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SUNFLOWER: SOME EXAMPLES OF CURRENT RESEARCH TOURNESOL : EXEMPLES DE TRAVAUX DE RECHERCHE

Changes in sunflower breeding over the last fifty years

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Abstract – This article discusses changes in sunflower breeding objectives since the introduction of hybrid varieties 50 years ago. After a reminder of the importance of some early programmes, Canadian in particular, the present situation for each breeding objective is compared with those encountered earlier. Breeding for yield has changed from maximum possible yield under intensive agriculture to yield with resistance to abiotic stresses, moderate droughts and shallow soils in particular, helped by collaboration with agronomists to produce crop models. Breeding for oil has changed from quantity to quality and the value of seed meal is again becoming economically important. Necessary disease resistances vary with agronomic practises and selection pressure on pathogens according to varietal genetics. The possibilities of new types of sunflower are also discussed. Advances in genomics will change breeding procedures, but with rapidly changing molecular techniques, international collaboration is particularly important.

Keywords: Hybrid / yield / oil / disease resistance / genomics

Résumé – **Sélection du tournesol : tour d’horizon de 50 années d’évolution.** Cet article discute des changements intervenus dans les objectifs de sélection du tournesol depuis l’introduction des variétés hybrides, il y a 50 ans. Après un rappel des premiers programmes, le canadien en particulier, la situation actuelle pour chaque objectif est comparée à celle rencontrée 50 ans auparavant. L’objectif de la sélection pour le rendement en grain ne vise plus en priorité un rendement maximum en conditions d’agriculture intensive mais un rendement maintenu sous stress abiotiques, sécheresses modérées ou sols peu profonds. Cette sélection est maintenant aidée par la collaboration avec des spécialistes en modélisation agronomique. La sélection relative à l’huile concerne maintenant plus souvent des qualités spécifiques que la teneur de la graine, tandis que le tourteau redevient de valeur économique significative. Les résistances aux maladies nécessaires pour les variétés actuelles varient selon les pratiques agricoles et les génétiques prépondérantes. La possibilité de changer radicalement d’architecture ou de cycle de culture est discutée. Les avances en génomiques vont modifier les procédures de sélection, mais une bonne collaboration internationale s’avère très importante vu les changements rapides dans les techniques moléculaires.

Mots clés : Hybride / rendement / huile / résistance aux maladies / génomique

1 Introduction and History

Breeding programmes and genetic research with the aim of developing hybrid sunflower varieties started about 50 years ago. Before discussing the present situation, I think it is worth looking back on where sunflower breeding came from.

With the requirement for field, laboratory and computing studies, the development of a new sunflower genotype is, at present, a large team effort. This is in contrast with the past, when a few small teams developed programmes on which modern sunflower are based. The work of Pustovoit at VNIIMK in Russia to develop high yielding, open pollinated

varieties (OPV) with oil contents of up to 50%, is well recognised as the main genetic base of modern sunflower breeding. For production of hybrids, the same is true for the cytoplasmic male sterility discovered by P. Leclercq at INRA in France in a cross between *Helianthus petiolaris* and cultivated sunflower (Leclercq, 1969) and its restoration from the same source and from wild *H. annuus* by Kinman at USDA, USA (Kinman, 1970).

Less well recognised is the importance of Canadian work and yet it was probably as important as that of the first three programmes. In 1944, Unrau and White were the first to publish the idea of hybrid varieties of sunflower, studies continued by the team led by Putt at Morden Manitoba, but they

