

Floral biology of hazelnut

(Review article)

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1 Blooming

Among the temperate-zone fruit trees the hazelnut is the unique one, which excels with a special life history between blooming, pollination and fertilisation. That period lasts in most plant species some hours or a few days, at most, whereas in hazelnut the respective time is much longer and is subject considerably to environmental influence (Trotter, 1930). Blooming of hazel ensues much earlier than the budburst of any other deciduous fruit tree in the temperate climate. That is an evolutionary consequence of the coenological status of the species, i.e. the hazel bushes underneath the leafless canopy of the wood had the only chance to release pollen, which was drifted by the wind at sunny days of the early spring, unhindered. Fertilisation, however, occurred much later, when weather conditions became suitable.

That early blooming as a special character was maintained in the cultivated varieties of the species. In Hungary (being on the northern border of the natural distribution of hazelnut) blooming started in some seasons during December already (Szentiványi, 1980). In Germany, blooming dates are much more dependent on the geographic site (micro-district) than on the season (Stritzke, 1962). In Slovenia, the interval was 36 days long between the dates of blooming, which varied depending on the year. Between the earliest and latest blooming varieties, however, there was 6-13 days difference (Modic, 1974).

In SW-France, female blooming of hazelnut lasts from early December to end of March, as early varieties (*Negret*) and late ones (*Cosford*) start at different dates (Germain & Leglise, 1973). At the same site, the male bloom of catkins starts in the second half of December (*Tonda Gentile delle Langhe*) and ends with the early March (*Merveille de Bollwiller*). In continental climatic conditions (lower temperature minima) blooming starts later and lasts shorter (Kavardzhikov, 1980).

It is independent from the season that female flowers bloom for a longer period than male flowers do. As average

of years, pollen release of individual catkins lasts 5.9-8.6 days, it means that the functional time of male flowers is much shorter than of female flowers (Modic, 1974). The blooming period of female flowers starts with the appearance of the bright red stigmata on the surface of mixed buds, and it ends when the long, curled stigmata turn



Figure 1 Bloom phenology of male and female flowers in filbert cultivars at Chieri (Torino) (after Zannini et al., 1983)

brown (*Romisondo et al.*, 1978). At that time, the two stigmata fused at the basis are connected with the ovule still rudimentary. In SW France, the blooming period of female flowers lasted 1–2.5 months. That period was especially long at the variety *Négret* as stated by *Bergougnoux et al.* (1978). The release of pollen lasted in the varieties one month, at most. The blooming period of male and female flowers varied greatly, according to the season, depending on the weather (*Germain*, 1983). Weather effects are relatively more expressed in the bloom of catkins (pollen release) as it stops, temporarily, as the temperature dropped below 0 C° (*Barbeau*, 1973).

Bergamini & Ramina (1968) determined the quantity of "cold hours" necessary to complete the rest period of the buds:

shoot buds	1050–1300,
mixed buds with female flowers	600–800,
catkins (male flower buds)	350–600 hours.

That high degree of dichogamy serves as a tool of avoiding self-pollination. Exceptionally mild winters may not fulfil the chilling requirement of mixed buds. Thus in Spain, when the bloom of varieties of higher chilling requirement is disturbed (e.g. *Ribet*, *Tonda Gentile delle Langhe*, *Amandi*) catkins are shed prematurely (*Ninot & Mena*, 1983).

The majority of varieties are proterandrous, however some varieties are homogamous or even protogynous (*Germain*, 1983). *Figure 1* and *2* show the blooming time and the type of dichogamy of hazel varieties. It is a reason of precaution that most of the varieties belong to transitory, yearly variable types. There are but a few consequently protogynous (e.g. *Barcelona*, *Guscio Tenero*, *Bandnuss*, *Neue Riesennuss*), or proterandrous (e.g. *Lambert Filbert*). Early blooming varieties are more inclined to be proterandrous (*Modic*, 1974). *Figure 3* gives an idea, how the female and male relative blooming time changed in 30 varieties during a period of 4 years. Taking into account the above information, reference varieties proposed by *Jona* (1986) might help to classify varieties according to blooming types:

- 1 highly protogynous *Négret*, *San Giovanni*
- 2 protogynous *Tonda Romana*
- 3 homogamous *Merveille de Bollwiller*, *Morell*
- 4 proterandrous *Barcelona*, *Duchilly*
- 5 highly proterandrous *Tonda Gentile delle Langhe*, *Segorbe*, *Bergeri*.

We have to remark, however, contradictions are found in that system too, e.g. the variety *Barcelona* is in many cases (sites and authors) considered to be protogynous.

