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INHERITANCE OF OLEIC ACID CONTENT IN F_2 AND A POPULATION OF RECOMBINANT INBRED LINES SEGREGATING FOR THE HIGH OLEIC TRAIT IN SUNFLOWER

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SUMMARY

Pervenets is a sunflower mutant having a seed oil oleic acid content greater than 65%. All lines derived from the mutant Pervenets population display seed oil with a high oleic acid content [HOAC], over 80%. Linoleic (LO) and [HOAC] genotypes carry specific RFLP markers, oleLOR and oleHOS, revealed by oleate-desaturase cDNA used as a probe. Linkage disequilibria between the OleHOS allele and Pervenets mutation, and oleLOR and [LO] were without any exception. We studied the inheritance of [HOAC] in F_2 progenies from a cross [LO] x [HOAC]. This study has shown one dominant allele for [HOAC] that co-segregated with the oleate-desaturase oleHOS, [HOAC]-specific RFLP. Variance analyses revealed almost complete dominance and that oleHOS marker explained 86% of the OAC variation. F_6 recombinant inbred lines segregating for [HOAC] / [LO] showed that all [HOAC] RI lines carried oleHOS, but half of the RI lines carrying oleHOS were [LO]. Conversely, the absence of [HOAC] RI lines carrying oleLOR is evidence against recombination having taken place between the oleHOS locus and the Pervenets mutation locus. The [HOAC] trait is therefore due to 2 independent loci: the locus carrying the oleHOS allele and another locus. One allele, supole, at this second locus may suppress the effect of the oleHOS allele on the [HOAC] trait. Preliminary results with SSR (170 microsatellites, 500 cM) indicated that the oleHL and the supole loci are independent and explained 47.14 and 32.2% of the OAC variation, respectively. The existence of the Pervenets mutation, supole and epistatic combinations for modifier alleles leading to [HOAC] trait has never been suggested. It may explain the discordant results found in our segregating populations and literature.

Key words: **high oleic acid content, mutant, oil composition, oleate-desaturase, RFLP, sunflower, suppression**

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INTRODUCTION

Pervenets is a sunflower mutant having a seed oil oleic acid content (OAC) greater than 65%. It was obtained after mutagenesis treatment on VNIIMK 8931 (Soldatov, 1976). Soldatov (1976) analyzed 6,000 oil samples by gas chromatography and only one displayed an OAC of 50.3%. He sowed the remaining seeds from the plants that have given the OAC of 50.3% and self-pollinated each of them. He used again 30 seeds per head to extract oil and mixed the seeds from all the progenies, which displayed an OAC higher than 40%. Thus, he constituted the Pervenets population. After two cycles of intercrossing he enhanced the average OAC of Pervenets to 65%. This report shows clearly that the Pervenets mutant came from only one plant (one pollen grain).

Previous works (Hongtrakul *et al.*, 1998; Lacombe and Bervillé, 2002) showed that [HOAC] and [LO] genotypes are differentiated by specific RFLPs, oleLOR and oleHOS, respectively, using oleate-desaturase cDNA as a probe. Linkage disequilibria between the OleHOS allele and Pervenets mutation, and oleLOR and [LO] have been found without exception (Lacombe and Bervillé, 2002). In practice now, all lines derived from the mutant population Pervenets display seed oil with the oleic acid content [HOAC] over 80%. However, the [HOAC] genotype carries not only the Pervenets mutation but also different factors that affect OAC. We therefore achieved to mark Pervenets mutation in order to follow it in segregating progenies. Thus we were able to separate the effect of Pervenets mutation from the ones of other factors. We also identified another factor that may suppress the effect of Pervenets leading to the [LO] phenotype.

MATERIALS AND METHODS

Plant materials

Diversity analysis: it was performed on 239 genotypes representing [HOAC] and [LO] from main public collections and companies worldwide.

Segregating F_2 population: the [LO] line BD40713 was used as the female parent in a cross with the [HOAC] line BE78079 from Monsanto. One F_1 plant was self-fertilized to produce the F_2 progeny, composed of 107 plants in a greenhouse in 1998. They were used both to determine OAC on half a cotyledon of each seed, and to detect RFLP carrying the oleate-desaturase similar sequences with a sunflower oleate-desaturase cDNA as a probe. Comparisons were made against the BD40713 and BE78079 (Monsanto) parent lines and F_1 plants of the same cross were treated in the same way.

