeds harvested in the recombination area are the improved seeds, finishing the first recurrent selection cycle.

After step 3, all the steps before can be repeated, or alternatively, the model adjusted in step 2 can be used in the follow recurrent selection cycle without recalibration. So the follow cycle has only two steps (step 4 and 5);

Step 4 Correspond on the first step in recurrent selection using the adjusted GWS model. One thousand seeds will be planted and the DNA for each plant will be extracted when the plants are still young (seedling stage), and the GEBV will be estimated using the GWS model adjusted in Step 2;

Step 5 Inferior plants will be eliminated before flowering maintaining 800 superior plants for recombination. These plants will be recombined, and their seeds will be harvested. These seeds are the improved population, and the second recurrent selection is completed.

Genotyping should be done after flowering to make steps 4 and 5 possible. In canola, this is not simple since the cycle is pretty short. One possible solution is to cultivate these plants under controlled environments trying to increase the cycle time (Bassi et al. 2015).

Another strategy that can be used is the reciprocal recurrent selection (Nasim et al. 2014). The reciprocal

recurrent selection strategy can be used on two ways: obtaining half-sib family (Wittenburg et al. 2016) or full-sib family, and GWS can be applied for both strategies. Five steps are need to use GWS in the reciprocal recurrent selection for obtaining half-sib family in canola as described below and also in Figure 10.

Step 1 100 plants are pollinated with pollen from 5 plants from another population (pollen bulk) meanwhile some siliques are self-pollinated. Breeders can use 50% of the siliques to obtain half-sib family and 50% to obtain self-pollinated plants. In addition, 400 plants for each population are just self-pollinated. After that, the 100 plants that were pollinated with the pollen bulk and the 400 self-pollinated plants for each population are genotyped resulting in 1000 genotyped plants;

Step 2 The 100 half-sib families from both population are evaluated in experiments with replicates to measure the phenotypic traits. GWS model is adjusted based on the phenotypic and genotypic information from each half-sib family. Then the GEBV from the 1000 plants can be estimated;

Step 3 Fifty superior plants for each population are selected based on the GEBV. Then, the self-pollinated seeds $S_{0\text{-}1}$ are mixed and planted on the recombination area. Then, seeds are harvested obtaining the improved population and ending the first reciprocal recurrent selection cycle.

After Step 3, all strategy explained from step 1 to 3 can be repeated making the next reciprocal recurrent selection, or the model adjusted in Step 2 can be used to estimated GEBV to next cycle without recalibration. So next cycle has just two steps (Step 4 and 5).

Step 4 Correspond on the first step in the reciprocal recurrent selection using the adjusted GWS model. Five hundred seeds per population are planted and the DNA for each plant is extracted when the plants are still young (seedling stage), and the GEBV is estimated using the GWS model adjusted in Step 2;

Step 5 Inferior plants are eliminated before flowering maintaining 800 superior plants for recombination. These plants are recombined and their seeds are harvested. These seeds are the improved population and the second reciprocal recurrent selection is completed.

Five steps are need to use GWS in the reciprocal recurrent selection for obtaining full-sib family in canola as described below and also in Figure 11.

Step 1 In this step, 200 plants from the first population are relocated in pairs with 200 plants from the second population, which 50% of the siliques are used to obtain the full-sib family and the respective reciprocal, and the other 50% of the siliques are used to obtain self-pollinated seeds. Therefore, each pair will result in full-sib families and self-pollinated families. In addition, 300 plants for each population are self-pollinated. After that, the 200 plants that were pollinated with the pollen from the another population (full-sib family) and the 300 self-pollinated plants for each population are genotyped resulting in 1.000 genotyped plants;

Step 2 The 200 full-sib family are evaluated in experiments with replicates to measure the phenotypic traits. GWS model is adjusted based on the phenotypic and genotypic information from each full-sib family and the GEBV from the 500 plants per population is estimated;

