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The sporophytic self-incompatibility mating system is conserved in *Olea europaea* subsp. *cuspidata* and *O. e. europaea*

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Abstract Fruit setting after self-pollination, crosses and free-pollination appears to be erratic in the cultivated olive tree [*Olea europaea* subsp. *europaea* L. (*O. e. europaea* L.)] because of a lack of a suitable model to enable prediction of rates. The same lack of prediction also applies to the wild taxon *Olea europaea* subsp. *cuspidata* (*O. e. cuspidata*). Because of their close phylogenetic relationships, we hypothesize that *O. e. cuspidata* and cultivated olive share the same self-incompatibility system. We used data recently published in a wide study involving four *O. e. cuspidata* accessions and four olive cultivars. Because the olive varieties have been deciphered for their *S*-allele pair, that infer determinants present in the stigma and pistil, and that coat the pollen, we deciphered the *S*-alleles carried by three of the *O. e. cuspidata* accessions. Data are too scarce and the number of accessions too small to speculate on the *O. e. cuspidata* genetic population structure. The working

hypothesis is confirmed. This study and data from the Italian team will enable us to embark on a large-scale hybridization program between the two subsp. to obtain a wide range of progenies for screening for responses to cold, diseases and pests.

Keywords Genetic resources · Hybridization · Olive

Introduction

Recently Cáceres et al. (2015) published new data on fruit setting after hybridization between two subspecies of *Olea europaea*, namely subsp. *europaea* L. (*O. e. europaea* L.) and subsp. *cuspidata* (*O. e. cuspidata* Wall ex G. Don.). Controlled crosses between four *O. e. cuspidata* accessions on the one hand and four olive cultivars—‘Dolce Agogia’, ‘Favolosa’ also called ‘Fs17’, ‘Frantoio’ and ‘Lec-cino’—on the other hand, led to fifteen hybrid plants saved in a nursery. Fruit setting between pairs of the subspecific taxon *O. europaea* appeared erratic because there was no way of predicting success or failure. However, we have already attributed *S*-allele pairs to three of the olive varieties within the framework of the sporophytic model. We thus questioned whether *O. e. europaea* and *O. e. cuspidata* have the same self-incompatibility system.

As reported by Besnard et al. (2001) seventeen hybrid trees, which are now 31 years old, were

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obtained by Villemur by 1984. Hannachi et al. (2009) studied oil yield and some phenotypic traits such as fruit color and size in these trees. These trees are maintained in dense conditions in the orchard collection at INRA—Montpellier; they have lost their juvenile traits and blossom and produce fruit regularly each year with each tree yielding several kilograms of fruit Table 1.

Natural hybrids between subspecies *O. e. cuspidata* and *O. e. europaea* occur in areas surrounding olive orchards in South Africa (Costa 1998; H. Sommerlatte pers comm). There are no published reports of natural hybridization in countries other than South Africa, but there are speculations that they may occur (Breton et al. 2008; Cáceres et al. 2015 for review).

Recently Gibbs (2015) published a complete review on the different aspects of self-incompatibility including architecture self-incompatibility (ASI) type and late-acting self incompatibility. We can omit aspects that are well documented in the review. However, most researchers ignore the fact that SI distribution in the evolutionary tree of the Plantae is not in concordance with the species phylogeny. It appears that SI has appeared several times either as architecture SI, gametophytic self-incompatibility (GSI) and sporophytic self-incompatibility (SSI) (Fig. 1). Moreover, for close species in different genera SI may have been lost and become self-compatible as in *Prunus* (*P. persica*), whereas other *Prunus* species (cherry, apricot and almond) harbor a GSI mechanism. *Arabidopsis thaliana* has lost SI whereas *A. lyrata* harbors a deep SSI system (Goubet et al. 2012).