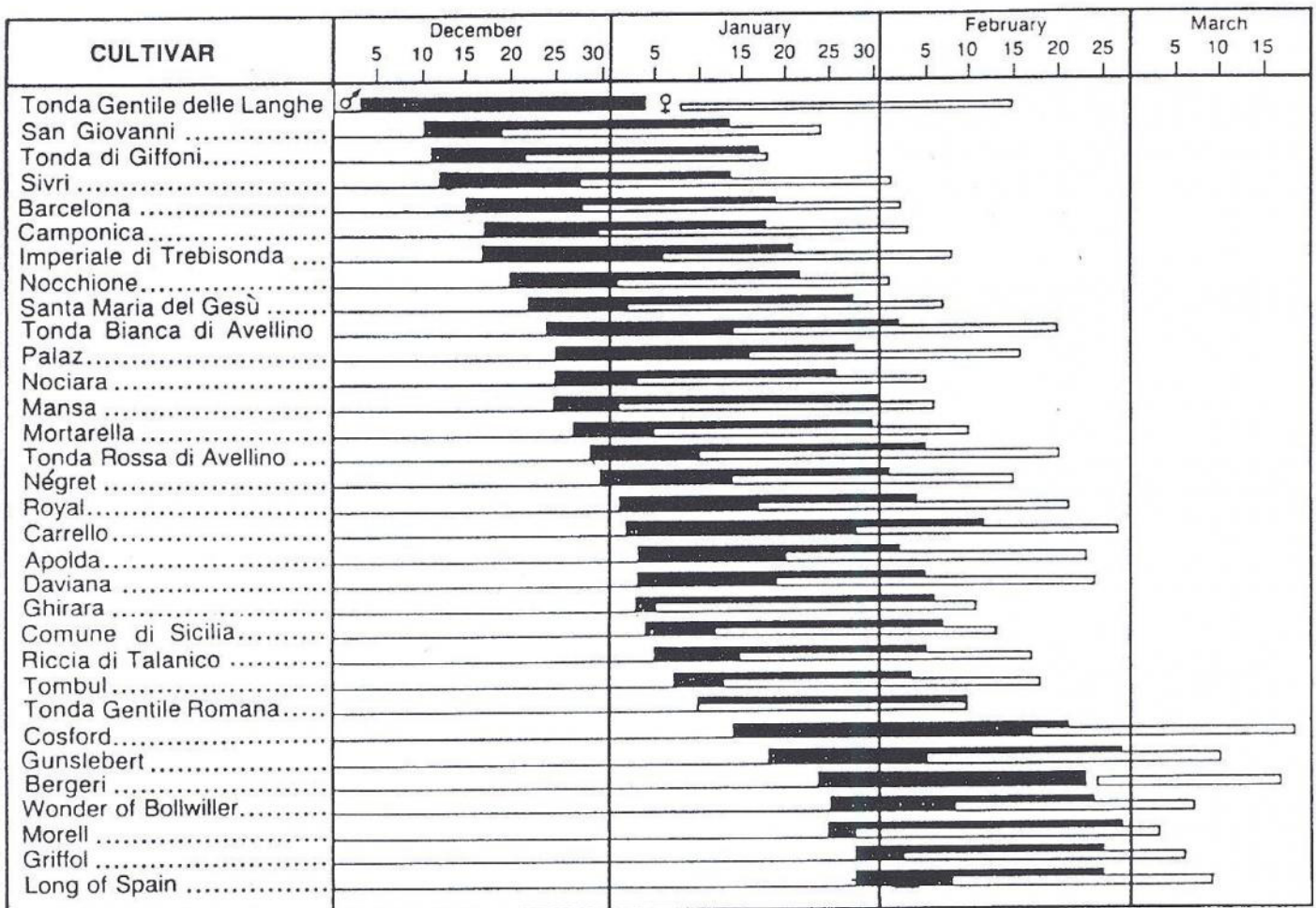
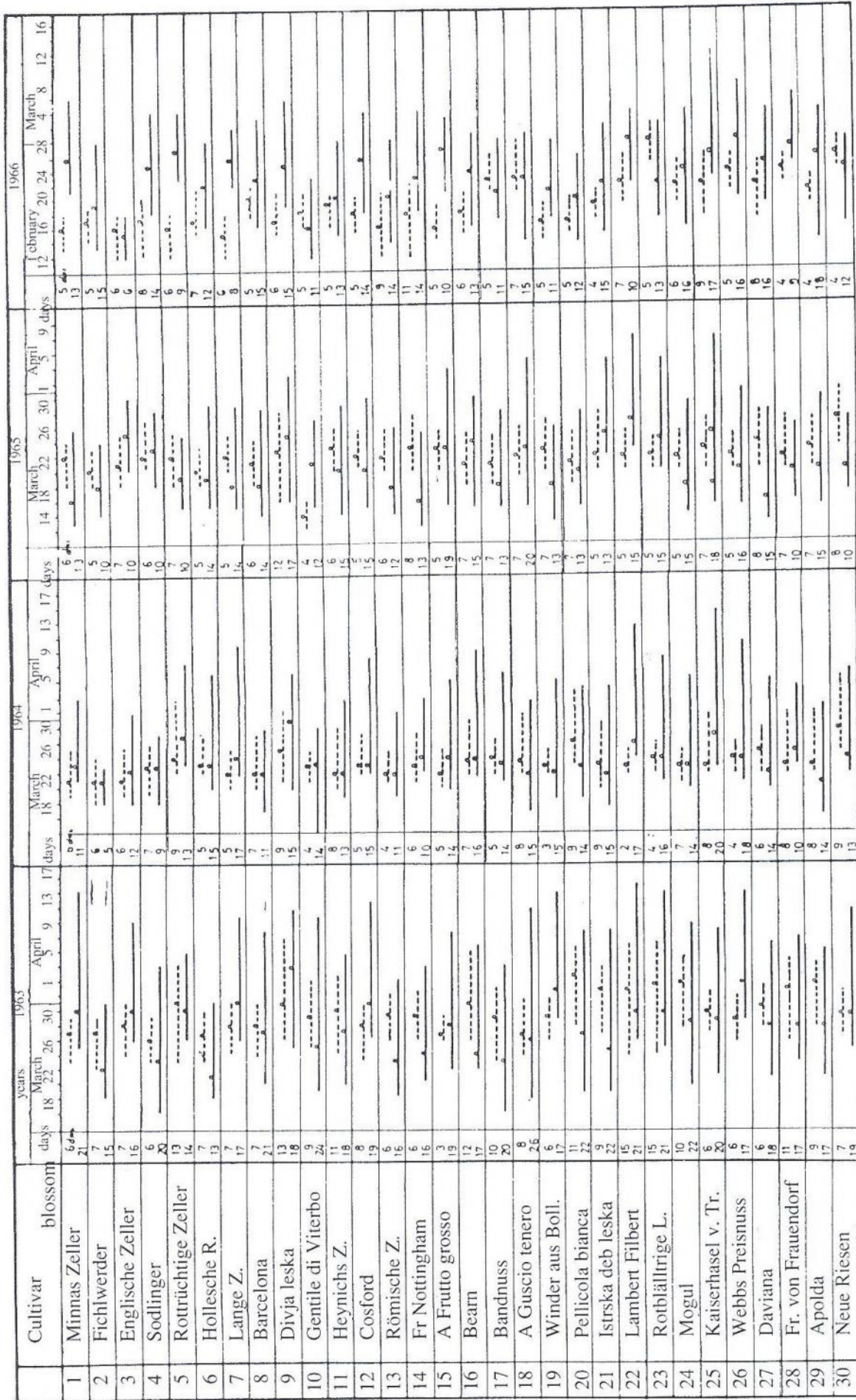


Figure 2 Flowering time of male and female flowers near Rome (average of observations of years 1975 to 1980). (From Manzo, P. and Tamponi, G. cit. *Jona*, 1986)



--- male inflorescence: ♂
 - - - female inflorescence: ♀

Figure 3 The phenophases and the duration of blossoming of filbert and hazel bushes (Modic, 1974)

Szentiványi (1980) claims that the rest period of mixed flower buds may change depending on their proterandrous or protogynous character. In highly proterandrous varieties the chilling requirement of the mixed buds may approach that of the vegetative shoot buds (Romisondo, 1978).

The sense and degree of dichogamy may change as a consequence of weather too. At high spring temperatures stimulate first of all the bloom of the male flowers (catkins), consequently, proterandry is stimulated in proterandrous varieties, whereas homogamy in protogynous varieties. On the contrary, cool weather may delay or prolong the bloom of male flowers; i.e. protogyny will be accentuated in protogynous varieties and homogamy in proterandrous varieties. The climate of the growing sites (geographic latitude and longitude, elevation above sea level, exposition) and weather conditions may modify in a complicated manner the blooming type of varieties. The variety *Tonda Gentile delle Langhe* is proterandrous at 70–80% in SE-France, whereas under continental climatic conditions it turned to be homogamous or even protogynous due to the cool autumn (Romisondo, 1978). Kavardzhikov (1980) states that the degree of dichogamy diminishes under continental conditions. In Germany, there is a higher degree of proterandry experienced during some years as a consequence of warm weather, whereas rather protogyny because of cooler weather (Stritzke, 1962). Those examples published in the literature prove that association of varieties in planning of plantations requires a careful and critical study of blooming dates referring to different types of dichogamy as well as to the natural conditions of the growing site (Modic, 1974).

In plantations of Oregon – in contrast to the European experiences – it was generally accepted that 90% of varieties used to be protogynous. Female bloom started, depending on the temperature, during the period between December and February, most frequently at the end of January (Olsen et al., 2000). The stigmata maintain their functionality during 3 months. Between pollination and fertilisation some 4–5 months elapsed in Oregon: thus fertilisation ensues between mid of May and end of June.