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lacked a satisfactory system of male sterility for large scale production. However, the line S37.388RR (a selection from Mennonite material), crossed with the variety Sunrise gave the “hybrid” Advent, in which the first resistance to downy mildew (*Pl1*) was identified by Vranceanu and Stoenescu (1966) at IC-CPT, Rumania. In progenies from natural crosses of Canadian breeding material with wild *Helianthus annuus*, in winter generations grown in Texas, the team at Morden, Manitoba obtained rust and *Verticillium* resistance (Putt, 1964a) and they developed lines known as 953.88 and 953.102. These were provided to M.Kinman, who crossed 953.102 with a CMS form of a French line selected from the Russian population Cernianka (PI343765) and led to his discovery of the restorer gene *Rf1* (Kinman, 1970). The first USDA “RHA” lines came from the cross (Peredovik × 953.102), while (953.88 × Armavir3497) gave HA61, the source of recessive branching (Putt, 1964b), the *Pl2* downy mildew resistance gene and a high level of *Sclerotinia* resistance (see details at <http://www.ag.ndsu.nodak.edu/aginfo/seedstock/varieties>). In addition, Putt and his colleagues bred lines from Russian open pollinated varieties (OPV); one of them was CM303 (CM: Canada-Morden). This line was considered as late for Canada, but a selection from it was released by USDA as HA89 in 1971. When P. Leclercq received CM303 from Morden, the letter said “CM303, which the Americans call HA89”. The Agriculture Canada team did not have the means to make the most of their discoveries but they certainly should not be forgotten.

In the period 1970–1985, once CMS and restoration were available (freely with no patents), commercial breeding started on a large scale in all the countries where sunflowers could be grown. At first, increases in yield were small compared with OPV, but hybrids were more uniform, making harvesting easier for farmers and breeders could more easily produce varieties adapted to particular conditions using different combinations of inbred lines. As a new crop, public research (especially USDA, USA; INRA, France; CSIC/INIA, Spain and INTA, Argentina) continued to provide part of the breeding effort, together with more basic research, and in return, private companies provided both some financial support and carried out some of the field work, in particular hybrid trials. This public – private collaboration is now widespread in genetic and plant breeding research but the sunflower industry was among the pioneers for such organisation. In France, the association “Promosol” was formed in 1975, between INRA, CETIOM (now Terres-Inovia), the technical research institute, and all French sunflower breeders and, in spite of many changes, it continues as such today.

In Eastern Europe, breeders (all in the public sector) had for long been interested in sunflower since it was one of their major crops. Being used to OPV, they changed to hybrid varieties more slowly than in Western Europe. However, once started, they were very successful; varieties from Hungary, Rumania, Serbia and Bulgaria were widely grown all over Europe in the period 1980–2000. In contrast, at VNIIMK in Russia, the home of OPV, the change did not come for many years, improved OPV were bred and, although these continued to be grown in the ex –Soviet Union, Krasnodar was no longer the source of world sunflowers.

Around 1990, politics led to change. From 1992, in Western Europe, farmers were no longer supported according to their production but to their acreage and sunflowers were moved from the best, irrigated land to areas with less fertile conditions. There was less profit from sunflower seed sales and the objectives of breeding programmes had to change. In France, in 1992, there were about 22 companies breeding sunflower (and participating in Promosol); by 2005 there were only six. In Eastern Europe, including Russia, with the end of communism, funds available to public research were considerably reduced and institutes had to be commercially successful to be able to survive and carry out research, with the IFVC, at Novi-Sad in Serbia, probably being the best example. In USA and Argentina, change came from the development of GMO maize and soybean. Highly profitable, these crops pushed sunflower to the drier poorer land, similar to the changes in Western Europe.

So, at present, there is a rather odd situation: sunflowers are still grown on good land in Eastern Europe, Ukraine and Russia but, with a few notable exceptions, the research effort is reduced. In contrast, Western Europe, USA and Argentina, where sunflowers are often considered as a not very profitable crop, concentrate the main research and breeding programmes. However, perhaps this is a good logic for the future in a changing climate and environmental situation, with need for reduced use of pesticides, fertilizers and irrigation. The sunflower crop that farmers expect to sow and harvest with little work between, adaptation to soil, climate and pests being expected to come from genetics, should have a promising future and confirm its use as an a symbol of ecology in agriculture.

2 Breeding objectives

What is going on at present, compared with the work of the pioneer teams? Vincourt provided an extensive update on present breeding and research projects quite recently (Vincourt, 2014). Here, I will try to discuss changes over the last 50 years concerning the main breeding objectives and international collaboration.