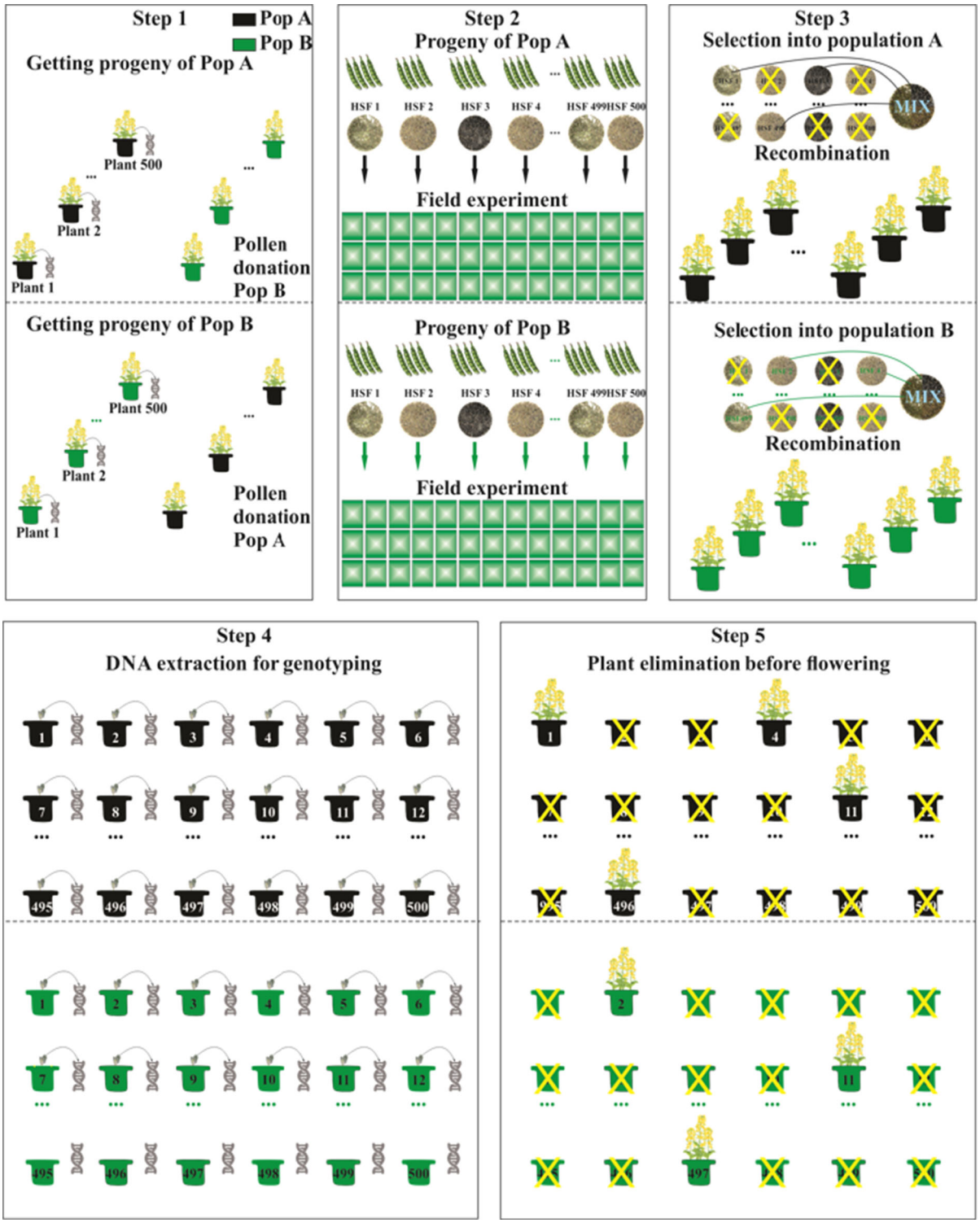
Step 3 Based on the GEBV 400 superior plants for each population are selected. Then, the self-pollinated seeds $S_{0\text{-}1}$ from these selected plants are mixed and planted for recombination. Then, seeds are harvested obtaining the improved population and ending the first reciprocal recurrent selection cycle.