2 Relations of fertilisation

2.1 Self-fertility and self-incompatibility

Hazelnut varieties having unisexual flowers are highly or entirely self-incompatible (Schuster, 1922, 1936, Griggs, 1953, McKay, 1966, Jacoboni et al., 1968, Tombesi & Cartechini, 1970, Vidal-Barraquer, 1974, Bergougnoux et al., 1978, Thompson, 1979a). Moreover, at the bloom of female flowers there is scarcely if any pollen of the same plant or variety available. In the variety *Tonda Gentile delle Langhe* the high degree of self-sterility is attributed to the sterility of its pollen, which is aggravated by adverse effects of the environment (Romisondo, 1963).

Some Italian varieties (*Carello*, *Santa Maria del Gesu*, *Tonda Romana*) some partial self-fertility has been experienced (Geraci, 1974), but in planning of plantations we had better to consider them as self-incompatible and provide for polliniser variety. That is valuable in the case of *Tonda di Giffoni*, which set fruit with artificial self-pollination at a rate of 14.7%, only (Limongelli, 1983). Low self-fertility has been stated in Spain to the variety *Gironell* (Vidal-Barraquer, 1974). *Barcelona* set fruit after self-pollination at a rate of 6.2%, which is a 1/6 fraction of the figure obtained by open pollination (Zielinski & Thompson, 1967). Partial self-fertility is often an artefact, i.e. result of technical mistake because it is difficult to prevent pollination by the very small pollen grains drifted by the wind (Thompson, 1971). Most recent results did not change the conclusion known since long (Schuster, 1922, Johansson, 1935, Rivals & Everinoff, 1955, Riera, 1958, Kolesnikov, 1959, Romisondo, 1965, Mc Kay, 1966, Paglietta, 1970, Modic, 1971 etc.), all varieties of the species *Corylus avellana* L. should be considered as self-incompatible.

2.2 Cross fertilisation

The moment of pollination does not depend on the viability (longevity) of the ovule (Romisondo, 1963, Baron & Stebbins, 1969). It was stated that the pollen tubes starting at February 1 reached the basis of the style within 10 days. The ovules, however, started to be visible at the end of March. Embryo sacs finish their formation at the end of May; thus fertilisation (cytological) cannot be completed earlier than that (Romisondo, 1965).

It is generally accepted that the success of cross fertilisation is conditioned by a possibly early pollination, the earlier the better. Painter (1965) found, on the contrary, that the receptivity of female flowers was better around the main bloom and immediately after that than at the beginning of bloom. Geraci (1968), Germain & Leglise (1973), as well as Bergougnoux et al. (1978) claim that the optimal receptivity of the stigma is about 15 days later than the start of bloom. On the contrary, the fertility of *Barcelona* (Thompson, 1965), and *Tonda Gentile delle Langhe* (Romisondo et al., 1978, 1978a) was not influenced by the time of cross-pollination. The stigma and style are receptive independently from the stage of bloom but weather conditions are more decisive. The quality of the pollen is more important than its quantity in fertilisation (Romisondo, 1965, 1968).

Compatible combinations proposed by Romisondo (1978) and those recommended by Jona (1986) are presented in Table 1 and 2. It is surprising that in some combinations also *Tonda Gentile delle Langhe* was included as polliniser in spite of the fact that studies prove the high rate of sterile pollen of that variety. The security of cross fertilisation is increased substantially by the conscious choice of varieties with different S-genotypes as far as explored (Table 3).

Table 1 Compatibility combinations in hazelnut cultivars (after Romisondo, 1978)

Cultivar	Pollinizer
A Guscio Tenero	Cosford, Istrski debeloplodni leski
Apolda	Cosford, Sodlinger
Bandnuss	Cosford, Garibaldi, Gunslebener Z., Hallesche R., Istrski debeloplodni leski
Barcelona (Fertile di Coutard, Castanyera)	Alpha, Avelline de Barcelona, Avelline Grosse Ronde, Bandnuss, Bellhuster n.2, Bergeri, Bollwiler, Brunswick, Butler, Chaperone Compton, Cosford, Creswell, Daviana, Duchilly Du Provence, English Zeller, Fichterwedersche Zellernuss, Fitzgerald 20, Gem, Gunslebert Hall's Giant, Henneman n. 2, Henneman n. 3, Impératrice Eugénie, Imperial de Trebizonde, Jemttegaard n. 19, Lansing, Longue d'Espagne, Luisen, Morell Negreta, Nonpareil, Nooksack, Nottingham, Pautet, Percy 14, Prince Arden, Purple Avelline, Royal, Selection, Segorbe, Sicily, Sodlinger, Tombul, Tonda Gentile delle Langhe, Tonda rossa, White Avelline, Willamette Woodford
Bearn	Cosford, Istrski debeloplodni leski
Butler	Ennis, Meraviglia di Bollwiler
Brixnut	Meraviglia di Bollwiler
Carrello	Mausa, Minnolina, S. Maria del Gesu
Cosford	Gunslebert, Istrski debeloplodni leski, Longue d'Espagne, Meraviglia di Bollwiler, Morell
Daviana	D'Alger, Du Chilly, Grosse Ronde, Istrski debeloplodni leski, Meraviglia di Bollwiler, Morell
Du Chilly	Alpha, Clackamas, Daviana, Gasaway
Englische Zellernuss	Cosford, Sodlinger
Ennis	Butler, Meraviglia di Bollwiler
Fichtwerder	Sodlinger
Fr. V. Fravendorf	Cosford, Istrski debeloplodni leski
Fr. V. Nottingham	Cosford, Istrski debeloplodni leski
Garibaldi	Bandnuss, Römische Nuss, Verbesserte Cosford, Webbs Preisnuss
Grossal (Gironell)	Daviana, Culpla, Gunslebert, Negret, Pautet, Segorbe, Tonda Gentile delle Langhe, Trenet
Gubener Zellernuss	Bandnuss, Gunslebener Zellernuss, Romische Nuss, Verbesserte Cosford, Webbs Preisnuss
Gunslebener Zellernuss	Bandnuss, Römische Nuss, Verbesserte Cosford, Webbs Preisnuss
Gunslebert	Cosford, Longue d'Espagne, Impératrice Eugénie, Meraviglia di Bollwiler, Morell
Hallesche Rieselnuss	Bandnuss, Istrski debeloplodni leski, Römische Nuss, Verbesserte Cosford, Webbs Preisnuss
Heynick's Zellernuss	Cosford, Sodlinger
Impératrice Eugénie	Gunslebert, Meraviglia di Bollwiler, Morell
Istrski debeloplodni leski	A Guscio Tenero, Bandnuss, Bearn, Frühe Nottingham, Frühe von Frauen, Kaiserhasel v. Tr., Lambert filbert, Neue Riesen, Rotblättrige, Webb's preiss, Wunder a Bollwiler
Lambert Filbert	Cosford, Istrski debeloplodni leski