Oleaceae are known to harbor different floral biology systems. In *Jasminum* heterostyly, either distyly and tristyly, is known in 24 families (Ganders 1979; Dommée et al. 1992). In *Fraxinus* different modes exist; *F. excelsior* and *F. angustifolia* (Mediterranean) are polygamous (Bochenek 2011) as each tree carries at least some hermaphroditic flowers and may be functionally dioecious. *F. ornus* displays androdioecy (Dommée et al. 1999). *F. lanuginosa* displays androdioecious behavior in northern Japan (Ishida and Hiura 2002); and *Phillyrea* displays androdioecy (Saumitou-Laprade et al. 2010). In *Olea* little is known apart from *O. e. europaea*; however, Hannachi and Marzouck (2012) recently discovered androdioecy in *O. e. subsp. sylvestris* (wild olive or oleaster). Although the GSI model has been considered as

functioning in the cultivated olive (Zhu et al. 2013) it is now established that the SSI model works (Breton and Bervillé 2012; Breton et al. 2014; Farinelli et al. 2015; Koubouris et al. 2014). SSI and GSI differ in other features by the stage of deposit of S-determinants onto the pollen coat. With SSI the S-determinants are deposited early before the tetrad stage, and thus all pollen grains are coated by the same S-determinants (Breton et al. 2014). Without dominance between the S-alleles, both determinants coat all pollen grains produced by the individual. However, when dominance is expressed, only the S-determinant of the dominant S-allele is present on the pollen coat. Gibbs (2015) reported the history of emergence of the SSI model, and stressed the difficulties it may cause in analysing cross data. The singularities are due to dominance relationships (>) whereby (i) each pollen grain may not be coated by the S-determinant of the S-allele it carries; that is, the determinant of the recessive S-allele is lacking, and (ii) in reciprocal crosses with $R2 > R3$ and $R1 = R3$ the cross ♀*R1R3* × *R2R3*♂ (determinant R2) is compatible, whereas the reciprocal cross ♀*R2R3* × *R1R3*♂ (determinant R1R3) is incompatible.

Differences in fruit setting after crossing, self-pollination or free-pollination between *O. e. cuspidata* and *O. e. europaea* resemble most olive cross data widely published in several countries and quoted by Cáceres et al. (2015). For three of these varieties Farinelli et al. (2015) have, within the framework of the sporophytic self incompatibility (SSI) system, already deciphered the S-allele pair in each variety. We aimed to verify if *O. e. cuspidata* harbors SSI as is the case in cultivated olive, and therefore we attempted to decipher the S-alleles in the four accessions from *O. e. cuspidata*. Based on the attributed S-allele pair of each olive variety we deduced the S-alleles in *O. e. cuspidata*. Cross fruit set is shown to match inferences from SSI for successes and failures. When reciprocal crosses were made the power of attributing a pair is higher than when crosses were made in only one direction. Data enabled us to decipher S-alleles in 16 crosses. It was fortunate that Cáceres et al. (2015) used several olive varieties that carry different S-allele pairs (including all S-alleles). Theoretical self-compatibility and self-incompatibility as open-pollination rates are discussed in relation to experimental data.

Table 1 Crosses reported by Cáceres et al. (2015) and S-alleles deduced from mating successes and failures based on reference parents and those deciphered in this study