After step 3, all strategy explained from step 1 to 3 can be repeated making the next reciprocal recurrent selection, or the model adjusted in step 2 can be used to estimated GEBV to next cycle without recalibration. So next cycle has just two steps (Step 4 and 5).

Step 4 This step is the first step in the reciprocal recurrent selection using the adjusted GWS model. Fifty seeds per population are planted and the DNA for each plant is extracted when the plants are still young (seedling stage), and the GEBV is estimated using the GWS model adjusted in step 2;

Step 5 Inferior plants are eliminated before flowering maintaining 800 superior plants for recombination. These plants are recombined and their seeds are harvested. These seeds are the improved population and the second reciprocal recurrent selection is completed.

Another strategy that can be used in canola breeding is getting inbred lines. Inbred lines are important to be used for crossings aiming the hybrid formation (Hallauer et al. 2010). Two strategies have been used for obtaining inbred lines: successive self-pollination and the production of doubled haploid.


Step 1
Pop A
Pop B
Getting progeny of Pop A
Plant 500
Plant 2
Plant 1
Pollen donation Pop B
Getting progeny of Pop B
Plant 500
Plant 2
Plant 1
Pollen donation Pop A
Step 2
Progeny of Pop A
HSF 1
HSF 2
HSF 3
HSF 4
HSF 499
HSF 500
Field experiment
Progeny of Pop B
HSF 1
HSF 2
HSF 3
HSF 4
HSF 499
HSF 500
Field experiment
Step 3
Selection into population A
MIX
Recombination
Selection into population B
MIX
Recombination
Step 4
DNA extraction for genotyping
1
2
3
4
5
6
7
8
9
10
11
12
495
496
497
498
499
500
Step 5
Plant elimination before flowering

◀**Fig. 10** Scheme of the application of Genome Wide Selection in a canola reciprocal recurrent selection using half-sib family. Steps 1 through 3 represents one cycle with phenotyping of half-sib families. Steps 4 and 5 represents the second cycle without phenotyping, i.e., plants were selected based on their GEBV estimated using the GWS models adjusted in step 2. Population A is represented by black color meanwhile population B is represented by green color

For obtaining inbred lines based on successive self-pollination in canola the follow steps should be performed and also can be observed in the Figure 12:

Step 1 Part of the seeds from $S_{0\text{-}1}$ progenies selected in the recurrent selection (Figure 10—Step 2) should be planted. Considering that 50 $S_{0\text{-}1}$ progenies were selected 20 individual for each progeny will be planted, and all 1,000 individuals will be genotyped. Based on the GWS model adjusted in the recurrent selection (Figure 10—Step 2), the GEBV of these individuals will be predicted. Fifty superior individuals from each family will be selected based on their GEBVs and they will be self-pollinated to obtain the $S_{1\text{-}2}$ progenies;

Step 2 Five individuals for each progeny will be selected randomly and self-pollinated to generate 50 $S_{1\text{-}3}$ progenies;

Step 3 Some individuals from the 50 subpopulations $S_{1\text{-}3}$ will be testing in field experiments with testers. Testers can be an open pollinated population from another heterotic group which individuals will be selected based on their general combining ability (GCA) with the testers. Researchers have reported that the correlation between GCA in S_3 and GCA in S7 is high, and therefore the evaluation using testers can be done in S_3 (Bernardo 1991; Souza 2011). Four individuals per subpopulation will be used for crossing with testers generating 200 half-sib families. One thousand individuals will be genotyped (20 per subpopulation) including individuals crossed with the testers. All genotyped individuals will be also self-pollinated generating 1,000 $S_{3\text{-}4}$ progenies;

