Theor. Appl. Genet, 54, 113-116 (1979)

Genetics of Incompatibility in *Corylus avellana* L.*

Maxine M. Thompson
Department of Horticulture, Oregon State University Corvallis, Oregon (USA)

Summary. Diallele crosses of sibs and parents of 3 parental combinations demonstrated sporophytic type of incompatibility in *Corylus avellana* L. One gene with multiple alleles was indicated. All 6 alleles present in the 4 parental cultivars and in their progeny exhibited dominance in pollen and independent action in the pistil. Individuals homozygous for *S*-alleles appeared in progeny of parents having one allele in common. Reciprocal differences occurred in some crosses. The stigmatic surface is the site of the incompatibility reaction. Incompatible pollen germinated abundantly but failed to penetrate into the stigma cells.

Key words: Incompatibility – Filberts – Hazelnuts – *Corylus*

Introduction

During the course of several years' breeding and pollination studies with filberts (= hazelnuts), *Corylus avellana* L., all cultivars tested were self-incompatible and considerable cross-incompatibility was found. Compatibility relationships, originally determined for the purpose of making successful hybridizations, suggested that the sporophytic type of incompatibility exists in this species; reciprocal differences occur, indicating dominance, and the site of the reaction is at the stigmatic surface. This type of genetic control was first reported for *Crepis foetida* (L.) (Hughes and Babcock 1950) and *Parthenium argentatum* Gray (Gerstel 1950) and has subsequently been reported in other members of the Compositae as well as in the Cruciferae and other families. This paper reports experiments designed to obtain more information on the genetics of incompatibility in filberts. Diallele crosses of siblings and parents were made for 3 different parental combinations involving 4 different parent cultivars.

Materials and Methods

Compatibility relationships were determined by observations of pollen tubes using stylar squashes in aniline blue dye (0.1 g aniline blue, 0.71 g K_3PO_4, 100 ml distilled water) and fluorescence microscopy. In compatible crosses masses of long tubes are evident in the styles, whereas in incompatible crosses abundant pollen germinates but only very short tubes are formed. These do not penetrate the stigmatic surface and often terminate with a more or less pronounced swelling, or bulb. For several years we have used this technique to determine compatibility for breeding and, in all cases, nut set was correlated with pollen tube tests.

Prior to female anthesis, catkins were removed and limbs were bagged on test trees. When catkins were about to shed, pollen was collected and stored in a cotton-stoppered vial in the freezer. Despite repeated thawing and freezing, which resulted from the same pollen being used on flowers of various selections as they reached anthesis at successive periods, viability remained good throughout several weeks. Female flower clusters at full anthesis were detached from trees and placed on damp filter paper in petri dishes. For each clone, 3 or more clusters, each consisting of about 8 to 24 stigmatic styles, were pollinated in the laboratory as soon as possible after they were detached, left in the petri dishes overnight at room temperature (18-20°C) to stimulate pollen tube growth, and then put in a freezer until convenient to analyze. Styles are very thin and soft enough to squash either fresh or frozen without using a softening agent. Storing the pollinated clusters in the freezer is preferable to storage in a killing fluid because in the latter case the short incompatible tubes may be washed off in the fluid. The absence of incompatible tubes on squashed styles could be confused with lack of germination which occurs either when stigma receptivity is lost or when pollen is inviable.

Diallele crosses were made for parents and progeny for each of 3 different crosses, 'Barcelona' X 'Lansing', 'Barcelona' X 'Extra Ghiaghli' and 'Fitzgerald 20' X 'Lansing'. Previous pollination trials had revealed reciprocal differences in compatibility of the 'Barcelona' X 'Lansing' combination. Tentative *S*-allele genotypes for 'Barcelona' (S_1S_2) and for 'Lansing' (S_1S_3) were assigned. Dominance in the pollen and independent action in the pistil was indi-

---

* Oregon Agricultural Experiment Station Technical Paper No. 4986, Corvallis, Oregon 97331

0040-5752/79/0054/0113/$ 1.00

cated, with S_1 dominant over S_2, and S_3 dominant over S_1. In addition to the parent and progeny diallele crosses, tester pollen from a different source, bearing the specificity of the recessive allele of 'Barcelona' (S_2), was used on progeny of both crosses involving 'Barcelona' in order to help elucidate their genotypes. Likewise, tester pollen having the specificity of the recessive allele in 'Lansing', (S_1) was used on progeny of 'Fitzgerald 20' X 'Lansing'.