The majority of breeding objectives change only slowly but a few change rapidly, because of a new requirement, a new product quality, a new resistance to disease or a change in the economic situation of the crop or because new techniques make possible studies that could not be undertaken in the past. In recent years, there have been many changes in research techniques, in particular, the possibility of determining the genotype of a plant and not just its phenotype. There have also been changes in agricultural practices, due to economic or environmental factors.

2.1 Seed yield

As with most crop species, sunflower seed yield has nearly always been a main subject of research, except for a short period in 1980–1990, when there was considered to be general agricultural overproduction in Western Europe. At that time, research projects to increase yield were badly looked on, acceptable projects concerned only yield regularity. Farm yields

in central France reached 4 t/ha and Skoric *et al.* (2007) suggested that it would be possible to obtain 6t/ha. However, after the change in Common Agricultural Policy in the EU in 1992, there was question as to whether recent sunflower varieties showed any genetic gain over old varieties. Large scale trials of varieties ranging from Peredovik to the most recently registered hybrids in France in 2001, and more recent analyses, showed that potential yield of the leading varieties was at least 150% that of Peredovik and the other varieties grown in 1960–70 (Salvi and Pouzet, 2010; Vear and Muller, 2011). However, mean yields in France have rarely exceeded 2.5 t/ha and now that sunflowers are grown without irrigation, there has been little change in mean yield (2015: 2.1 t/ha). So the need is for genotypes which maintain good yields in stressed conditions.

This is one objective that has become easier to study using new techniques, in particular genomics and crop models. In the past, drought resistance was difficult to measure; when comparisons were made for yield under dry conditions/yield under irrigation, it was very often the hybrids with the lowest yields under irrigation which had the best ratio. Now, response to such abiotic stress is the principal objective of the French “Investments for the future” research programme “Sunrise”, running from 2012–2019 (<http://www.sunrise-project.fr/en/project/presentation>). It has already been possible to identify markers and genes active under stressed conditions (Marchand *et al.*, 2013). In other collaborative programmes, markers have been found for good yield under dry conditions, but since this is a most competitive aspect of sunflower breeding, results remain largely confidential.

Helianthus argophyllus, which grows in semi-desert conditions in Texas and Florida, and is quite easy to cross with cultivated sunflower, has long been suggested as a source of drought resistance. The genome of this species has been partially sequenced (http://compgenomics.ucdavis.edu/compositae_data.php?name=Helianthus+argophyllus) so, after interspecific crosses, it should now be possible to determine whether introgression from this source can provide genes that are of interest in maintaining good yields under stressed agricultural conditions, rather than just survival in the desert.

One of the most interesting aspects of research on yield at present is the renewed collaboration between agronomists and breeders and geneticists. In spite of all the laboratory work on DNA, field observations have increased with automatised measurements and the possibility of aerial photography using drones. Agronomic models can now take account of environmental conditions, and plant architecture in the field to define the best environments for field trials and to predict yields of hybrid combinations according to environmental conditions (Casadebaig *et al.*, 2015). It remains to be seen whether the varieties produced to yield well in stressed conditions will also perform well in deep soils with sufficient water available.

2.2 Oil content

Since the work of Pustovoit, high seed oil content has always been a breeding objective (at least for oilseed sunflower, for confectionary, a low oil content is required). Up to about 1970, it was necessary to press seed to determine oil content,

but with the development of very rapid, non-destructive measurement by NMR, oil content, which is highly heritable, has become one of the easiest characters for the breeder. Modern varieties show 50% oil regularly under good field conditions. The maximum possible is probably about 60%, but this may be too high to obtain the best combinations with other characters. Oil requires more energy per gramme produced than cellulose so that the highest yielding genotypes often do not have very high oil contents. At least one QTL has been identified on a wide range of material (Merah *et al.*, 2011; unpublished results) so it might one-day be possible to introduce the genes involved into very high yielding genotypes, but whether the result would be a strict sum of yield and oil production would need to be checked.