Cross	Possible S-alleles	Pollen determinant	Cáceres code	No flowers ^a	No fruit	Fruit set (%)	No SEC	No SO	No GE
<i>OeSA-A</i> × <i>DA</i>	<i>R1R3R4R5R6</i>	<u>R2</u>	C1	173	2	1.16	2	2	2
<i>OeDA</i> × <i>SA-A</i>	<i>R2R3</i>	<u>R6</u>	C16	47	3	6.38	3	3	2
<i>OeSA-A</i> × <i>Fs17</i>	<i>R4R6</i>	<u>R6</u>	C2	449	0	0	0	0	0
<i>Fs17</i> × <i>OeSA-A</i>	<i>R4R6</i>	<u>R6</u>	C19	22	0	0	0	0	0
<i>OeSA-A</i> × <i>Fra</i>	<i>R4R6</i>	<u>R5</u>	C3	204	6	2.94	6	10	10
<i>OeSA-A</i> × <i>Lec</i>	<i>R4R6</i>	<u>R1R5</u>	C4	308	4	1.30	4	7	7
<i>OeSA-A</i>	<i>R4R6</i>	<u>R6</u>	S1	709	4	0.56	2	2	1
<i>OeSA-A</i>	<i>R4R6</i>		OP1	2720	293	10.77	10	17	9
<i>OeSA-B</i> × <i>DA</i>	<i>R1R3R4R5R6</i>	<u>R2</u>	C5	374	28	7.49	18	11	0
<i>OeSA-B</i> × <i>Fs17</i>	<i>R1R3R4R5</i>	<u>R6</u>	C6	51	6	11.76	6	7	0
<i>OeSA-B</i> × <i>Lec</i>	<i>R3R4</i>	<u>R1R5</u>	C7	267	3	1.12	2	3	0
<i>OeSA-B</i> × <i>Fra</i>	<i>R3R4</i>	<u>R5</u>	C8	126	0	0	0	0	0
<i>OeSA-B</i>	<i>R3R4</i>	<u>R3</u>	S2	362	1	0.28	1	1	0
<i>OeSA-B</i>	<i>R3R4</i>		OP2	365	23	6.30	2	2	0
<i>OeCH</i> × <i>DA</i>	<i>R1R3R4R5R6</i>	<u>R2</u>	C9	21	1	4.76	1	1	1
<i>DA</i> × <i>OeCH</i>	<i>R2R3</i>	<u>R1R5R6</u>	C17	28	1	4.29	4	4	3
<i>Chin</i> × <i>Fs17</i>	<i>R1R4R5R6</i>	<u>R6</u>	C10	43	0	0	0	0	0
<i>OeCH</i> × <i>Lec</i>	<i>R5R6</i>	<u>R1R5</u>	C11	12	0	0	0	0	0
<i>OeCH</i> × <i>Fra</i>	<i>R5R6</i>	<u>R5</u>	C12	49	0	0	0	0	0
<i>OeCH</i>	<i>R5R6</i>	<u>R6</u>	S3	656	0	0	0	0	0
<i>OeCH</i>	<i>R5R6</i>		OP3	1424	26	1.83	3	3	3
<i>OeIN</i> × <i>DA</i>	<i>R1R3R4R5R6</i>	<u>R2</u>	C13	209	1	0.48	1	1	0
<i>DA</i> × <i>OeIN</i>	<i>R2R3</i>	<u>R1R5R6</u>	C18	20	1	5.00	1	1	1
<i>OeIN</i> × <i>Fs17</i>	? <i>R6</i>	<u>R6</u>	C14	100	0	0	0	0	0
<i>Fs17</i> × <i>OeIN</i>	<i>R4R6</i>	<u>R6</u>	C20	198	6	3.03	6	6	4
<i>OeIN</i> × <i>Lec</i>	<i>R1R5</i> or <i>R1R4</i> or <i>R4R5</i>	<u>R1R5</u>	C15	12	0	0	0	0	0
<i>OeIN</i>			S4	332	1	0.30	0	0	0
<i>OeIN</i>			OP4	100	2	2.00	0	0	0
Self-pollination	<i>DA</i>		S5	74	7	5.18	2	2	2
	<i>Fs17</i>		S6	112	6	5.36	1	1	1
Open-pollination	<i>DA</i>		OP5	120	12	10.00	3	3	3
	<i>Fs17</i>		OP6	336	40	11.90	6	6	4

OeSA-A *Olea europaea* subsp. *cuspidata* from South Africa, *OeSA-B* *Olea europaea* subsp. *cuspidata* from South Africa, *OeCH* *Olea europaea* subsp. *cuspidata* from China, *O. e. europaea* *OeIN* *Olea europaea* subsp. *cuspidata* from India, *DA*: dulce agogia, *FR* frantoio, *Lec* leccino, *No* number, *SEC* number of stones used for embryo culture, *GE* germinated embryos, *SO* seed obtained