Segregating recombinant inbred line population: the [LO] line 83HR4 (INRA), male-sterilized by gibberellin, was crossed with the [HOAC] line RHA345 (USA) in our INRA nursery during the summer of 1996. Nine F_1 hybrid seeds were obtained and the F_1 plants were inter-crossed to produce an F_2 generation in a greenhouse

during the following winter. From these F_1 plants we obtained 174 F_6 progenies. These progenies were used to determine OAC separately on half a cotyledon of five seeds for each F_6 family. These seeds were sown in Jiffypots and after 6 days in a greenhouse they were transferred to the field. For each F_6 family, the RFLP genotype of plant number 2 in the field was determined with the oleate-desaturase cDNA probe. 83HR4 and RHA345 parental lines were included as controls.

Measurement of OAC

Measurements of oil composition were performed using gas chromatography (GC) (Conte *et al.,* 1989). However, the method on half a cotyledon does not allow repeats. We also performed OAC determination using both GC and the refractometer method (Goss *et al.,* 1978) on the mixed oil from 20 F_7 seeds of some of the RI line progenies. The results from both methods were comparable.

Molecular methods

Molecular hybridization: DNA preparation, restriction analyses, Southern transfers, and hybridization were done according to Gentzbittel *et al.* (1994). DNA from [HOAC] or [LO] lines or hybrid genotypes were restricted by *Hind*III and the Southern transfers were probed with the oleate-desaturase cDNA.

Probes: oleoyl-PC-desaturase (oleate-desaturase) corresponds to an entire cDNA sequence. The complete sequence has not yet been published (A.G. Abbott, unpublished); it corresponds to accession number U91341 (Genebank) by Hongtrakul *et al*. (1998).

Data management

RFLP profiles revealed on autoradiograms were scored visually. The Qgene package (Nelson, 1997) was used to perform analysis of variance and to compute linkage, additive and dominance effects.

RESULTS

Diversity analysis

It was performed on 114 LO and 125 HO genotypes. No polymorphism for the Δ9-desaturase was correlated to this high content. The linoleic or [LO] genotypes carry the RFLP marker oleLOR corresponding to the 8 kb *Hind*III fragment revealed by an oleate-desaturase cDNA used as a probe. The diversity analysis showed that HO genotypes carry another *Hind*III fragment (oleHOS), a specific RFLP marker of more than 15 kb was detected exclusively for [HOAC] genotypes, which corresponds to the oleLOR allele. Linkage disequilibrium between the OleHOS allele and the Pervenets mutation was verified and probably due to genetic linkage between the two loci.

Segregation between alleles at oleHL locus and Pervenets mutation

We studied the inheritance of [HOAC] in two segregating populations.

F_2 segregation population

The first study concerned 107 F_2 progenies from the cross BD40713 [LO] x BE78079 [HOAC]. [HOAC] and [LO] F_2 population parents displayed oleHOS and oleLOR, respectively. OleLOR : oleHOS segregated 1:2:1 (33 oleLOR/oleLOR : 50 oleLOR/oleHOS : 24 oleHOS/oleHOS) in the F_2 population, in agreement with 2 alleles at one locus: oleHL (χ^2 test, $p>0.3$). All F_2 plants with the OAC higher than 65% displayed oleHOS in the homozygous or heterozygous state, whereas all F_2 plants with OAC lower than 65% displayed homozygous oleLOR (Figure 1).