Cultivar	Pollinizer
Lange Zellernuss	Cosford
Lansing	Meraviglia di Bollwiler
Longue d'Espagne	Cosford, Daviana, Gunslebert, Impératrice Eugénie, Meraviglia di Bollwiler, Morell
Meraviglia di Bollwiler	Cosford, Daviana, Longue d'Espange, Impératrice Eugénie, Istrski debeloplodni leski, Morell
Minnas Zellernuss	Cosford, Sodlinger
Mogul	Cosford, Sodlinger
Morell	Cosford, Daviana, Gironenc, Grifoll, Impératrice Eugénie, Longue d'Espange, Martorella, Meraviglia di Bollwiler.
Negret	Artellet, Cosford, Daviana, Fertile de Coutard (Castanyera), Gironell, Gironenc, Grossal, Gunslebert, Meraviglia di Bollwiler, Negret Garrofi, Pautet, Pinyolenc, Planeta, Ross, Segorbe, Tonda Gentile delle Langhe, Tonda di Giffoni, Trenet.
Neue Riesen	Cosford, Istrski debeloplodni leski
Northamptonshire	Princess Royal, White Lambert
Pautet	Castanyera, Gironell, Negret, Ross, Trenet
Pellicola Bianca	Cosford
Römische Zellernuss	Cosford
Rotblättrige Zellernuss	Cosford, Istrski debeloplodni leski
Rotfrüchtige Zellernuss	Cosford, Istrski debeloplodni leski
Santa Maria Del Gesu	Carrello, Favigna lunga, Favigna tonda
Segorbe	Butler, Cosford, Daviana, Ennis, Fertile de Coutard, Grossal, Gunslebert, Impératrice Eugénie, Lansing, Longue d'Espagne, Meraviglia di Bollwiler, Morell, Negret
Tonda Gentile delle Langhe (T.G.L.)	Apolda, Bearn, Barcelona, Camponica, Carrello, Con Frutto Grosso, Cosford, Daviana, Emperor, Fichtmans, Fichtwerder, Grossal, Gunslebert, Imperiale di Trebisonda, Inghilterra, Henneman n. 4., Heynich, Lansing, Meraviglia di Bollwiler, Mogul, Mortarella, Negret, Neue Riesen, Nocchia lunga, Nocchione, Payrone, Pellicola bianca, Riccia di Talanico, San Giovanni, Segorbe, Tonda Romana, Ibridi T.G.L. x Sodlinger: S 1/3; Ibridi Corylus maxima x T.G.L.: BB10; Ibridi Centile di Viterbo x Bearn: H1; Ibridi Payrone x Gentile di Viterbo: G1
T.G.L. x Cosford: 10I	Tonda Gentile delle Langhe
T.G.L. x Cosford: 104E	Tonda Gentile delle Langhe
T.G.L. x Cosford: 3L	Tonda Gentile delle Langhe
Tonda di Giffoni	Cosford, Daviana, Fertile de Coutard, Grossal, Gunslebert, Negret, Segorbe, Tonda Gentile delle Langhe
Tonda Romana	Cosford, Fertile de Coutard, Nocchione, Tonda Gentile delle Langhe, Tonda di Giffoni
Trenet	Castanyera, Culpla, Gironell, Pautet
Webb's Preiss	Cosford, Istrski debeloplodni leski
Whiete Aveline	Barcelona, Daviana

Table 2 Pollen-Stigma compatibility of various cultivars (Germain et al., 1976; Romisondo, 1965, 1977; cit. Jona, 1986)

	Cultivar	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.
1.	Barcelona	-		+	++	D	-	++	++	++	D	++		++	-	-	+	-	++
2.	Bergeri		-					++											++
3.	Cosford	++	-	-	-	-		++		++	++			++			+	-	++
4.	Daviana	++		-	-	-		D	-	-	D								++
5.	Empress Eugenia			-	-	-		++		-	++								++
6.	Grossal			D	++	D	-	++		D	D	++		++		D	++		D
7.	Gunslebert	++	++	++	D	++		-		++	++	++		++					-
8.	Imperiale of Trebisonde	++			+									++		+			++
9.	Long of Spain		++	++	+	++		++		-	++			+					++
10.	Morell			++	++	++		D		++	-								++
11.	Négret	++		++	++	D	++	++		D	D	-		++		+	++		++
12.	Riccia di Talanico																+	++	
13.	Ségorbe	+		++	++	++	+	++		++	++	+		-		D	-		++
14.	Tonda di Biglini	-												+					
15.	Tonda di Giffoni	++		+	+		+	+	+			+	++	++		-	++		
16.	Tonde Gentile delle Langhe	++		++	++	D	+	+	++	D	D	++	+	++	+	-	-	++	-
17.	Tonda Romana	++		+					+				+			++	D	-	
18.	Wonder of Bollwiller	-	+	++	+	+		-	-	+	+			-		+			-

Note: - = Incompatible crossing
 + = Partially compatible crossing
 ++ = Compatible crossing
 D = Dichogamy

Table 3 Hazelnut cultivar and pollinizer combinations. Incompatibility alleles noted in parentheses (Olsen et al., 2000)

Cultivar	Pollinizer
Barcelona (S ₁ S ₂)	Hall's Giant (S ₅ S ₁₅) Gem (S ₂ S ₁₄) Lewis (S ₃ S ₈) VR4-31, VR11-27 (S ₁ S ₃) VR20-11 (S ₂ S ₃)
Ennis (S ₁ S ₁₁)	Casina (S ₁₀ S ₂₁) Hall's Giant (S ₅ S ₁₅) Jemtegaard #5 (S ₂ S ₃) VR20-11 (S ₂ S ₃) VR23-18 (S ₁ S ₃)
Willamette (S ₁ S ₃)	Tonda di Giffoni (S ₂ S ₂₃) Hall's Giant (S ₅ S ₁₅) Gem (S ₂ S ₁₄)
Lewis (S ₃ S ₈)	Tonda di Giffoni (S ₂ S ₂₃) Barcelona (S ₁ S ₂) Hall's Giant (S ₅ S ₁₅) Gem (S ₂ S ₁₄)
Clark (S ₃ S ₈)	Hall's Giant (S ₅ S ₁₅) Gem (S ₂ S ₁₄)

The intrusion of pollen tubes into different regions of the stigma and style depends on the stage of bloom, first the tip of the stigma appeared, then gradually the second third of its length. The receptivity, i.e. its effect on pollen tube growth of that middle part of the style depends greatly on the time of pollination as well as on the actual weather conditions. Hazelnut is the species, which is hardly amenable to find correlation between in vitro pollen tests and the results of cross fertilisation (Romisondo, 1963).

2.3 Inter-incompatibility

Some combinations of known varieties proved to be sterile, as Schuster (1927) reported of *Barcelona x Fertile*

Coutard, Slate (1930) of *Barcelona x Rush*, Stritzke (1962) *Römische Nuss x Bandnuss*, Baldini et al. (1968) *Tonda Gentile delle Langhe x Locale di Romagna*, Thompson (1971) *Barcelona x Montebello*, *Barcelona x Kruse*, *Barcelona x Clackamas*, *Barcelona x Ennis*, *Barcelona x Ryan*. Also interspecific crosses of *Corylus colurna x Barcelona* proved as sterile (Zielinski & Thompson, 1967). Those authors concluded that the sterility of the combination *Barcelona x Hajeski Orijaski* is an additional proof of the identity of the two varieties.

