Genet. Pol., 35(1-2), 1994, pp. 43-51

Genotypic polymorphism of monogerm character in sugar beet (*Beta vulgaris* L.)

Stanislav MALETSKY, Ryszard KRYSIŃSKI

Institute of Cytology and Genetics, Siberian Division of Russian Academy of Sciences, Novosibirsk
Kutno Sugar Beet Breeding Co. Kutno, Poland

A b s t r a c t. MA-SA phenotypes of 137 hybrid combinations derived from crosses of 46 fertile 0-type MA lines (0-type populations) with four sterile, genotypically different MA tester lines were studied. The offsprings of a cross between the 0-type populations and tester lines were shown to split into two or three segregation groups, depending on the ratio of MA-SA phenotypes. The occurrence of SA phenotypes in the hybrids of two MA plants is regarded as a result of gene (intra- and interlocus) interactions via MA genes differing the crossed forms. The distribution of hybrids produced on the basis of one of the four tester lines into segregation groups agrees with the distribution of the 0-type lines under study into MA genotypes. As follows from this that populations of the monogerm 0-type lines and the monogerm tester lines have two or three genetic factors differentiating them. The occurence of SA phenotypes in the hybrids of MA plants is contrary to the monohybrid scheme of the MA-SA character inheritance and allows one to believe that this character is determined by a gene system with gene interactions of a complicated pattern.

Key words: *Beta vulgaris*, genotypic polymorphism, monogerm, sugar beet.

In sugar beet, the features of sowing units (fruits, balls) as regards the mono- and multigerm quality can be predicted long before their formation, since fruits and balls are derivates from the number of flowers on induvidual inflorescences. In view of this the terms mono- (MA) and synanthousness (SA) are used in this paper as characteristics of the type of flower primordium instead of mono-, multigerm which characterize technological features of the seed unit. In MA plants the flowers are largely alone on the shoots, whereas the SA type plants form clusters with 2-4 flowers (MALETSKY 1988).

Received: August 1993.
Correspondence: S. MALETSKY, Institute of Cytology and Genetics, Siberian Division of Russian Academy of Sciences, Novosibirsk, Russia.

Genetic control of the MA character is no longer a problem. The works still considered as classic (BORDONOS 1938, 1941, SAVITSKY 1950, 1952, 1954) put it down as follows: MA is a recessive character, SA is a dominant character. The MA-SA character is controlled by one locus (*M-m*) with one recessive and several dominant alleles. The genotype of MA crops is *mm*, that of SA plants are *MM* or *Mm*. However, the examples suggested by later works neither entirely confirm nor disagree with this statement (MALETSKY et al. 1988). Edgar Knapp, who studied genetics of the MA character in the forms received from different countries, concluded that the MA character in Savitsky's materials from the USA is inherited according to a monohybrid scheme, whereas that in the materials from the USSR, Poland and Germany remains polyhybrid (KNAPP 1962, 1967). Our study provides evidence that the inheritance of the MA character is quite far from a monohybrid scheme, but the polyhybrid type of segregation has not been confirmed yet anyway (nor Knapp's conclusion appears to be reasonable). We have found some new genes whose effects are readily observable in crossing experiments (MALETSKY, SHAVRUKOV 1991).Therefore, we may extend our discussion from just a single *M-m* locus to a system of genes whose interaction provides the formation of the MA–SA character in sugar beet.

We selected MA lines with different genotypes and obtained sterile analogs. The use of MA testers in breeding programme allows to carry out genetic differentiation of crossed forms into groups. It is, however, impossible to genetically indentify MA genotypes of a particular breeding sample.

The aim of the present paper was to describe the polymorphism of MA genotypes from the Polish breeding collection using four genetically different MA testers obtained from the Plant Population Genetics Laboratory of the Institute of Cytology and Genetics of the Siberian Division of the Russian Academy of Sciences (SD RAS).