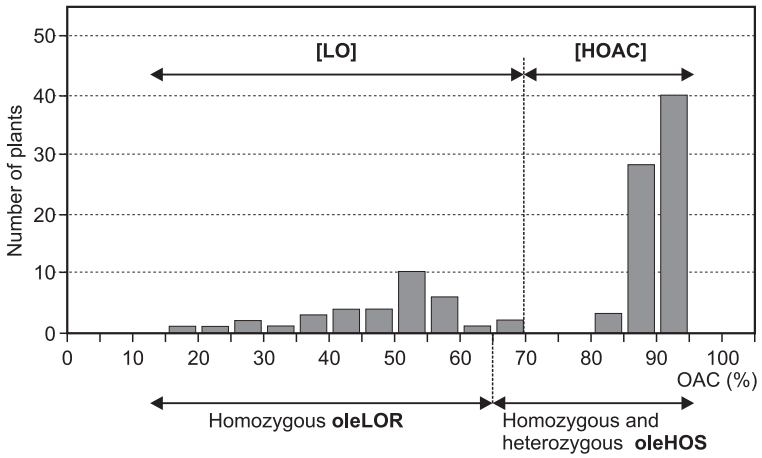

Figure 1: Distribution of OAC for 107 F_2 progenies. Upper dotted vertical lines indicate the OAC threshold between the [LO] and [HOAC] classes and upper horizontal arrows indicate the [LO] and the [HOAC] classes. Lower horizontal arrows indicate the distribution of the oleHOS and oleLOR alleles at the oleHL locus and lower dotted vertical lines indicate the OAC threshold between oleHOS and oleLOR classes.

On the basis of genotype at the oleHL locus, (whether homozygous oleLOR, or homozygous oleHOS and heterozygous), the OAC threshold was 65%, whereas the OAC threshold between [LO] and [HOAC] was 70%. All plants were correctly classified as [LO] or [HOAC] with respect to both OAC and the alleles at the oleHL locus, except for 2 plants that were classified in [LO] even though they carried oleHOS. Linkage between the oleHL locus and the locus directing [HOAC] was computed. The oleHOS allele explained most of the variation in OAC ($R^2 = 0.8642$), with strong linkage ($p<10^{-4}$) between the oleHL locus and the locus directing [HO]. Additivity (a = 22.07%) and dominance (d = 19.57%) were highly significant for oleHOS on OAC.

F_6 recombinant inbred lines

[LO] and [HOAC] parents of the RI lines displayed an average of 19 and 84% OAC, respectively. For the 174 F_6 RI lines, OAC varied from 12 to 92%. The OAC histogram is shown in Figure 2. The [HOAC] and [LO] parents of RI lines displayed oleHOS and oleLOR, respectively. For RI lines, only 6 plants were heterozygous at the oleHL locus and eliminated for further analyses. The OAC threshold between [HOAC] and [LO] RI lines could obviously be placed at 55%. The segregation pattern, 35 [HOAC] RI lines and 139 [LO] RI lines, agreed with a 1:3 [HOAC] : [LO] ratio (χ^2 test, $p>0.1$). This ratio supports the hypothesis that [HOAC] is directed by two independent loci. The other 168 RI plants were fixed at the oleHL locus. OleLOR:oleHOS segregated 1:1 (90:78), in agreement with two alleles at the oleHL locus (χ^2 test, $p>0.05$). All RI plants displaying the oleLOR (90) were [LO]. The seventy-eight RI lines displaying the oleHOS allele are distributed equally between [HOAC] (35) and [LO] (43) (1:1, χ^2 test $p>0.3$). Thus, the class of RI lines with oleLOR and [HOAC] is lacking (Figure 2, Table 1).