Thompson (1971) listed the inter-incompatible combinations, which have been published during the period 1921-1970:

<i>A de Piedmont</i>	<i>Fertile de Coutard</i>
<i>Avelline de Provence</i>	<i>Fitzgerald 30</i>
<i>Avelline Rouge Ronde</i>	<i>Gentile di Viterbo</i>
<i>Barcelona</i>	<i>Goodpastore</i>
<i>Blanche Ronde</i>	<i>Grosse Blanche</i>
<i>Brixnut</i>	<i>Haleski-Orijaski</i>
<i>Camponica</i>	<i>Kruse</i>
<i>Clackamas</i>	<i>Late Barcelona</i>
<i>Comun - Type A</i>	<i>Montebello</i>
<i>D'Alger</i>	<i>Ryan</i>
<i>Emperor</i>	<i>Tonda Romana</i>
<i>Ennis</i>	<i>White Barcelona</i>

Germain et al. (1976, 1976a) also reported mutual inter-incompatibility of some variety combinations.

In hazel it is relatively easy to prove the compatibility relation between varieties because the tracing of pollen tubes throughout the length of style is a convenient test (Thompson, 1971). That was confirmed in Turkey on an assortment of varieties (Beyhan & Odabas, 1997).

The incompatibility belongs to the sporophytic type with one single locus and a series of alleles (Thompson, 1979b, Germain et al., 1981, Latorse, 1981, Me & Radicati, 1983).

Scanning electron microscopic tests prove that the reaction of incompatibility is located on the surface of the stigma. Reciprocal (mutual) incompatibility is rare among hazel varieties. The genetic analysis of varieties is difficult because of the unilateral incompatibility, which is frequently met (Thompson, 1971, Bergougnoux et al., 1978, Romisondo et al., 1978a). Orientation is helped by the information presented by Romisondo (1978) on the incompatible combination of varieties (Table 4). Information concerning the S-genotype of varieties facilitates prediction of the compatibility relation (Zannini et al., 1983). The new method is suitable to clear earlier contradictory reports on inter-incompatible combinations of varieties (e.g. Johansson, 1935, Schuster, 1936, Stritzke, 1962, Modic, 1974, etc.).

Groups of inter-incompatible varieties have not been distinguished some 40 years ago (Griggs, 1953) but later they have been established in hazel too. Johansson (cit. Romisondo, 1963a) mentioned two groups of inter-incompatible varieties:

Table 4 Incompatibility combinations in hazelnut cultivars (after Romisondo, 1978)

Cultivar	Incompatibility pollinizer
A Frutto Grosso	Cosford, Sodlinger
Barcelona	Avelline de Piemont, Avelline de Provence, Avelline de Rouge Ronde, Blanche Ronde, Brixnut, Camponica, Clackmas, Comun Type A, Culpla, D'Alger, Emperor, Ennis, Fitzgerald 30, Gironell, Goodpasture, Grossal, Grosse Blanche, Haleski Oriaski, Kruse, Late Barcelona, Montebello, Rian, Ross, Tonda Romana, Tonda di Giffoni, White Barcelona
Braunschweiger	Lambert Filbert, Veisse Lambert
Cosford	Bergeri, Daviana, Impératrice Eugénie
Daviana	Cosford, Longue d'Espagne, Impératrice Eugénie
Fertile de Coutard	Ennis, Grossal, Tonda di Giffoni
Gentile di Viterbo	Sodlinger
Grossal	Fertile de Coutard, Ross
Hallesche Rieselnuss	Cosford
Hempels Zellernuss	Lngliche Rieselnuss, Meraviglia di Bollwiller
Impératrice Eugénie	Bergeri, Cosford, Daviana, Longue d'Espagne
Istrski debeloplodni leski	Cosford, Sodlinger
Lambert Filbert	Braunschweiger, Veisse Lambert
Lange Zellernuss	Sodlinger
Lange Rieselnuss	Hempels Zellernuss, Meraviglia di Bollwiller
Lansing	Fertile de Coutard
Meraviglia di Bollwiller	Gunslebert, Hempels Zellernuss, Lngliche Rieselnuss
Negret	Culpla, Grifoll, Negret primerenc
Pauetet	Culpla
Romische Zellernuss	Bandnuss, Soldlinger
Tonda Gentile delle Langhe	Barcelona x T.G.L. (C 3/4), Locale di Romagna, Tonda di Giffoni
Trenet	Culpla, Ross

– *Bolwyller, Hempels Zellernuss, Langliche Rieselnuss*

– *Braunschweiger, Veisse Lambert, Lambert Filbert.*

Recently, the S-genotype of the varieties is noted as the basis of classification (Table 5). Germain (1983) listed 14 inter-incompatible groups on the basis of literature and also on his own experiments. A single locus was only determined

Table 5 Complete or incomplete S allelic formula of 52 filbert varieties (dominant and codominant alleles are underlined> (after Germain, 1983)

Incompatibility group	Cultivar
<u>S1S2</u>	Fertile de Coutard (Syn. Barcelona) (a, b), Camponica (a, b), Kruse (b), Santa Maria di Gesu (Syn. Montebello) a, b), Riccia di Talanico (b), Grossal (a), Morell (a)
<u>S1S10</u>	Tonda di Biglini (a)
<u>S2S11</u>	Fitzgerald 20 (b)
<u>S3S1</u>	Lansing (a, b), Nonpareil (b), Percy 14 (b)
<u>S3S2</u>	Bellhusker (b), Butler (a, b), Compton (b), Jemstegaard 5 (b)
<u>S5S2</u>	Badem (b)
<u>S5S10</u>	Red Lambert (b), White Avelline (b)
<u>S6S10</u>	Henneman 3 (Syn. Macrocarpa) (a, b)
<u>S7S2</u>	Tonda Gentile delle Langhe (Syn. Ronde du Piemont) (a, b, c)
<u>S8S4</u>	Tombul Ghiaghli (b)
<u>S8S10</u>	Nottingham (a, b)
<u>S10S2</u>	Creswell (b)
<u>S12S13</u>	Tombul (b)
<u>S14S2</u>	Gem (b)
<u>S1S?</u>	Brixnut (b), Ennis (a, b), Jemstegaard 21 (b), Ryan (b), Tonda Bianca (b)
<u>S2S?</u>	Tonda di Giffoni (a, b)
<u>S3S?</u>	Cosford (a, b, c), Daviana (a, b), Gassoway (b), Imperatrice Eugénie (a, b), Royal (b), Woodford (b), Bergeri (a)
<u>S5S?</u>	Du Bearn (b), Gunslebert (a), Pellicule Rouge (b), Merveille de Bollwiller (a, b)
<u>S6S?</u>	Rodzeller (b), Corylus Avellana Fusco Rubra (b)
<u>S10S?</u>	Campanica (a, b), Casina (b), Imperiale de Trebizonde (a, b), Longue d'Espagne (Syn. Duchilly) (a), Negret (a, b), Tonda Romana (a)
<u>S15S?</u>	Italian Red (b)

According to (a) E. Germain, INRA Bordeaux, France
(b) M.M. Thompson, University of Corvallis, U.S.A.
(c) P. Romisondo, University of Torino, Italia

in 26 varieties. Associations will be planned much easier with varieties of known genetic constitution than to start with the tedious experiments of cross-pollinations.