^a Refers to number emasculated for different crosses, or sampled for self- and open-pollination studies

Materials and methods

The origin of the *O. e. cuspidata* studied in Montpellier was Stellenboch, South Africa. Elia Psillakis brought it from Chania (Greece) in the 1970s as fresh

scions that were grafted onto an olive stock in a greenhouse in Montpellier. *O. e. cuspidata* was grafted onto the cultivated olive ‘*Olivièrè*’, and local varieties from the Hérault area were grown in the greenhouse. The grafted *O. e. cuspidata* tree was exposed to

Fig. 1 Schematic phylogenetic tree of the Plantae showing occurrences of *SSI* sporophytic self-incompatibility, *GSI* gametophytic self-incompatibility, *LSI* late self-incompatibility

pollination by each of the mixture of varieties cultivated in the same greenhouse. Seeds were obtained naturally from free-pollination. They were harvested and germinated without hormone treatment in pots. Seventeen hybrid trees are conserved in the olive tree collection at INRA-Montpellier.

The genetics of SI depend on one locus with several *S*-alleles; thus two *S*-alleles are expected for each variety. Until now six *S*-alleles have been hypothesized for olive, and named *R1* to *R6*, thus the two by two pairwise combinations lead to fifteen host pairs (Breton and Bervillé 2012). Dominance relationships were revealed when one reciprocal pairwise combination leads in one direction to fruit set, and in the other direction to failure of the cross (Moutier 2002; Farinelli et al. 2006, 2015). Dominance relationships established by Breton and Bervillé (2012) were $R6 > R2 > R1 = R3 = R5 > R4$; that is, four levels of dominance were found. Among olive varieties for any *S*-allele pair, the higher the difference in dominance level the higher the self-compatibility level of the tree (Breton et al. 2016). However, on the male side the most important feature is that each pollen grain is coated by the same *S*-determinants—all pollen grains emitted by one tree carry the same *S*-determinant. *S*-proteins remain undetermined in olive at present. Consequently, to avoid any ambiguity in the coding of *S*-alleles and *S*-determinants for varieties the

S-allele pair is italicized (*S_xS_y*), whereas the pollen determinants are presented with regular characters and underlined (S_x, when $S_x > S_y$). Obviously, for one variety the *S*-allele pair in the stigma and the pollen determinant(s) is conserved, whether or not the other variety is male or female.

From all data published on olive crosses one can deduce that data from a cross that succeeded are more reliable than data from a cross that failed. In all publications, repeats of one cross in several bags shows that successes occur for about half of the expected compatible bags (Farinelli et al. 2015).

Routinely, when a variety is mated as male or female with a series of other varieties all with known *S*-allele pairs, then the *S*-alleles enabling success are identified. We proceeded with other cross data in a stepwise manner. It is only necessary to eliminate *S*-alleles to reduce the number to two potential *S*-alleles. Thus, choice of the reference varieties for crossing is vital to complete deciphering. In the Cáceres et al. (2015) study all host varieties were emasculated, thus there was no risk of interference in fruit set by self-pollination, and therefore we can be confident with the data. However, emasculation may have damaged the stigma and pistil because the average fruit set appeared low for self-pollination and free pollination in the varieties. The C1 to C20 codes refer to crosses made and examined by Cáceres et al. (2015).

Results

The open-pollinated grafted *O. e. cuspidata* tree grown in the greenhouse at Montpellier produced many fruits. After sowing viable seedlings were grown in a greenhouse. After 31 years 17 viable adult trees remain in the INRA collection at Montpellier.

Cáceres et al. (2015) published a set of data after crossing four cultivated olive varieties (*Dolce-Agogia*, '*Favolosa*', *Frantoio* and *Leccino*) with four *O. e. cuspidata* individuals from South Africa (SA), China (CH), and India (IN). Farinelli et al. (2015) attributed the S-allele pairs *R2R3-R2* (female genotype-pollen determinant), unknown; *R4R5-R5*, and *R1R5-R1R5* to these varieties, respectively.