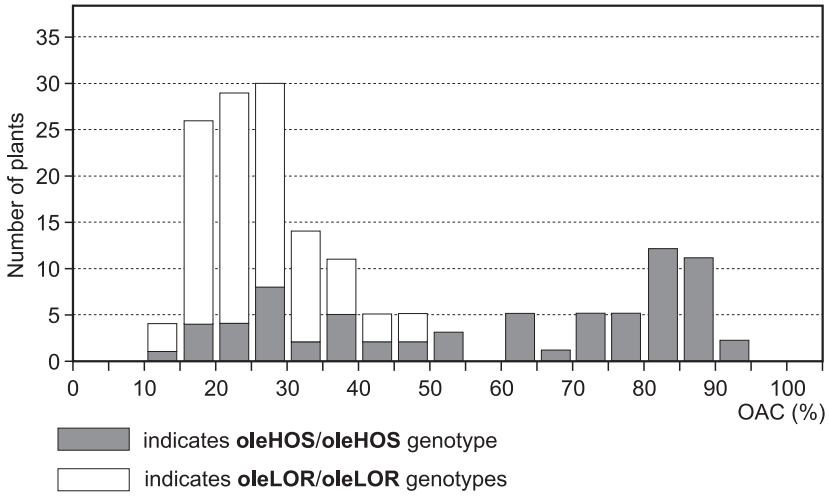

Figure 2: Distribution of OAC for 174 RILs. Upper dotted vertical line indicates the OAC threshold between the [LO] and [HOAC] classes and upper horizontal arrows indicate the [LO] and the [HOAC] classes. Lower horizontal arrows indicate the distribution of the oleHOS and oleLOR alleles at the oleHL locus and lower dotted vertical lines indicated the OAC threshold between oleHOS and oleLOR classes.

DISCUSSION

One or two loci directed HO trait depending on the crosses

We characterized strong linkage disequilibrium for oleHOS and Pervenets mutation alleles. We can therefore conclude that it is the oleHOS allele at the oleHL

locus that carries, or is very close to the Pervenets mutation allele (Lacombe and Bervillé, 2001).

Table 1: Number of RI lines in each [HOAC] or [LO] class according to the oleLOR or oleHOS alleles at the oleHL locus

	OleLOR	oleHOS
All RILs	96	78
[LO] RILs	96	43
[HOAC] RILs	0	35

The oleHL locus carries the 8 kb *Hind*III fragment in the [LO] genotypes whereas it carries the oleHOS allele characterized by the *Hind*III fragment of more than 15 kb for the [HOAC] genotypes (Hongtrakul *et al.*, 1998; Lacombe and Bervillé, 2001). In the F_2 segregating population, we observed co-segregation between the oleHOS allele and OAC higher than 65% ([HOAC] trait). Thus, we revealed a strong genetic linkage between an oleHL locus carrying oleHOS/oleLOR alleles and the Pervenets mutation allele (R^2=0.8642, $p<10^{-4}$). This suggests that the Pervenets mutation allele is either at the oleHL locus or is strongly linked to it. Moreover, the dominance/additivity ratio (90%) reveals an almost complete dominance effect of the oleHOS region on OAC. This is in agreement with the observed 3:1 [HOAC] : [LO] segregation ratio in the F_2, strong evidence that the [HOAC] trait is directed by the oleHOS region carrying the dominant allele.

Despite the strong genetic linkage, two [LO] plants of our F_2 population displayed the oleHOS allele of the [HOAC] parent. These two F_2 plants had oleHOS, but [LO] were in the upper extreme range of the [LO] class. In order to explain these F_2 plants, we asked whether:

1. routine OAC determination through a short GC procedure might introduce erroneous OAC data;
2. recombination had occurred between the oleHL locus and the locus carrying the Pervenets mutation allele;
3. modifier genes could enhance OAC variation leading plants in the lower extreme of the [HOAC] class to shift to a higher [LO] class and vice versa.

Concerning the point 1, OAC determination on an F_2 cotyledon is a unique measure. It cannot be repeated on the same F_2 plants to verify whether OAC was erroneous or not. However, for some RI line families, we performed OAC determination on the mixed oil of 20 F_7 seeds using the same GC procedure as for the F_2 population and the refractometer method. The results from both methods appeared consistent (not shown). Thus, we rejected hypothesis 1. This demonstrates the advantage of RI lines in such a comparison procedure.

Recombination between the oleHL locus and the locus carrying the Pervenets mutation allele in the F_2 population (point 2) cannot be excluded. However, there is no reason for the two recombinants to be located in the extreme upper [LO] and lower [HOAC] classes. To check whether recombination were possible or not, we

examined if such events had occurred in RI lines. We observed 43 [LO] RI lines carrying oleHOS, but we did not observe the expected complementary recombination product: [HOAC] RI lines carrying oleLOR (0:43). Moreover, this is supported by the fact that we did not detect any HO line carrying oleLOR. We therefore eliminated the hypothesis that recombination had taken place between the oleHL locus and the locus carrying the Pervenets mutation allele.

The hypothesis involving modifier genes (point 3), has already been put forward in the literature (Miller *et al.,* 1987; Schmidt *et al.,* 1989). We consider that these genes lead to a modification in [OAC] making extreme [LO] or [HOAC] positions uncertain. They may also explain the two F_2 plants with oleHOS in the upper extremity of the [LO] class. They should have a small effect on OAC in comparison to the Pervenets mutation allele, but their effect may be sufficient to explain the shift of the OAC threshold from 70% to 65%.