In cross-incompatible combinations (like in auto-incompatibility tests) pollen tubes are lagging and developing distorted tubes, which cannot penetrate the stigma (Germain, 1983, Hampson et al., 1993). Mehlenbacher (1997b) applied fluorescence microscopic techniques for the diagnosis of inter-incompatibility.

The S-alleles are already known in some varieties (Thompson, 1979c, Mehlenbacher & Thompson, 1988). Germain (1983) contributed to the list with the identification of 15 alleles. Zannini et al. (1983) made reciprocal crosses

between varieties of known and unknown S-constitution in order to complete the knowledge of S-alleles. So the varieties *Jann's* and *Jemtegaard 19* proved to be $S_{10}S_2$. In other varieties the identification of one allele succeeded only:

S_{10}	<i>Apolda, Payrone</i>
S_2	<i>Aveline Barcelona</i>
S_2	<i>Ribet, Tonda Rossa</i>
S_2	<i>Carello, Mortarella.</i>

The variety *Meraviglia di Bolwiller* remains enigmatic as for its genetic constitution if the model of sporophytic mechanism of hazel was applied. As indicated by Latorse (1981) that variety carries in addition to the dominant allele S_2 also other alleles (S_1, S_2, S_8, S_{12}) as recessives. Zannini et al. (1983) stated incompatibility reaction in pollination with S_{10} pollen too.

With the progress of investigations the S-locus of *Corylus avellana* L. proved to contain, alternatively, as many as 25 alleles (Thompson, 1997a). Recent studies are centred, increasingly, to the biochemistry and the physiological-molecular background of the inter-incompatibility mechanism. Pomper et al. (1998) identified two RAPD-markers in the alleles S_1 and S_2 .

In the selection of polliniser varieties attention ought to be paid to the genetic constitution of the S-locus, let alone the quantity and quality of viable pollen to be dispersed. (Olsen et al., 2000).

Diploid varieties harbour two alleles in their somatic cells as well as in the female flowers. There is no dominance among them, both are manifested. The pollen may contain 1 or 2 alleles, which are dominant or co-dominant. If one of those alleles and one of the alleles of the stigma are identical, the respective cross combination is incompatible. As e.g. the female flowers of the variety *Barcelona* of S_1S_2 genotype were pollinated by the variety *Ennis*, which's pollen carries the S_1 allele, the cross will fail to set fruit. In the pollen of varieties the dominance relations prevail with the only exception recognised up to now, the variety *Tonda di Biglini* (Thompson, 1979a).

2.4 The quantity, viability and sterility of the pollen

The pollen yield of hazelnut is very abundant, i.e. at least 5 million grains are produced per catkin as calculated in earlier papers (Trotter, 1930). The number of pollen grains per anther was estimated in a sample of ten varieties and found to be between 10 thousand (*Tonda Rossa di Avellino*) and 22 thousand (*Noccia lunga*) as reported by Pisani & Giulivio (1968) and Romisondo (1977). Baldini & Pisani (1968) calculated 15 thousand grains per anther as they estimated the pollen yield. Barbeau (1972) took 130-260 male flowers per catkin, whereas Pisani & Giulivio (1968) 180-290. Each flower bears 8 stamina; thus one catkin produces normally 22-35 million pollen grains (Szentiványi, 1980).

Varieties producing high rates of sterile pollen are not suitable to serve as polliniser in a plantation. E.g. the variety *Tonda Gentile delle Langhe* with a genotype of S_2S_7 ,

produces many irregular pollen grains, which are not viable or grow weak tubes (Riera, 1958, Romisondo, 1963, Olsen et al., 2000). The rate of empty grains may attain 36% (Me et al., 1983). It was also found that grains even of regular size and shape are, all the same, unable to fertilise because of some alleged hormonal or nutritional troubles, which may aggravate the sterility of genetically determined reduced viability in affected varieties (Romisondo, 1978). Among the 40 varieties observed in Germany as for their pollen viability (tube-growing ability in vitro) significant fluctuation was observed over the experimental years (Stritzke, 1962).

Pollen quality is an important varietal character, but the quantity is also decisive. Thus low quantity is a property of *Ribet* and *Tonda Romana* (Jona, 1986). Some varieties produce pollen with a high (30-50%) rate of empty grains (Barbeau, 1972). Considering the huge quantity of pollen produced with the reduction of that extent should still supply the plantation with the amount necessary (Germain, 1983).

The effect of weather, especially the temperature preceding immediately the enlargement of catkins and the dispersion of pollen, is decisive from the point of view of viability. During the long period, which elapses between pollination and fertilisation, the generative nucleus of the pollen tube may starve because of the lack of reserve nutrients or even of excesses in weather conditions. Unfavourable conditions of the site may increase the disadvantage of genetically determined reduced viability of the pollen; thus the chances of cross-pollination may become critical (Szentiványi, 1980). Griggs (1953) claims that in North-California 600 m above sea level hazelnut production is baffled because the pollen dispersion ensues prematurely, at the end of summer or during the autumn.

Frost may kill the pollen or impair its ability of fertilisation. Hazel is most eligible among the temperate zone fruit species to suffer that damage. Frost may threaten just at the beginning of pollen tube growth. Later on cold tolerance increases as the pollen tube penetrated the stylar tissue. According to Romisondo (1965) minima as $-5, -6$ C° are tolerated though the speed of growth is braked. Thus the time necessary for the pollen tubes to reach the base of the style may attain 20 days.

2.5 Fruit set of open pollinated flowers

Hazelnut produce plenty of flowers; thus the yields are less limited by the number of generative shoots, in contrast to chestnut and walnut. The primary condition of fertility is the process of fertilisation. Mixed buds with female flowers are grown abundantly in the leaf axes of shoots. The number of female flowers depends on the length of shoots (Barbeau, 1972, Germain & Leglise, 1973, Heitz, 1973, Barbe, 1974). The mean length of fruit bearing shoots is about 15-20 cm, but in old plantations without adequate pruning and at weak condition 10-15 cm or even shorter shoots mean the risk of low yields. Not only the low number of generative buds but rather the weak vitality of the female flowers is decisive. Shoots shorter than 5 cm are considered as entirely unfruitful (Romisondo, 1966).

Mixed buds are expected to appear in the leaf axes or even in the lower part of the axis of female inflorescences. In the last case the presence of growing fruits may inhibit the differentiation of mixed buds completely (Barbeau, 1972).

Optimal size of the bearing shoots depends on the variety, the age of the bush or small tree, its health and nutritional condition (Szentiványi, 1980). On young, healthy, vigorous plants the relatively longer (within reasonable limits) shoots bear the most developed female flowers. Female inflorescences inserted immediately below the catkins are usually larger and the chance to find empty fruits on them is lower than else (Pisani, 1968).