2.3 Protein content and hullability

The other question concerning seed quality is the importance given to seed protein content, since there is generally a negative correlation between oil and protein contents. This question was studied in the period 1970–1980, especially by the Bulgarian team at General Toshevo, but the economic importance of sunflower seed meal varied considerably according to the price of soybean meal so oil content was of more direct economic interest to farmers and organisations collecting the sunflower harvest. Up to about 1970, before NMR, when only small quantities of seed were available, the character used to breed for high oil content was % kernel in whole seed, which had the advantage of reducing hull content and not affecting the oil/protein ratio. The question of protein content recurs regularly but little research on its genetics has been carried out recently. The possible variation in cultivated sunflowers, independent of oil content is not well known but this topic may become of importance (Dauget *et al.*, 2016).

The alternative method to increase the protein content in seed meal is to hull seed. A European project (France, Spain, and Italy) was devoted to this subject in the 1990s. Techniques were developed to measure hullability on small quantities of seed, environmental conditions were found to be important, but there was moderate heritability although genotypes with thick hulls were the most easily hulled (Denis *et al.*, 1994). However, when the programme was completed, the price of soybean meal fell and, at least in Europe, crushers had no incentive to hull seed before oil extraction.

Recently, there is renewed interest in Europe, since hulled sunflower meal would be good alternative protein source to replace imported soybean and hulls are now an economic fuel (Dauget *et al.*, 2015). However, the question of whether hullability will become a necessary breeding objective has not yet been answered.

2.4 Fatty acids

A further important quality character for sunflowers (and other oil crops) is the proportion of the different fatty acids in oil. The high oleic mutation obtained by Soldatov (1978) was one of the first artificial mutations to have a favourable effect

(although negative in its action since it blocked enzymatic conversion to linoleic acid) and to be incorporated into a widely grown crop. Since few genes are involved, they are now known and marker assisted selection is widely used to obtain oleic versions of successful varieties. It remains to be seen whether other specialist types of oil could be economically successful.

2.5 Minor constituents

Concerning minor constituents of sunflower seed which could be of interest, such as tocopherols and phytosterols, the question is whether varieties with increased contents would provide a significant increased value, for compounds that only represent about 0.03% of sunflower seed weight. Genetic studies have shown differences within cultivated sunflower, with identification of QTL (Merah *et al.*, 2011), and since the enzyme pathway for sterols is known, the genes involved could probably be identified quite quickly. Would it be worthwhile to introduce the best alleles into modern sunflower varieties?

3 Pest and disease resistance

3.1 Downy mildew

This disease, caused by the oomycete *Plasmopara halstedii*, has been known for more than 50 years in Canada and Russia (Sackston, 1949). It was probably introduced into Western Europe in seed of Russian OPV. The first races identified in the USA and in Europe were different (races 300 and 100 respectively), but we do not have an explanation of how this may have come about. In Soviet Russia in the period 1960–1980, long rotations were practised so downy mildew was not too much of a problem. In Europe, breeding programmes led to all widely grown varieties carrying the resistance genes *P11* and *P12* and there followed almost 20 years (until 1988) with no problem from this disease. However in the USA, problems appeared more quickly, with new races from 1980 (Gulya *et al.*, 1991), which could be considered to be logical co-evolution. Chemical control (by metalaxyl seed treatment) was only of very temporary use, the parasite soon showed resistance (Albourie *et al.*, 1998). Since 2000, many new races have appeared, probably as a result of natural selection pressure when most varieties contain the same major resistance genes (see review of the present race situation by Viranyi *et al.*, 2015). The search for new genes has been successful but some have been overcome quite quickly (Tourvieille de Labrouhe 2003; Bertero de Romano, personal communication). In the period 2004–2010, studies of quantitative resistance were made, in the hope that it would be less race-specific. Genetic differences were observed and a few QTL identified from field observations but no laboratory test is yet quite satisfactory (Mestries *et al.*, 2016). It is perhaps illusory to expect that such a test is possible when all other quantitative resistances in sunflower are still measured in field trials. Until a satisfactory method, in laboratory or field, is developed, major genes will continue to be the basis in breeding for downy mildew resistance. Wild *Helianthus annuus* appears

to be a good source of genes, several new ones have been identified recently (Qi *et al.*, 2015, 2016; Vear *et al.*, 2008). In the last publication, the authors made the interesting remark that many ecotypes with downy mildew resistance come from dry or desert areas (Texas) where no downy mildew is observed. If there has not been co-evolution, could there be some other selective advantage linked to downy mildew resistance genes? Concerning breeding for downy mildew resistance, I think it is most important to emphasise the need to maximise the diversity of genes in widely cultivated varieties to reduce selection pressure on *P. halstedii*.