Sup locus

We assumed that since we found only 6 RI lines heterozygous for oleHOS / oleLOR, each RI line family verified to be fixed at oleHL locus and could be represented by a single plant. The mode of inheritance of the [HOAC] trait was directed by one locus in the F_2, so we expected the trait to be directed by one locus in the RI lines also. However, the 3:1 [LO]: [HOAC] ratio was evidence that the [HOAC] trait was directed by two loci in the RI line population.

We hypothesized a suppressor locus because we observed that RI lines carrying oleHOS were split equally into [LO] and [HOAC] classes (1:1, χ^2 test, $p>0.3$), whereas plants carrying oleLOR were all [LO]. The oleHOS region is therefore required for the [HOAC] trait. As we had eliminated the possibility of recombination between the oleHL locus and the locus carrying the Pervenets mutation allele, this distribution indicates another independent locus controlling the [HOAC] phenotype of RI lines. In the [LO] RI lines carrying oleHOS, the effect of the oleHOS region on the [HOAC] trait could be suppressed by one allele at another locus (supole allele) (Table 2). We therefore explain the 3:1 [LO]: [HOAC] segregation pattern by 2 loci directing the [HOAC] trait.

Table 2: Prediction of classes for RI lines according to three loci: oleHL, suppressor and modifiers assuming oleHOS as reference led to 65% OAC. Sup0 corresponds to a null allele on [HOAC]

Genotypes		OAC classes	
locus oleHL	locus Supole	[LO]	[HOAC]
oleLOR	Sup0	[LO]	
oleLOR	Supole	[LO]	
oleHOS	Sup0		[HOAC]
oleHOS	Supole	[LO]	

Full dominance of the [HOAC] trait is quite surprising. It has not been reported for rapeseed or peanut, for which high oleic mutants do exist, but in which muta-

tions are never dominant (Moore and Knauft, 1989; Schierholt *et al.*, 2000). Dominance occurred when the trait was of transgenic origin (i.e., antisens oleate-desaturase construct) (Lacombe and Bervillé, 2000b).

Perez-Vich *et al.* (2000) have also shown in sunflower by QTL analyses that the QTL peak for OAC, explaining 84.5% of the variation, coincided with an oleate-desaturase locus. Moreover, several authors have shown under-accumulation for oleate-desaturase transcript in the developing embryos between 10 to 20 days after fertilization (Kabbaj *et al.*, 1995; Hongtrakul *et al.*, 1998; Lacombe and Bervillé, 2000a). All plants of these preceding studies had also been characterized for oleHL locus by Lacombe and Bervillé (2001) and they displayed oleHOS when [HO]. The strict correlation in [HOAC] plants between under-accumulation of the oleate-desaturase transcript and oleHOS suggests a functional relationship between these features leading to the absence of oleate-desaturase activity giving rise to the [HOAC] trait (Lacombe and Bervillé, 2000).

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HERENCIA DEL CONTENIDO DE ACIDO OLEICO EN LA POBLACION F_2 DE LAS LINEAS CONSAGUINEAS DEL GIRASOL, QUE SE SEPARAN SEGUN LA PROPIEDAD DEL ALTO CONTENIDO DE ACIDO OLEICO