Pruning, nutrition and irrigation of aged plants must be carefully observed in order to induce well-developed shoots and maintain the balance between vegetative and reproductive functions. (Romisondo, 1978). At similar conditions those shoots, which enjoy better illumination will bear 1.5–3 times more female flowers and later fruits than in the shaded ones (Bergougnoux et al., 1978).

Hazel is provided with special morphological tools in order to keep up with the conditions of the early season when its bloom is timed. Pollen is captured on the whole surface of the stigma. The club-shape papillae of the stigma is extended on the 4/5 of the style (Romisondo, 1965). If the tip of the stigma is damaged by a spell of frost the continuous growth of the style exposes new healthy stigmatic surface, which is able to receive pollen grains which arrive later (Szentiványi, 1980).

It is also a peculiarity of temperate zone fruit tree species that cold resistance of the anthers and the pollen is equal or a little higher than that of the pistils. The fully developed catkins may resist to frost as to temperature minima of -16 , -18 C°, at the time of the elongation of the catkin's axe to -8 , -10 C°, whereas at the time of pollen dispersion to minima of -5 , -7 C°, only. Meanwhile, the resistance of female flowers is about -7 , -8 C° (Romisondo, 1978).

The long interval between the end of the rest period and the fertilisation is charged with many risks and adversities, which afflict the buds and later the flowers. In Italy, sometimes 40–45% of the mixed buds were shed (Geraci, 1974). The variety *Tonda Gentile delle Langhe* lost during the interval from end of January to May altogether 62% of buds and female flowers in the year of 1976 (Romisondo, 1978). The cause of heavy losses in female flowers is the lack of fertilisation as well as the frosts, which are incident after bud-burst (Germain, 1983). Moreover, the position of female inflorescences is also a condition of fertility as far as the upper part of the reproductive shoots issued from mixed buds are most eligible to bear fruit (Figure 4).

The initial growth of the ovary is conditioned by the pollination with compatible pollen grain (Germain, 1983). As a consequence of the lack of pollination the ovary stops growing at a size about half a mm, and soon the gradual abscission of female flowers ensues (Romisondo, 1966a, Barbeau, 1973, Dimoulas, 1979, Thompson, 1979a, Mussano et al., 1983). First those female inflorescences abscise, where not a single flower got pollinated. The rate of

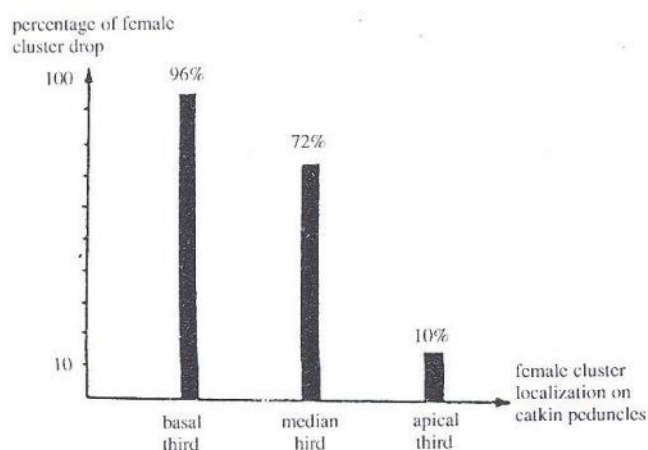


Figure 4 Percentage of female cluster drops in connection with their position on catkin peduncle. Fertile de Coutard cv., Bordeaux. 1978. (Germain, 1983)

abscised female inflorescences without being fertilised may attain 35–45% (Thompson, 1967).

The growth of ovaries after the flowers having been pollinated with compatible pollen starts when the pollen tubes arrived to the base of the stigmatic apparatus (Trotter, 1951). The cavity of the ovary increases and the ovules become visible (Barbeau, 1972, Barbe, 1974, Geraci, 1974, Dimoulas, 1978). Later, their growth speed up, and at the end of April or early May the micropyle and the nucellus are well recognised. Two weeks later, the ovules turn to adopt a hanging (epitropic) position.

The pollen tubes, which arrived much earlier, some months ago, to the spot remain still dormant, but the appearance of the megaspore in the embryo sac of the nucellus triggers their resumption of growth (Germain, 1983). So a pollen tube reaches the tip of the ovules within 5–6 days between the chalaza and the micropyle after having penetrated the tissue of the obturator. The tip of the pollen tube arrives to the chalaza of the ovule and the two nuclei enter the embryo sac, where the double fertilisation ensues between end of May and early June.

There are two ovules in each ovary but after one of them got fertilised the other used to be aborted regularly. According to the former authors the incidence of fertilisation, being though variable, is within the range of 55–99%, depending on variety and season. Geraci (1974) states that some varieties develop frequently two seeds per fruit shell. There is a chance, obviously, that the two ovules were equally developed and got fertilised synchronously.

At the moment of fertilisation (end of May – early June) the size of acorns reached about 1 cm (Geraci, 1974, Bergougnoux et al., 1978), and their growth continues (Romisondo, 1978). The following 2–3 weeks the growth is intense (Germain, 1983), though that of the embryos is still lagging (Figure 5). At the time when lignification started in the pericarp the growth of the embryo accelerates, and it fills out the space available within a 3–4 weeks' interval.

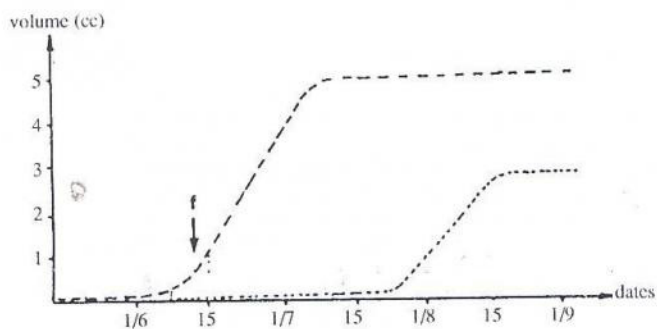


Figure 5 Growth curves of fruit (a) and kernel (b) in 1978 in BORDEAUX area. Fertile de Coutard cv. - f: period of fertilization. (Germain, 1983)

The eventual lack of fertilisation (after pollination) results in the development of empty fruits. The rate of empty acorns may attain even 80–90% (Germain, 1983). It is generally accepted that a female inflorescence (glomerule) contains 8 flowers, but that value may vary between 4 and 20 (Barbeau, 1973a).

The alleged causes of the premature shedding being, 1–45%, and emptiness of acorns are divers (Lagerstedt, 1977, Romisondo, 1978):

- genetic incompatibility between the variety and its polliniser,
- reduced fertility of the variety in question,
- reduced viability of the pollen,
- lack of double fertilisation,
- abortion of the embryo,
- adverse environmental conditions (winter and spring frosts, lack of water, parasites, etc).