Step 4 Two hundred half-sib families will be evaluated in field experiments and 1,000 $S_{3\text{-}4}$ progenies will be stored. Then, GWS model will be adjusted based on the phenotypic data from the half-sib families. Subsequently, GEBV will be predicted for all genotyped individuals;

Step 5 Twenty superior individuals will be selected based on their GEBV and their $S_{3\text{-}4}$ progenies will be planted in rows. All plants will be self-pollinated and seeds within each line will be harvested in bulk generating 20 subpopulation $S_{3\text{-}5}$;

Step 6 Twenty subpopulations will be planted in rows. All plants will be self-pollinated and seeds within each line will be harvested in bulk generating 20 subpopulation $S_{3\text{-}6}$;

Step 7 Twenty subpopulations will be planted in rows. All plants will be self-pollinated and seeds within each line will be harvested in bulk generating 20 subpopulation $S_{3\text{-}7}$;

It is necessary to obtain the maximum number of seeds over the self-pollination steps (Step 5 through 7) because the selected plants will be evaluated in several locations.

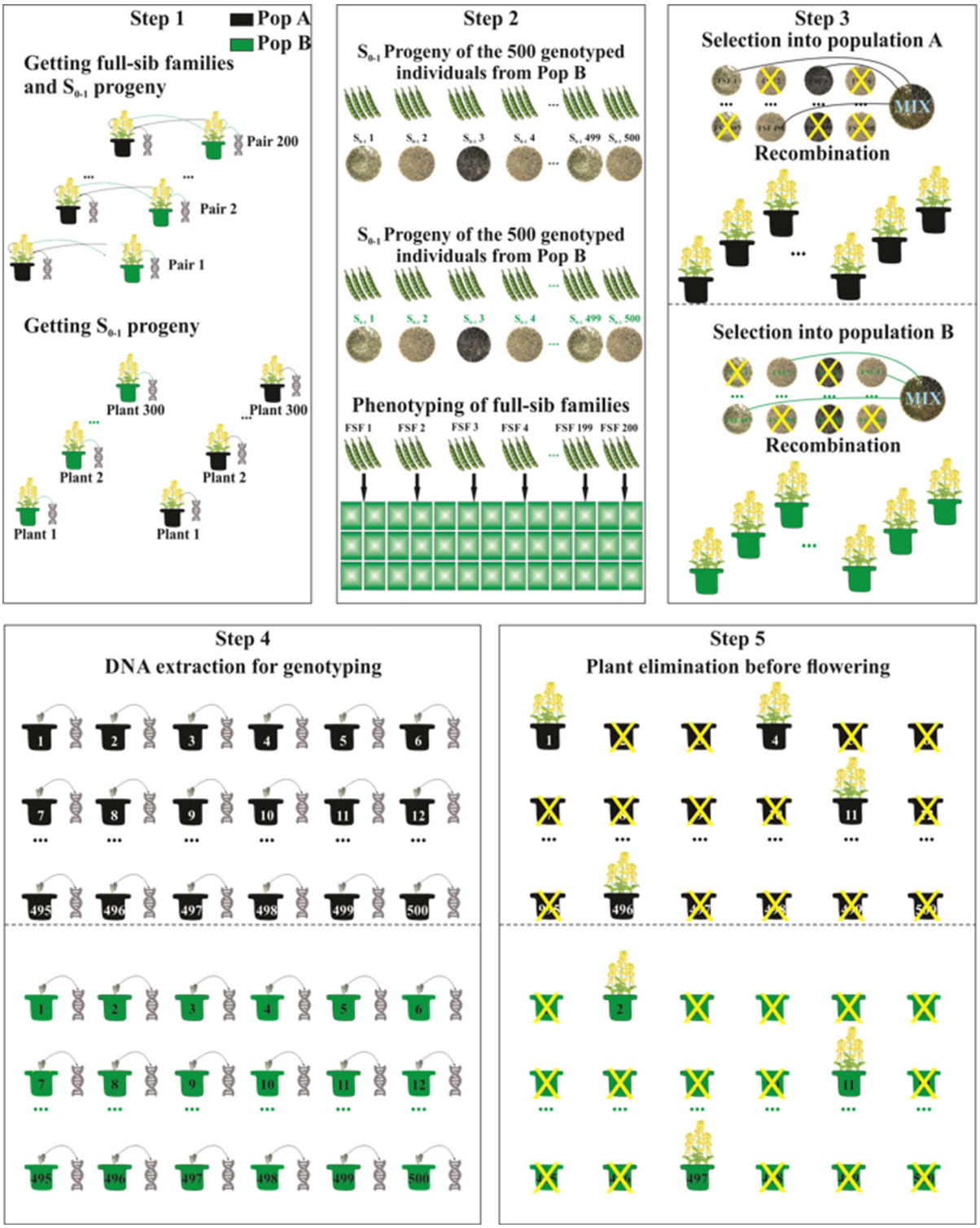
Doubled haploids is an important strategy to obtain inbred lines faster in canola (Fritsche-Neto et al. 2012). GWS can be used to select superior individuals to produce the doubled haploids and also to select superior doubled-haploids (Bernardo and Yu 2007). Therefore, four steps are used to obtain doubled haploids as described below and in Figure 13:

Step 1 Part of the seeds from $S_{0\text{-}1}$ progenies selected in the recurrent selection (Figure 10—Step 2) should be planted. Considering that 50 $S_{0\text{-}1}$ progenies were selected 20 individuals for each progeny will be genotyped, i.e., 1000 individuals will be genotyped. All these plants will be self-pollinated. Based on the GWS model adjusted in the recurrent selection (Figure 10—Step 2) the GEBV of these individuals will be predicted and the 50 superior plants will be selected;

Step 2 $S_{1\text{-}2}$ progeny from the 50 selected plants will be used for producing the doubled haploid which will be genotyped and multiplied for posterior phenotypic evaluation;

Step 3 Two hundred doubled haploids (4 seeds per $S_{1\text{-}2}$ progeny) will be crossed with a tester. The tester can be an open pollinated population, a variety, or a breeding population. All the 1,000 doubled haploids from $S_{1\text{-}2}$ progeny (20 seeds per progeny) will be self-pollinated and genotyped;

Step 4 Self-pollinated seeds will be stored meanwhile the 200 half-sib families will be evaluated in the field experiment and these families will be phenotyped for the important traits. Then, the GWS model will be adjusted based on the phenotypic values from these half-sib families and their genotypes. After that the GEBV for all doubled-haploids will be estimated and


Step 1
Pop A
Pop B
Getting full-sib families and S0-1 progeny
Pair 200
Pair 2
Pair 1
Getting S0-1 progeny
Plant 300
Plant 300
Plant 2
Plant 2
Plant 1
Plant 1
Step 2
S0-1 Progeny of the 500 genotyped individuals from Pop B
S0-1 Progeny of the 500 genotyped individuals from Pop B
Phenotyping of full-sib families
FSF 1
FSF 2
FSF 3
FSF 4
FSF 199
FSF 200
Step 3
Selection into population A
MIX
Recombination
Selection into population B
MIX
Recombination
Step 4
DNA extraction for genotyping
Step 5
Plant elimination before flowering

◀**Fig. 11** Scheme of the application of Genome Wide Selection in a canola reciprocal recurrent selection using full-sib family. Steps 1 through 3 represents one cycle with phenotyping of full-sib families. Steps 4 and 5 represents the second cycle without phenotyping, i.e., plants were selected based on their GEBV estimated using the GWS models adjusted in step 2. Population A is represented by black color meanwhile population B is represented by green color

the 20 superior doubled-haploids will be selected based on their GEBV.