Because *O. e. cuspidata* SA-A as female was successfully mated by '*Dolce Agogia*' (C1)-*R2R3* as host and *R2* as male (C16)-in both directions of crossing, SA-A cannot carry *R2* or *R3* but could carry *R1*, *R4*, *R5*, or *R6*. ♀SA-A was successfully mated by *Frantoio* (*R5*) (C3) and *Leccino* (*R1R5*) (C4), and consequently *R1* and *R5* can be eliminated as the possible S-alleles for SA-A leaving *R4R6* as the genotype for SA-A. The SA-A cross by '*Favolosa*' failed (C2, C19) as both SA-A and '*Favolosa*' carry the common S-allele *R6*. Consequently SA-A and '*Favolosa*' carried *R4R6*.

SA-B was mated by *Dolce Agogia* *R2* (C5), '*Favolosa*' *R6* (C6), *Frantoio* *R5* (C8), and *Leccino* *R1R5* (C7) thus *O. e. cuspidata* cannot carry *R2*, *R6*, *R5*, or *R1*, and consequently SA-B carries *R3R4* and thus behaves as *R3*.

Olea europaea cuspidata China (OeCH) and *Dolce Agogia* *R2* mated successfully in both directions (C9, C17); OeCH may carry *R1*, *R4*, *R5*, or *R6*. But the other three varieties failed as male (C10, C11 and C12). Thus OeCH cannot carry *R1* and *R4* but could carry *R5* and *R6*, thus Oe-CH is confirmed as *R5R6* and *R6*.

Olea europaea cuspidata India (OeIN) and *Dolce Agogia* mated successfully in both directions (C13, C18), OeIN and '*Favolosa*' also mated successfully in both directions (C14, C20), but *Leccino* *R1R5* failed as male (C15). Thus OeIN should carry *R1* and/or *R5* and therefore *R1* or *R5* remain undetermined along with *R4*. The cross with *Frantoio* if incompatible would indicate *R5*, and if compatible would indicate *R1*. Consequently OeIN could be *R1R5* or *R1R4* or *R4R5*.

Data of Cáceres et al. (2015) concerning self-pollination for SA-A, SA-B, OeCH and OeIN are 4/709–0.56%, 1/362–0.28%, 0/656–0% and 1/332–0.30% in comparison to varieties '*Dolce Agogia*' (7/74–5.18%) and '*Favolosa*' (6/112–5.36%). Thus *O. e. cuspidata* after self-pollination displayed low seed set in comparison to '*Dolce Agogia*' and '*Favolosa*'. However, it is indicative that those data cannot be compared with data from Farinelli et al. (2006) and Breton et al. (2014) obtained on more hermaphrodite flowers.

Data concerning open-pollination of SA-A (293 fruit/2720 flowers), SA-B (23/365), OeCH (26/1424), OeIN (2/100), *Dolce Agogia* (12/120), and '*Favolosa*' (40/336 or 11.90% cannot be easily compared because open-pollination of each female variety depends on the genotypes of surrounding varieties rather than the tree itself.

Discussion

Comparison of progeny size from *O. e. cuspidata* in Montpellier (present results) and in Italy (Cáceres et al. 2015) shows that embryo rescue is useless. The determination of self-incompatibility in olive is expensive and requires considerable investment.

S-alleles were identified for the cultivated olive variety '*Favolosa*' as *R4R6* using three *O. e. cuspidata* accessions, namely, the two from South Africa (SA-A *R4R6* and SA-B *R3R4*) and one from China (*R5R6*). The fourth *O. e. cuspidata* accession from India remains partially deciphered as *R1R5*, *R1R4* or *R4R5*. *R4* is the lowest ranking recessive S-allele and thus did not influence the outcome of crosses unless the parent was homozygous for *R4*, but a homozygous *R4R4* olive individual has not been documented. Data on self-pollination shows that all these pairs are partially self-compatible—thus *R1R4* could be eliminated based on the Breton et al. (2016) model, and open-pollination data showed that all host varieties received some compatible pollen. The Chinese accession is the first occurrence of *R5R6* pair reported for an *Olea* individual.