Material and methods

M a t e r i a l s. 46 0-type lines from Polish breeding were scored at random, so they could be regarded as a sample of genotypes from a population. Sterile analogs of four lines, SOAN-22, SOAN-31, SOAN-243 and SLC91, created as a result of breeding and genetic work in the Laboratory of Plant Population Genetics of the Institute of Cytology and Genetics SD RAS (Novosibirsk), were examined for the ability to differemtiate MA genotypes. Two lines,

SOAN-22 and SOAN-31, were derived from the cultivars of Soviet breeding: Ramonskaya monogerm and Uladovskaya monogerm, respectively; the line SOAN-243 was derived from the German population 140361 (Klein Wanzleben, GDR): SLC91 is a recombinant of SLC91 (supplied by the National Institute of Plant Industry, Leningrad) selected from the progeny after crossing with SA form. The four testers have different MA genotypes. Cross-pollination (in any direction) between three testers – SOAN-31, SOAN-243 and SLC91 – leads to restoration of the wild phenotype (SA forms) in F_1. On the other hand, crossing of SOAN-31 and SOAN-243 with SOAN-22 plants results in exclusively MA offsprings. The line SOAN-22 has a dominant inhibiting gene which suppresses the development of additional flowers in the clusters (dominant alleles of *I-i* locus). The cross of SLC91 and SOAN-22 results in mixed offspring, partly MA and partly SA (MALETSKY, SHAVRUKOV 1991).

Identification of the MA genotype in the investigated lines is based on an analysis of phenotypic effects produced by gene interactions in hybrids resulting from cross-pollination of two MA forms. The MA phenotype is often referred to as a mutant (SAVITSKY, 1950). The SA phenotype is called "wild". Like all tester lines, the MA lines under study are uniform in phenotype: they are classified as MA phenotypes. However, genes controlling the development of the MA phenotype may be different in the crossed lines. Gene interactions between maternal and paternal genomes may cause that part of (or entire) F_1 progeny will have the SA phenotype. A comparison of respective shares of MA or SA phenotypes in different hybrids, can show differentiation or similarity of MA forms with respect to the MA-SA control genes.

Crosses were performed on the isolated plots placed in the hemp stripes. Each plot was allotted for 2-4 sterile MA testers and one fertile MA line. The crosses were performed during the summer of 1991 at the Plant Breeding Station in Straszków. Hybrid seeds were sown in a greenhouse: in the spring 1992, they were checked for the MA-SA phenotypes. A sample of the hybrid plants ranged from 10 to 40 individuals (depending on the number of plants which completed the formation of floral shoots).

The plants were classified into those with MA and SA phenotypes in accordance with the previous criteria (MALETSKY et al. 1988) and classification scheme adopted in Straszków which is equally good for the identification of the two phenotypes. There must be two reasons why the MA-SA segregation takes place in the offspring of the test crosses: a) either the MA line used for the experiment was not homozygous for the MA genes, or the tester was not homozygous, or neither of the components of the cross was homozygous; b) it

is liable that, despite homozygosity for the MA genes of both components of the cross, segregation may take place in F_1, as the wild phenotype may appear because of gene interactions and incomplete expression of the MA character in the hybrids.

If there are only MA plants in the test cross offspring, then the two following conclusions should be made: a) the line under study and the MA tester have the same MA genotype, b) either the MA line or the tester line carries alleles of the dominant inhibitor locus which suppress gene interactions. Otherwise, if the offspring of the test cross is entirely or partly represented by SA plants, then the respective MA genotypes of the tester line and the line under study are not the same, but there is no way to determine the exact number of the genes differing the parental forms. A pairwise comparison of the share of MA phenotypes in the offspring was made for a statistic estimate of the SA-MA phenotype segregation. If the number of hybrids derived from one tester line is n, then $n(n-1)/2$ pairs should be compared. The startpoint hypothesis was that the genotype of a pollinator has no influence on the SA-MA phenotype ratio in the offspring of the test cross. This hypothesis was verified by Fisher's u-criterion. The u values were calculated by the formula

$$u = (\Phi_1 - \Phi_2)\sqrt{\frac{n_1 n_2}{n_1 + n_2}},$$

where n_2 and n_2 are the numbers of MA phenotypes in the first and second progenies, Φ_1 and Φ_2 are the shares of the MA phenotypes (p) calculated from $\Phi = 2\arcsin\sqrt{p}$.