Several strategies for the application of GWS in a canola breeding were discussed. However the success of the GWS strategy depends on several factors such as training population size (Asoro et al. 2011), number of markers (Peixoto et al. 2016), number of QTLs

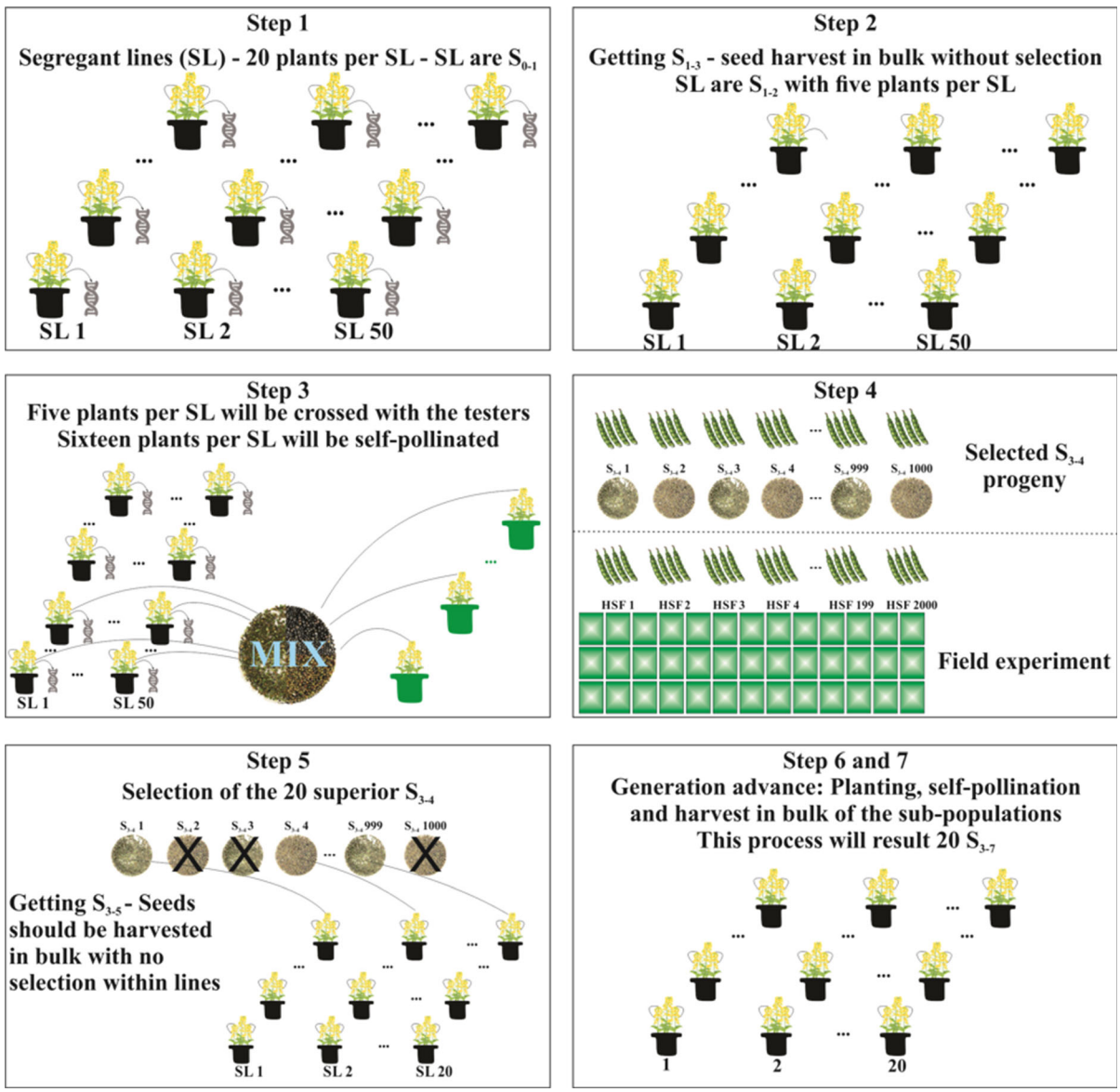


Fig. 12 Scheme of the application of Genome Wide Selection in a canola breeding for obtaining pure lines by successive self-pollination. This scheme initialized with the selection of 50 S_{0-1} progenies selected in one recurrent selection cycle