The pedigree of '*Favolosa*', a selection from open-pollinated progenies from *Frantoio* *R4R5*, infers that '*Favolosa*' should carry either *R4* or *R5* and an unknown S-allele from the pollination source. '*Favolosa*' received *R6* from free pollination. It is logical to suppose that a pollen grain coated by *R5* had not

pollinated *Frantoio*. However, *R6* was not detected previously in Central Italy and is infrequent in Central Italy, but it is present in '*Nostrale Rigali*' in Sicily (Farinelli et al. 2015). The frequency of *R6* among about eighty varieties was 9/155 (0.06), whereas the frequency of *R3* was 35/155 (23%) (unpublished statistics). The number of *O. e. cuspidata* individuals here is too low to speculate on the frequency of *R6* in its populations.

The self-compatibility rate is expected to be higher for the *R6R4* pair because of three levels of dominance difference between *R6* and *R4* (Breton et al. 2016). Mehlenbacher (1997) found nine levels of dominance among 39 *S*-alleles in Hazelnut, and self-fertility was present in cutleaf hazelnut (Mehlenbacher and Smith 2006). Self-fertility occurs in genotypes combining *S28* and *S1*, *S2* or *S26* *S*-alleles—all three being recessive to *S28*. However, the possibility that *S28* alone leads to self-fertility by mutation in the male part cannot be eliminated.

There is concern because *OeSA-B* was mated by the other three accessions, but not by *Frantoio*. This is not important because '*Leccino*' and '*Frantoio*' carry the *R5* *S*-allele. However, it is frequent that a mate predicted to succeed, leads to no fruit set (Farinelli et al. 2015). This does not contradict the SSI model.

Cáceres et al. (2015) used % for O-PR and self-pollination of 100 emasculated flowers. However the results are ambiguous, because they did not say whether they had or had not counted male-sterile flowers, the proportion of which is variety dependent. The exact description should be 'fruit set for 100 hermaphrodite flowers' that standardizes data to enable comparison of fruit sets between varieties.

Self-pollination for the *R3R4* pair is expected to be relatively low. Thus 0.28 (0.28 fruit for 100 emasculated flowers calculated for 1 fruit / 362 emasculated flowers) is probably overestimated, and the range in variation could be important on a larger sample.

Unambiguously *O. e. cuspidata* from China carries, for the first time, the *R5R6* pair, a combination not found in cultivated varieties (Breton et al. 2014; Farinelli et al. 2015). Self-compatibility is expected to be relatively high (with *Frantoio* for reference). Open-pollination is low probably because varieties carrying *R5* are frequent in the area (Farinelli et al. 2015). All varieties that do not harbor *R6* release compatible pollen for the host *O. e. cuspidata* in the Perugia collection. This illustrates the paradoxical inference

from SSI as in any location free pollination of one host variety does not depend on the host variety itself, but on the surrounding varieties. Thus trees carrying *R6* even at low frequency are pollinators for 99% of host varieties, and consequently it is not surprising that '*Favolosa*' harbors *R6*. This is one of the consequences of the SSI model, and does not happen with the GSI model.

Conclusion

The olive subspecies *O. e. europaea* and *O. e. cuspidata* share many molecular markers and a few are specific of each species (Cáceres et al. 2015). Moreover they share the same self-incompatibility system. This study and that of Cáceres et al. (2015) will now enable us to start on a largescale hybridization program between the two subspecies to obtain large progeny populations for screening for agronomic traits such as resistance to cold, diseases and pests. This study shows that crosses can be chosen based on compatibility.

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