Critical values for u were taken from tables (URBACH 1963). If $u < 1.96$, the shares of the MA phenotypes are similar in the comparable hybrids, and the hybrids fall in with the same segregation group. If $u > 1.96$, the shares of MA phenotypes are statistically different, and the offsprings fall in with different segregation groups. Four segregation groups, denoted as 1, 2, 3 and 4, were revealed in the actual experiment. The share of the MA phenotype reliably decreases with the increase of the group number.

To estimate the number of genetic factors, differing the lines under study and affecting the occurrence of MA-SA phenotype, we deliberately suppose that the adjacent segregation groups differ only in one genetic factor, whereas the occurrence of four segregation groups provides evidence that there are at least three genetic factors, the interaction of which with MA genes of the tester lines causes the hybrids to manifest SA phenotypes.

Results

The distribution of hybrids with each of the four test crosses is presented in Table 1. The data show that the tested lines fall into several groups: msSOAN-22 and msSLC91 gave two groups each, msSOAN-243 and msSOAN-31 gave three groups each. The total number of different segregation groups was four.

Table 1. The distribution of hybrids from the crosses of 46 MA sugar beet lines with four sterile MA tester lines into different segregation groups

Tester line	F_1 offsprings No.	Plants Total	MA	SA	MA %	Segregation group
A. ms SOAN-22						
	6	97	94	3	96.91	1
	2	55	40	15	72.72	2
Total	8	152	134	18	88.16	1, 2
B. ms SOAN-243						
	8	109	104	5	95.41	1
	24	617	432	185	70.02	2
	13	322	134	188	41.61	3
Total	45	1048	670	378	63.93	1, 2, 3
C. ms SLC91						
	13	181	141	40	77.90	2
	26	425	180	245	42.35	3
Total	39	606	321	285	52.97	2, 3
D. ms SOAN-31						
	3	87	54	33	62.07	2
	37	983	301	682	30.62	3
	5	108	7	101	6.48	4
Total	45	1184	368	816	31.08	2, 3, 4

Segregation group 1: the offspring has only MA plants and/or occasional SA plants. MA plants in that group make up 95-97%. Segregation group 2: the offsprings are mostly with MA phenotype (the share of MA plants within that group ranged from 70 to 78%). Segregation group 3: predomination of

SA plants (MA plant made up about 42%). Finally, segregation group 4 was largely formed by SA plants (MA individuals constituted only 6.48%).

A. Tester line msSOAN-22. A small sample of hybrids (8 offsprings) from two segregation groups 1 and 2 was subjected to analysis. Group 1 consisted of six and group 2 of two progenies. This tester line yielded the highest number of MA plants due to the dominant inhibitor locus carried by this line (MALETSKY, SHAVRUKOV 1991).

B. Tester line msSOAN-243. Forty five offsprings were analysed for the MA-SA ratios and were divided into three segregation groups (1, 2 and 3). Segregation group 1 is observed among the offsprings of msSOAN-22 and msSOAN-243. Still, in the former case this group occurs due to the activity of the inhibitor locus, whereas in the latter case, it must be due to the identity of the tester line and pollen parents with respect to MA genes. We know that msSOAN-243 carries no inhibitor genes and that there are no MA forms with the inhibitor dominant genes in the Polish materials involved (explained below).

Most of the offsprings (24) were referred to group 2 (MA plants made up about 70%). Our method of MA genotype identification permitted to assume that the tested MA tester lines msSOAN-243 have the same genetic factor causing partial recovery of the wild phenotype.