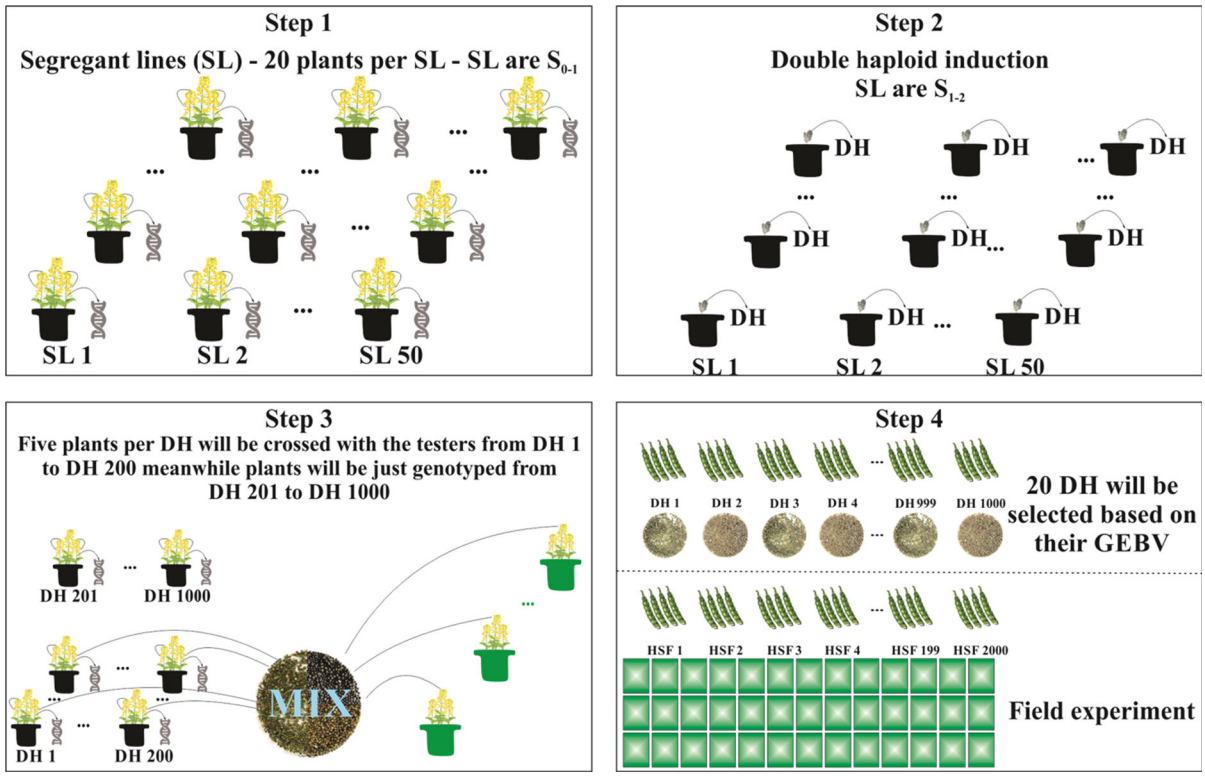


Fig. 13 Scheme of the application of Genome Wide Selection in a canola breeding for obtaining pure lines by doubled haploids. This scheme initialized with the selection of 50 S_{0-1} progenies selected in one recurrent selection cycle

(Grattapaglia and Resende 2011), heritability (Resende et al. 2012), population structure (Collard et al. 2015) and statistic model (Bhering et al. 2015).