Results

'Barcelona' x *'Lansing' Progeny*

Compatibility relationships of a diallele cross of 'Barcelona' x 'Lansing' progeny and parents, and of progeny and parents crossed with tester pollen previously established as having S_2 specificity are given in Table 1. In the 11 progeny clones only 2 types of pollen were formed, S_1 and S_3, indicating that, in pollen, S_1 and S_3 are dominant over S_2 and that S_3 is dominant over S_1. Pistil reactions in the sib diallele also fell into 2 groups. Assuming no dominance in the pistil a third group, represented by S_1S_3, was expected but did not occur. Presumably this deficiency was because there were too few individuals to recover all 4 genotypes in the progeny. The 2 genotypes postulated for the first group, S_1S_1 and S_1S_2, were differentiated from each other by the tester pollen obtained from selection No. 20-58, known to be homozygous for S_2. The ratio of progeny genotypes (S_1S_1, S_1S_2, S_1S_3, and S_2S_3), expected to be 1:1:1:1, actually was 2:3:0:6. In this progeny, as in the others, the small number of individuals of each type precluded the use of X^2 tests.

'Fitzgerald 20' x *'Lansing' Progeny*

Compatibility relationships of a diallele of 'Fitzgerald 20' x 'Lansing' progeny and parents and of progeny and parents crossed with S_1 tester pollen obtained from 'Barcelona' are given in Table 2. 'Fitzgerald 20' pollen was designated S_2 because it is incompatible on pistils of 'Barcelona' (S_1S_2) but compatible on those of 'Lansing' (S_1S_3). The other allele in 'Fitzgerald 20' was arbitrarily designated S_{11}. Amongst the 11 sibs there were 2 types of pollen, S_1 and S_3. Neither of the 'Fitzgerald 20' alleles, S_2 or S_{11}, were found as pollen specificities in the progeny, indicating that both of them are recessive to both 'Lansing' alleles, S_1 and S_3. The 2 progeny genotypes comprising the first pistil group, S_1S_2 and S_1S_{11}, and the two genotypes comprising the second, S_2S_3 and S_3S_{11}, were discriminated from each other by S_2 pollen of 'Fitzgerald 20'. 'Barcelona' pollen behaved the same as pollen of the 5 progeny bearing the S_1 specificity.

'Barcelona' x *'Extra Ghiaghli' Progeny*

Compatibility relationships of a diallele of 'Barcelona' x 'Extra Ghiaghli' progeny and parents and of progeny and

Table 1. Compatibility relationships in a diallele cross of 'Barcelona' 'Lansing' sibs, in reciprocal backcrosses of progeny to parents, and in crosses of parents and progeny to S_2 tester pollen

		Pollen specificity				
		S_1		S_3		S_2
Clone	Pistil genotype	'Barcelona' 18-19 18-17	13-13 13-19 18-22	'Lansing' 13-22 13-31 13-45	 18-20 19-20 19-30	20-58
18- 9 18-17 13-13 (?)	S_1S_1	–[a]		+[b]		+
'Barcelona' 13-19 18-22	S_1S_2	–		+		–
'Lansing'	S_1S_3	–		–		+
13-22 18-20 13-31 19-20 13-45 19-30	S_2S_3	+		–		–

[a] (–) = incompatible combination
[b] (+) = compatible combination

Table 2. Compatibility relationships in a diallele cross of 'Fitzergerald 20' 'Lansing' sibs, in reciprocal backcrosses of progeny to parents, and in crosses of parents and progeny to S_1 tester pollen