3.2 Broomrape

Orobanche cumana is the other parasite of sunflower for which major resistance genes are the main control method. This is unusual and not known for most *Orobanche*/crop interactions. *O. cumana* was probably adaptation of an *Orobanche* parasite on other species onto sunflower, since it is not observed in North America and appeared first around the Black Sea, followed by appearance in Spain in 1958, becoming important in the 1970s (Moliner-Ruiz and Domínguez, 2014). With considerable importation of sunflower seed from Spain to France, for many years we wondered why there was no broomrape in France, it has only appeared since 2010. Climatic change may be involved, since higher temperatures and absence of rainfall favour broomrape development. Research problems are different from those for downy mildew, where apparently homogeneous races were obtained very quickly, since broomrape appears to exist in the field as populations, heterogeneous for their virulence patterns. In recent years, there has been considerable international cooperation in Europe (for example the 3rd ISA symposium on Broomrape held at Cordoba, Spain in 2014) but there is still no satisfactory identification of the pathotypes of some new broomrape isolates. However, knowledge should progress very quickly, making use of recent techniques. Highly homozygous lines and segregating populations of *O. cumana* have now been produced, at CSIC in Spain in particular. Several QTL/resistance genes have been mapped (Fernandez-Martinez *et al.*, 2010) and the *Orobanche* genome is being sequenced by INRA in a France-Spain collaborative project. So, it should soon become clearer what resistance genes are necessary in sunflower varieties. Resistance sources have so far been cultivated sunflower or other annual *Helianthus* species (Velasco *et al.*, 2011) In contrast with downy mildew, where introduction of resistances from wild *H. annuus* is relatively easy, if broomrape resistance requires interspecific crosses, the procedure for introduction of genes from such origins will require new research. More general knowledge of how best to make the most of the 50 *Helianthus* species which exist would be of great benefit to research on many breeding objectives.

3.3 Phomopsis

Phomopsis stem canker (*Diaporthe helianthi*) is the example for sunflower of a recent adaptation of the parasite to this crop. First observed in Serbia in 1980

(Mihaljčević *et al.*, 1980), it can be compared with broomrape in that this disease is most important in Europe and has only recently become a problem in North America (Mathew *et al.*, 2015). Perhaps, for both phomopsis and broomrape, the fact that Southern Russia and Eastern Europe was the first and largest area of cultivated sunflower meant that there was a selective advantage to be able to infect this crop on a large scale. Quantitative but quite strong resistances to phomopsis were soon identified, in Serbia (Mihaljčević *et al.*, 1982) and then in France (Viguie *et al.*, 2000) and, although phomopsis resistance is still an essential part of sunflower breeding programmes, the disease can be said to be under control. QTL have been identified (Bert *et al.*, 2002) but since disease reactions vary significantly with climatic conditions, even if markers are obtained within resistance genes, it is questionable whether it would be possible to rely only on laboratory work in breeding for resistance.

3.4 Sclerotinia

Sclerotinia wilt or rot is one of the most widespread disease problems for sunflower, a problem for breeders since the start of the crop. *Sclerotinia sclerotiorum* can attack all crops except grasses and cereals and no complete resistance is known in sunflower. Considerable work on quantitative resistance has been carried out, in particular in France and Argentina concerning head rot (Fusari *et al.*, 2012; Vear and Grezes-Besset, 2010) and in the USA concerning stalk or root rot (Talukder *et al.*, 2014). Many QTL have been identified, on almost all linkage groups, so that marker-assisted selection would be quite difficult. In recent years *Sclerotinia* has not caused much yield loss as a whole. This may be due to the movement of the sunflower crop to dryer conditions and, with climate change, it might even be suggested that this disease will not be a major problem in the future. However, on the other hand, the areas like Central France where yields are best and it would be good to see more sunflower acreage, have more humid climates and thus more risk of *Sclerotinia* attack. Good resistance to this disease must thus remain an objective in sunflower breeding. Probably the best source would be perennial *Helianthus* spp. As for broomrape resistance, there is a real need for research on interspecific introgression methods maximising the possibilities offered by genomic studies and available to the sunflower community.