RESUMEN

Pervenec es el mutante del girasol que tiene el contenido de acido oleico en el aceite mas grande que 65%. Todas las lineas derivadas de la poblacion mutante de Pervenec tienen el alto contenido de acido oleico [HOAC], sobre 80%. Los genotipos oleicos [LO] y esos con alta oleina [HOAC] poseen los marcadores especificos RFLP, oleLOR y oleHOS, cuya presencia se descubre por medio de oleato-desaturase con respecto a cDNK. El desequilibrio entre los alelos oleHOS y la mutacion de Pervenec, asi como entre oleLOR y [LO] aparecia sin excepcion. La herencia del alto contenido de acido oleico [HOAC] era investigada en los descendientes F_2 del cruce [LO] x [HOAC]. Esta investigacion ha mostrado que el alto contenido de acido oleico [HOAC] es bajo el control de un alelo predominante, lo que fue confirmado por el analisis especifico RFLP del efecto de oleato-desaturase sobre oleHOS. Loa analisis de variacion mostraron la dominacion quasi completa, si que el marcador oleHOS explicaba 86% de variacion en la composicion de acidos grasos. Las lineas consanguineas recombinantes, que se segregaban a [HOAC]/[LO], mostraron que todas las lineas [HOAC] contenian oleHOS, pero la mitad de esas lineas era de tipo linoleico. Por lo contrario a eso, cuando las lineas [HOAC], que contienen oleLOR, no aparecen, eso indica que no se hizo la recombinacion entre el locus oleHOS y el locus que contiene la mutacion de Pervenec. Eso siggnifica que existen dos locus independientes que controlan la propiedad [HOAC]: el locus que contiene el alelo oleHOS y aun un locus. Un alelo, supol, a ese otro locus puede suprimir el efecto del alelo oleHOS sobre la propiedad [HOAC]. Los resultados preliminares con SSR (170 microsatelitas, 500 cM) indican que el locus oleHL y el locus supol son reciprocamente independientes y esos explican 47.14% y 32.2% de variacion en la composicion de acidos grasos. Hasta ahora no se presento la hipotesis con respecto a la mutacion de Pervenec, supol y las combinaciones epistaticas del alelo que moduifican la propiedad [HOAC]. Esta hipotesis explica el desacuerdo entre nuestros resultados para la poblacion en la separacion de resultados tambien literarios.

TRANSMISSION DU CONTENU EN ACIDE OLÉIQUE DANS UNE POPULATION F_2 DE LIGNES INBRED DE TOURNESOL QUI SE DIFFÉRENCIENT PAR LA CARACTÉRISTIQUE DE NIVEAU ÉLEVÉ D'ACIDE OLÉIQUE

RÉSUMÉ

Le Pervenets est un mutant du tournesol dont l'huile contient plus de 65% d'acide oléique. Toutes les lignes dérivées de la population mutante Pervenets ont un niveau élevé d'acide oléique [HOAC], plus de 80%. Les génotypes linoléiques [LO] et [HOAC] possèdent des marqueurs RFLP spécifiques,

oleLOR et oleHOS, révélés par le cADN oléate-désaturase. Dans tous les cas, sans exception, un déséquilibre est apparu entre les allèles oleHOS et les mutations Pervenets et entre oleLOR et [LO]. Nous avons étudié la transmission de [HOAC] dans la progéniture F_2 du croisement [LO] x [HOAC]. Cette étude a démontré que le contenu élevé d'acide oléique [HOAC] est sous le contrôle d'un allèle dominant et ceci a été confirmé par l'analyse spécifique RFLP de l'effet de l'oléate-désaturase sur oleHOS. Les analyses de variances ont révélé une dominance presque complète de telle façon que le marqueur oleHOS expliquait 86% de la variation dans le contenu en acides gras. Les lignes inbred recombinantes F_6 qui se sont séparées en [HOAC]/[LO] ont montré que toutes les lignes [HOAC] contenaient oleHOS, cependant, la moitié de ces lignes était de type [LO]. Au contraire, l'absence des lignes [HOAC] RI contenant oleLOR montre qu'il n'y a pas eu recombinaison entre le locus oleHOS et le locus contenant la mutation Pervetets. Ceci signifie qu'il existe deux loci indépendants qui contrôlent la caractéristique [HOAC]: le locus qui contient l'allèle oleHOS et un autre locus. Un allèle, supole, sur cet autre locus peut réduire l'influence de l'allèle oleHOS sur la caractéristique [HOAC]. Les résultats préliminaires avec SSR (170 microsatellites, 500 cM) ont montré que le oleHL et les loci supole sont indépendants et ils expliquent 47.14 et 32.1% des variations de contenu en acides gras. Jusqu'à maintenant, l'existence de la mutation Pervetets, de supoles et de combinaisons épistatiques des allèles modifiant la caractéristique [HOAC] n'a pas été suggérée. Cette supposition pourrait expliquer la discordance entre nos résultats pour ces populations et les données bibliographiques.