Thirteen offsprings were ascribed to segregation group 3. Their MA plants constituted about 42%. According to our suggestion, there are, therefore, two genetic factors differing the 0-type pollinators from the tester line of this group.

C. Tester line msSLC91. Crosses involving this line as a tester, yielded 39 hybrids, but because of delayed flowering the number of plants analysed within each progeny was small (8-20). It should be noted that none of the 39 fertile pollinator lines was genetically identical to the tester line: one-third of the lines had only one differentiating factor each, whereas the remaining lines had two factors each.

D. Tester line msSOAN-31. Forty five hybrid offsprings were analysed and it should be noted that this tester line shows the highest degree of difference when compared to the tested 0-type lines. The MA hybrid plants from this combination were accounted constituted, on average, for 31% which makes up about one third as compared to other tester lines. Most of the hybrids were identified to belong to segregation group 3. Only the msSOAN-31 tester produced hybrid offsprings belonging to segregation group 4 – i.e. predominantly plants of SA phenotype. The lack of hybrids belonging to segregation group 1 indicates that no fertile lines have MA genotypes like the tester line and that the Polish MA lines carry no dominant alleles of the inhibitor locus.

As to the ability of the four tester lines to differentiate MA genotypes in the pollinator lines, the best was the tester line msSOAN-243 with three segregation groups, including group 1, which indicates that there is a similarity between part of genotypes of the pollinators and tester line. We failed to reveal genotypes of the pollinators identical to those of three other tester lines. Probably due to this failure it is difficult to assess the mutual correspondence of segregation groups at pollination by any line. The msSOAN-22 line gives an excess of MA phenotypes because of the presence of inhibitor genes whereas the msSOAN-31 line gives an excess of SA plants in the hybrid offspring. We failed to use msSLC91 line in our work, since its hybrids are retarded: many of the them have no shoots at all, or produce only vegetative shoots. Small samples impede the assessment of genotypes of pollen parents, although with this tester line, two segregation groups were also distinguished.

Discussion

As mentioned in the introduction, during the last 40 years, Savitsky's concept has been the leading one and according to it the MA phenotype is an attribute of plants which are homozygous in respect of the recessive allele (*m*), whereas SA plants carry dominant alleles of the locus *M-m* in the genotypes. This, without doubt, is a wrong and misleading hypothesis, which follows from the fact that results obtained from one experiment on the MA character control were generalized for the cultured sugar beet. The practice of breeding and genetic analysis do not agree with the monogene concept of the MA character inheritance. There is the most obvious disagreement, namely, the existence of several donors of the MA character discovered in different countries. And there is another disagreement – numerous cases of deviations in the F_2 from the monogene scheme of inheritance (it is not seldom that MA plants do not occur in F_2 at all). This question is beyond the scope of our studies, and those interested in it are referred to our reviews dealing with this subject (MALETSKY et al. 1988). The way we considered differentiation of genes controlling the MA-SA character formation is presented in the materials of the studied Polish MA lines. The source of differentiation were, on the one hand, tester lines, and on the other, 0-type lines. As described previously cross pollination of SOAN-31, SOAN-243 and SLC91 after a diallelic scheme always leads to restoration of the wild phenotype. This result may be explained by the effect of gene interactions. It should be noticed that the three lines were derived from

different populations (different sources of the MA character: Soviet, German and American).

The results presented in this paper as well as numerous data in the literature provide one-to-one evidence that there should be a system of genes controlling the MA-SA character in sugar beet. All the facts known cannot support in a way Savitsky's standpoint about one-locus (*M-m*) control over this character. The idea that the MA-SA character is polygenic (KNAPP 1962, 1967) is scarcely right either, provided that polygeny is understood as a uniform participation of the genes considerable effect on the character formation of the alternative (wild) phenotype. To reveal the exact number of MA genes and to analyse the effects of their interactions, futher studies are necessary.