3.5 Other diseases

The other main disease problems for sunflower vary according to country or region and also with crop practises and the genetic origins of varieties grown. In France, when breeding started, *Botrytis cinerea* head rot was the main problem, but this disease has almost disappeared since about 1990. This could be because sunflowers are harvested earlier, before the onset of autumn rains (when they occur!) or because of a change in varietal genotype. (Was Peredovik particularly susceptible to grey rot?) Also in France, *Phoma macdonaldii* (*Leptosphaeria lindquistii*) became of economic importance in south west France around 2000, when farmers stopped ploughing, to reduce costs and limit soil erosion. Genetic and agronomic studies showed that although there are

significant differences in susceptibility between genotypes, control would be easiest by agronomic factors and cultivation methods (Sessau *et al.*, 2010). *Verticillium dahliae* and *Alternaria helianthi* have been known for a long time, in France of importance in the 1970s and 1980s and again at present. In Argentina, they have been studied for a long time, and both major genes and quantitative resistances have been proposed (Bertero and Vazquez, 1983; Kong *et al.*, 2004). Rust resistance was studied by Sackston in Canada in the 1960s, at present this disease occurs in the USA and in semitropical climates, where breeding efforts are necessary. A more general interesting point about rust resistance genes is that they are very often found linked to downy mildew resistance genes. It remains to be seen whether there are common genes active in the defence reactions.

It may be the genetics of widely grown varieties that determine the importance of these parasites but it is often difficult to judge the relative importance resistance to these diseases should be given in future breeding programmes.

3.6 Insects (including bees)

This subject can be divided into two: resistance to insect pests and attractivity to bees and other pollinating insects. Fortunately for most of the world, the first subject only really concerns the USA. It is to be hoped that it will remain that way. For those interested, the review by Prasifka (2015) should be consulted. In Europe, aphids can infect sunflowers and there are quite distinct differences in attractivity between varieties but since no important viruses are known for sunflower, yield loss is probably not significant. The effect of seed treatment was probably more cosmetic than real. It was suggested at one time that aphid attack gave an entry to *Sclerotinia* leaf and terminal bud attack, but, in fact, it was probably that some factor like a highly concentrated sap was appreciated by both insects and fungal pathogens.

In contrast, all sunflower growers, and more especially producers of hybrid seed, must be interested in pollinating insects. There are significant differences in nectar sugar composition (Vear *et al.*, 1990) and some differences in hybrid seed yield may partly be due to differences in attractivity of parental lines, but with the provision of hives, there have rarely been difficulties in seed production. The subject has reappeared with the problems of disease and reduction in bee populations. Beekeepers have suggested that modern sunflowers are less attractive than varieties grown 30 years ago. For a serious answer to be provided, a lot of phenotyping would be necessary: pollen and nectar composition, tubular floret length etc. This comes as an extra research subject and I do not know if the necessary means are available.

3.7 Height, earliness, changes in architecture or vegetation cycle

Plant height at flowering, flowering date and per cent humidity of seed at harvest are characters regularly measured in sunflower breeding programmes, mostly to avoid very tall or very late material and to have a good knowledge of an inbred line or a hybrid.

In the 1980s, there was considerable work on dwarf material, measuring only 1 m even in good growing conditions. Several sources of dwarf genes were available, including that from gamma-mutation (Leclercq and Phillipon, 1978). In 1980–1985, some quite nice looking hybrids were in trial (Fick *et al.*, 1985), but, whatever the source, seed set was not good. It appeared that vascularisation of the capitulum was impaired. So most research programmes stopped and, although farmers like shorter varieties, there is no close relation with lodging and many of the highest yielding varieties have been the tallest of those available.