The number of QTL that affects a quantitative trait has influence on the prediction accuracy mainly due to it influences on the right choice of the statistics method, which some methods have better performance for traits controlled by few QTLs with large effects meanwhile others have better performance when the trait is affected for several QTLs with small effect (Daetwyler et al. 2013). According to Zhong, Dekkers (Shengqiang et al. 2009) the prediction accuracy seems like to be inversely proportional on the number of QTLs. In general, Bayesian methods are better to estimated traits controlled by few QTLs with large effect while mixed models methods are better to estimate traits affected by several QTLs with small effects (Meuwissen et al. 2001; Shengqiang et al. 2009; Daetwyler et al. 2013).

Heritability is one of the most important effects that affects GWS analysis and its interaction with other effects such as the number of QTLs should be evaluated since this interaction can influence the GWS method and consequently the prediction accuracy (Peixoto et al. 2016). Despite the heritability can be not controlled by the breeder the use of replications can improve the heritability and it can also increase the prediction accuracy estimated by GWS methods (Crossa et al. 2010). In addition, heritability has a large influence on training population size since they have negative correlation, which if heritability is low training population should be larger while if heritability is big training population should be smaller (Daetwyler et al. 2013).

Simulations studies have demonstrated that small training population are not capable to estimate the GEBV with a suitable prediction accuracy when the heritability is low (smaller than 0.7) or the traits is controlled by several QTLs (Resende 2008; Peixoto et al. 2016). It probably happens because the allelic effects amplitude is not suitable in this condition, and the effects of the QTLs may be not being very well estimated (Grattapaglia and Resende 2011; Peixoto et al. 2017b).

The number of markers should be large for training the GWS model since at least one marker should be in disequilibrium linkage with the QTL (Heffner et al. 2009; Erbe et al. 2013; Ren et al. 2015). However, several researches have demonstrated that the use of few specific markers can be better that the use of a large number of markers (Habier et al. 2009; Wellmann et al. 2013; Peixoto et al. 2016; Sollero et al. 2017). Moreover GWS models fitted with the known QTL as fixed effect and other markers as random effect present a higher accuracy than GWS models with all markers fitted as random effect (Bernardo 2014; Collard et al. 2015; Arruda et al. 2016).

Population structure is positive correlated with the number of individuals in the training population. Populations with no structure requires more individuals for training the GWS model meanwhile structured population requires less individuals (Collard et al. 2015).

Several GWS methods have been described and usually they are divided in two groups: frequentist methods represented by RRBLUP (Endelman 2011), GBLUP (Daetwyler et al. 2010), PLS (Solberg et al. 2009) and LASSO (Azevedo et al. 2015), and Bayesian methods represented by Bayes A (Peixoto et al. 2017b), Bayes B (Guo et al. 2012), Bayes Cπ (Desta and Ortiz 2014), Bayesian LASSO (Bhering et al. 2015), and Reproducing Kinship Hilbert Space Regression (RKHS) (Heslot et al. 2012).

Therefore, GWS is a suitable tool to help breeders to improve the efficiency selection in a canola breeding program increasing the selection accuracy or even reducing the cycle time. In addition, before the application of GWS in the canola breeding the breeders should evaluated all factors explained in this paper to fit GWS model that can get the highest selection accuracy.

Conclusions

We demonstrate the main breeding strategies that can be used to increase your oil production. We propose here a breeding strategy for canola, in which some strategies previously mentioned are integrated. The purpose of this strategy is to enhance the selection and efficiency at the beginning of a breeding program. Among these, genome wide selection (GWS) is a suitable tool to help breeders to improve the efficiency selection in a canola breeding program increasing the selection accuracy or even reducing the cycle time. In addition, all factors explained in this paper should be evaluated before the application of GWS in the canola breeding seeking to fit GWS model that can get the highest selection accuracy.

Availability of data and material The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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