Clone	Pistil genotype	Pollen specificity S_1	S_3	S_2
		'Barcelona' 25-32 25-50 26-22 25-83 26-3	'Lansing' 26-2 26-11 26-17 26-7 26-9 26-35	'Fitzgerald 20'
25-32 25-50 26-22	$S_1 S_2$	–[a]	+[b]	–
25-83 26-3	$S_1 S_{11}$	–	+	+
26-2 26-11 26-17	$S_2 S_3$	+	–	–
26-7 26-9 26-35	$S_3 S_{11}$	+	–	+
'Lansing'	$S_1 S_3$	–	–	+
'Fitzgerald 20'	$S_2 S_{11}$	+	+	–

[a] (–) = incompatible combination

[b] (+) = compatible combination

Table 3. Compatibility relationships in a diallele cross of 'Barcelona' 'Extra Ghiaghli' sibs, in reciprocal backcrosses of progeny to parents, and in crosses of parents and progeny to S_2 tester pollen

Clone	Pistil genotype	Pollen specifificity S_1	S_x	S_2
		'Barcelona' 23-10 23-17 23-24 23-31 23-35 23-38 23-42 23-48 23-51 23-52 23-55	'Extra Ghiaghli' 23-7 23-59	20-58 23-6 23-61
23-10 23-17 23-35 23-48 23-51 23-52 23-55	$S_1 S_x$	–[a]	–	+[b]
23-24 23-31 23-38 23-42	$S_1 S_y$	–	+	+
23-7 23-59	$S_2 S_x$	+	–	–
23-6 23-61	$S_2 S_y$	+	+	–
'Barcelona'	$S_1 S_2$	–	+	–
'Extra Ghiaghli'	$S_x S_y$	+	–	+

[a] (–) = incompatible combination

[b] (+) = compatible

parents crossed with S_2 tester pollen obtained from selection No. 20-58 are given in Table 3. The alleles of 'Extra Ghiaghli' are designated S_xS_y because they have not been tested against all of the 11 alleles thus far identified in unpublished studies. Three different pollen specificities, S_1, S_x, and S_2 are represented in the 15 sibs. Thus, in the pollen S_1 is dominant to S_x and S_y, S_x is dominant to S_2 and S_y, and S_2 is dominant to S_y. With no dominance in the pistil and with 4 different alleles segregating in the progeny, the expected 4 genotypes, S_1S_x, S_1S_y, S_2S_x, and S_2S_y, resulted in 4 mating groups which were expected to occur in a ratio 1:1:1:1. They were actually 7:4:2:2.

Discussion

The small number of mating groups found in all 3 progenies support the hypothesis of monofactorial control with multiple alleles. Reciprocal differences in compatibility between some sib groups and between some parent-progeny crosses are evidence of dominance. The 6 alleles present in the 4 parents and their progeny exhibited dominance in the pollen but independent action in the pistils. The dominance relations in the pollen are as follows: S_3 is dominant S_1, S_2, and S_{11}; S_1 is dominant over S_2, S_{11}, S_x, and S_y; S_x is dominant over S_2 and S_y; and S_2 is dominant over S_{11} and S_y. However, the possibility is not excluded that with additional alleles, not included in this study, independent action in the pollen or dominance in the pistil may occur. In other species, with sporophytic control, both types of gene expression have been reported in both pistils and pollen, as for example, *Iberis amara* (Batemen 1954) and *Cosmos bipinnatus* (Crowe 1954).

Acknowledgement

The author wishes to express appreciation to Monica Ray and Susan Thomas for technical assistance and for contributions on interpretation of the data.

Literature

Bateman, A.J.: Self-incompatibility systems in Angiosperms II. *Iberis amara.* Heredity *8*, 305-332 (1954)

Crowe, L.K.: Incompatibility in *Cosmos bipinnatus.* Heredity *8*, 1-11 (1954)

Gerstel, D.U.: Self-incompatibility studies in guayule II. Inheritance. Genetics *35*, 482-505 (1950)

Hughes, M.B.; Babcock, E.B.: Self-incompatibility in *Crepis foetida* (L.) subsp. *rhoeadifolia* (Bieb.) Schinz et Keller. Genetics *35*, 570-588 (1950)

Received October 17, 1978
Communicated by H.F. Linskens

Dr. Maxine M. Thompson
Department of Horticulture
Oregon State University
Corvallis, Oregon 97331 (USA)