One of the ideas for developing short sunflowers was that they could be sown at higher density and thus increase yield, with a crop of many small heads, covering the ground more quickly in spring and maturing more rapidly, permitting an earlier harvest. This could be considered as an alternative to breeding short season hybrids while maintaining high yields. Concerning earliness more directly, since QTL or association studies have been published for flowering date (Cadic *et al.*, 2012) and water content at harvest, it may be possible to explicit the relation between the two, which is not very clear at present. Whether it will be possible to introduce “earliness” genes into longer season genotypes without losing yield remains to be seen.

Involving both these characters, revolutions in plant type can be, and have been, imagined. Rather than reducing height directly, one idea would be to have sunflower plants with several stems to obtain a high density of small heads. However, the branching type of restorer lines at present, that flower, and mature, over about 4 weeks, would not be very satisfactory; all the heads need to be harvestable at one time. “Y-branched”, with 2 heads flowering at the same time, appeared of more interest (Brigham and Young, 1980; Liu and Leclercq, 1988), but the source (from VIR 1629) rarely gave 100% plants with this character, very often the two heads were joined and irregularly formed.

The other way to obtain such a change in plant type might be to change earliness characters and cropping seasons. In areas of the world with little risk of frost, modern sunflower varieties can be sown in the autumn (for example in Morocco in November) and harvested in April (Gosset and Vear, 1995). Research on cold resistance has been carried out (Allinne *et al.*, 2009), but with two different objectives: germination at low temperatures (to sow early and avoid summer droughts, an alternative to drought resistance) and resistance to frost. When young sunflower plants are frosted, the terminal bud is at least weakened and plants are more or less branched. Could autumn sowing in some climates give a branched crop in the spring, comparable with oilseed rape?

However, are such suggestions useful, with all the research and development necessary, when the Amerindians first, and perhaps unintentional, selection produced a single headed sunflower from its wild multi-branched relatives? Whatever the objective, maintenance of wild and cultivated sunflower genetic resources is essential but costly. Since it is the interest of all research and breeding programmes, international collaboration, including research on methodologies, must be encouraged, as it could free means for new research objectives.

3.8 Genomic developments to boost sunflower research and breeding programmes

In recent years dense genetic maps, largely based on Single Nucleotide Polymorphism (SNP) have become available, so, as discussed for each character, markers can be found for major genes or QTL. However, the genes actually involved in the character are known only in a few cases. A new step forward for sunflower in 2010 was the International sequencing initiative, led by Rieseberg at British Columbia University, Canada (a return of Canada to the sunflower research scene), together with American, French and Argentinean collaboration (Kane *et al.*, 2011). Using the Illumina/454 technique, the sequence of the USDA inbred line HA412OL should be available very soon, together with those of two French lines (XRQ and PSC8), sequenced by INRA using the new technique PacBio. This new method has the advantage of producing very long DNA sequences, which help assembly of the complete genome sequence. This is because they span some of the large repeated sequences particularly present in the sunflower genome, which is not possible when shorter sequences are used. Having the complete genome sequence should make it possible, for any character, to find closer SNP markers, which should be in some cases part of the genes involved. It should also be possible to search for candidate genes known to be involved in similar traits in model species like *Arabidopsis*.

We will have to wait until some experience is obtained to be able to judge how this knowledge will modify breeding techniques and results. Constructing new sunflower plants depends on the identification of a combination of many chance genetic recombinations. Although it will be possible to estimate their expected frequency, the plants will have to be found and their behaviour checked under varied environmental conditions.

Nevertheless, one of the indirect positive aspects of this genomic research is that it opens a new field, with methods that change very rapidly and so much remains to be discovered that international collaboration is encouraged. As for maintenance of genetic resources, costs are high so they could advantageously be shared. Also, there is a lot of basic research that can be accomplished in common before competitive interests take over. It is rather the same situation as when hybrid sunflowers were first imagined and international collaboration was the basis of their success.

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