REFERENCES

BORDONOS M.C. (1938). A mode of segregation and some peculiarities of sugar beet plants with separate flowers. Breeding and Seed Farming 6: 24-27 (Russ.).

BORDONOS M.C. (1941). Monogerm forms of sugar beet. Proceeding of VASHNIL. 11: 3-4 (Russ.).

KNAPP E. (1962). Genetische Erfahrungen mit einzelfruchtigen Zuckerruben. 25th Winterkongress IIRB. – Brussel. pp. 325-331.

KNAPP E. (1967). Die genetischen Grundlagen der Einzelfruchtigkeit (monokarpie) bei *Beta vulgaris* L. Tag. ber. Dt. Acad. Landwirtsch. Wiss DDR. – Bd. 89(2): 189-219.

MALETSKY S.I. (1988). About the terminology and classification concerning mono-and multigerm plants. In: A Monogerm beet: Embriology, Genetics, Breeding (F.E. Reimers ed.). Nauka, Novosibirsk pp. 5-12 (Russ.)

MALETSKY S.I., SHAVRUKOV Yu.N. (1991). The genetical control of monoanthousness and synanthousness in sugar beet. (I.M. Surikov, ed.) Nauka, Novosibirsk pp. 60-113 (Russ.).

MALETSKY S.I., SHAVRUKOV Yu.N., MGLINEC A.V. (1988). Inheritance of monoanthousness and synanthousness in sugar beet. In: Monogerm Beets: Embriology, Genetics, Breeding (F.E. Reimers ed.) Nauka, Novosibirsk pp. 79-131. (Russ.)

SAVITSKY V.F. (1950). Monogerm sugar beets in the United States. Proc. Amer. Soc. Sugar Beet Technol. 6: 156-159.

SAVITSKY V.F. (1952). A genetic study of monogerm and multigerm characters in beets. Proc. Amer. Soc. Sugar Beet. Technol. 7: 331-338.

SAVITSKY V.F. (1954). Inheritance of the number of flowers in flower clusters of *Beta vulgaris* L. Proc. Amer. Soc. Sugar Beet Technol. 8(2): 3-15.

URBACH V.Yu. (1963). A comparison two sampling share of variant. In: A Mathematical Statistics for Biologist and Physicians Man. Nauka, Moscov, pp. 215-217 (Russ.).

Genotypowy polimorfizm cechy jednokiełkowości u buraka cukrowego (*Beta vulgaris* L.)

Streszczenie

Badano dziedziczenie rozdzielno- i zrosłokwiatkowości u buraków cukrowych. 46 płodnych linii rozdzielnokwiatkowych (MA) typu 0 skrzyżowano z czterema sterylnymi testerami MA różniącymi się pod względem genetycznym. Występowanie cechy rozdzielno- (MA) i zrosłokwiatkowości (SA) obserwowano w potomstwie 137 kombinacji krzyżówkowych. Wykazano, że potomstwa uzyskane ze skrzyżowania linii typu 0 z testerami segregują na dwie lub trzy grupy w zależności od udziału w nich roślin o fenotypach MA i SA. Występowanie w obrębie mieszańców między dwiema formami MA roślin o fenotypie SA jest interpretowane jako rezultat allelicznej i nieallelicznej interakcji genów MA. Podział mieszańców będących potomstwem jednego z czterech testerów na grupy segregacji odpowiada podziałowi linii typu 0 według genotypów MA. Wynika z tego, że populacje jednokiełkowych linii typu 0 różnią się od jednokiełkowych testerów dwoma lub trzema czynnikami genetycznymi. Występowanie roślin SA w potomstwach mieszańców między formami MA przeczy monogenicznemu schematowi dziedziczenia cechy rozdzielno- i zrosłokwiatkowości. Można sądzić, że cecha ta determinowana jest więcej niż jednym genem.