The variety *Barcelona* being pollinated by *Daviana*, *Woodford* and *Nottingham* produced fruit sets at equal rate but the rate of seedless fruits attained 23% when the polliniser was *Woodford* (Zielinski & Thompson, 1967). In the seedless acorns there are remnants of fertilised seeds; thus the reason of sterility is not the consequence of the lack of pollination (Thompson, 1967). Seedless fruits characterise varieties too, which reveal themselves in the irregularity of the formation of microspores because of chromosome anomalies (Germain, 1983). Seedless fruit may brought into relation with the number of fertilised ovules or also with the inclination to produce twin seeds (Geraci, 1974). The neglect of pruning or poor illumination of the bushes may increase the rate of seedless fruits (Baron & Painter, 1965). The adverse effect of drought was incriminated already by Jannaccone (1937). Poor reserves in potash (K) are mentioned as well. The seasonal effect seems to be more decisive that the growing site. Rainy, cool weather after fertilisation increases the rate of sterile fruits. Ferrán et al. (1997) explored the effect of Boron on fruit set. The time of fruit shedding influences the amount as well as the quality of the yield (Azarenko et al., 1997).

Germain (1983) summarised the relevant literature and his own experiences as a system of the causes influencing fruit set in hazel:

- Maximum of shoot growth is coincident with the growth of ovaries as well as with initiation of catkins.
- In June, fertilisation and the growth of the fruit coincide with shoot growth. The vigour of shoot growth influences highly the induction of mixed buds, which is also actual at the end of that month.
- In July and early August the initiation of male and female inflorescences is coincident with the growth of the seeds.

It is not unexpected that as a consequence of auto-regulation, first the shedding of female inflorescences, then seedless fruits appear. All those indicate that the culture of hazel should observe the rules of intense technologies in order to achieve economically acceptable yields.

3 Association of varieties in the plantations

Because of the high degree of dichogamy, association of varieties is necessary let alone the possibility of accidental self-pollination. The use of two varieties only may prove to be insufficient in spite of the coincidence of bloom; thus considering the prolonged receptivity of female flowers, several polliniser varieties blooming successively one after the other are recommended (Szentiványi, 1980). The varieties selected should be inter-compatible. The unilaterally compatible combinations would increase the list of varieties and mean unnecessary burden in finding optimal associations (Romisondo, 1978, Zannini et al., 1983).

Pollen spreading should be prolonged all over the blooming period (Romisondo, 1963a). The author gives some examples of association for Italian conditions, where the individual polliniser varieties represent most frequently 10–33% of the plantation:

- *Piazza Armerina* : *Racinante* + *Jannusa*
- *Catania* : *Del Comercio* + *Selvaggiol*
- *Cuneo* : *Tonda Gentile delle Langhe* + *Bearis*, *Cosford*, *Sodlinger*, *Heynich*.

For Spain the following recommendations are given (Everinoff, 1958):

- 2 rows *Negret* (66 %) + 1 row *Grossal de Costanti* (34 %)
- 2 rows *Negret* (50 %) + 1 row *Grossal de Costanti* (25 %) + 1 row *Negret primerene* (25 %)
- *Negret* (84 %) + *Grossal de Costanti* (16 %)
- *Negret* (87,5 %) + *Grossal de Costanti*, *Negret primerene* (12,5 %).

Ninot & Mena (1983) recommend as pollinisers of *Negret* the varieties *Vermellet*, *Rosset* and *Girondell*, for *Girondell* the varieties *Vermellet*, *Trenet* and *Pauetet*.

In France unfruitful plantations have been transformed to successful ones by the planting of polliniser varieties blooming at different time (Rivals & Everinoff, 1955).

Germain (1983) recommended 8-15% assigned to polliniser varieties. That rate depends on the system whether the pollinisers are planted in every third row at every third position or whole rows are assigned to one polliniser variety. In any case, the distance between the partners should not exceed 30 m.

In Turkey varieties are planted for the only purpose to serve as pollen source (Romisondo, 1963a). Low yielding orchards may be improved by the use of purposefully collected and stored catkins exposed at the right time of bloom when pollen is supposed to be a shortcoming (Stritzke, 1962).

Plantations in Oregon are provided generally with 10% of polliniser plants with a maximum distance of 20 m to the target plants (Olsen et al., 2000). Pollinisers represent 2-3 varieties with different blooming data in order to overlap the whole period of receptivity of female flowers.

The floating ability of hazel pollen is excellent; i.e. it is carried by the wind easily to a distance of 600 m (Pisani & Giulivio, 1968). The pollen density in the air diminishes rapidly with the distance from the pollen source. Consequently, the planned distance between pollen source and the target variety should not exceed 50 m (Soltész, 1996). The floating pollen is very susceptible to high humidity, which may diminish, substantially, the carrying distance of the wind (Romisondo, 1978). Data are lacking in hazel,

which may prove the decline of fruit set with the increasing distance from the pollen source (Thompson, 1967). However, there are heavy arguments, which prove the losses due to the lack of pollinisers in plantations (Ninot & Mena, 1983).

There are also other purposes to be considered with the association of varieties in addition to the knowledge of opportunities of pollination and fertilisation. Those are related to the conditions of the growing site. In Oregon State (USA), e.g. the eastern filbert blight causes heavy losses (Pinkerton et al., 1992, Johnson et al., 1996). Therefore, the planting of susceptible varieties should be avoided, even as pollinisers they should not exceed 5% of the stands. Earlier, several varieties are recommended as polliniser for *Barcelona*: *White Aveline*, *Nottingham*, *Daviana*, *Du Chilly*, *Bolwyller*, *Du Provence* (Schuster, 1944, Griggs, 1953). The list of potential pollinisers was reduced, gradually. It is of concern that in 70% of hazel plantations in Oregon are planted to *Barcelona* and with the polliniser, *Daviana* that is susceptible to the disease. For new plantations the resistance should be taken into account much more than earlier (Table 6).

The main obstacle of the planting pollinisers in sufficient quantity is the anguish to impair the quality of the harvest with inferior fruits. Therefore the quality of fruit should be also a decisive criterion in choosing pollinisers (Romisondo, 1963a). As an additional argument the xenia (metaxenia) should not be neglected (Soltész, 1996).

Research workers do not want to renounce the opportunity to give recommendations not only for the varieties to be associated but also furnish the optimised technology of cultivation and harvest securing the desired quality of the produce (Romisondo et al., 1977). In the hazel orchards of Oregon, the variety *Barcelona* excludes the planting of pollinisers within the rows because of the mechanised harvesting procedures (Thompson, 1967). Similar quality of the product of varieties may facilitate mechanised operations conspicuously (Thompson, 1971). A good example should represent the combinations *Tonda Romana x Riccia di Talanico* (Tombesi, 1980) or *Tonda di Giffoni x Riccia di Talanico* (Limonelli, 1983). Varieties of extremely tender shell, though representing a minor fraction as polliniser, may offer an easy target to birds, which are undesired consumers and risk the rest of varieties too (Zielinski & Thompson, 1967).

References

- Azarenko, A.N., McCluskey, R.L. & Hampson, C.R. (1997): Time of shading influences yield, nut quality, and flowering. *Acta Hort.* 445:179-181.
- Baldini, C. & Pisani, P.L. (1968): Attuali conoscenze sui principali aspetti della biologia floreale del nocciuolo. *Atti Conv. Naz. Studi Nocciuolo*, Viterbo, 1-20.
- Baldini, C., Pisani, P.L. & Bergamini, A. (1968): Contributo allo studio della biologia floreale del nocciuolo cv. "Tonda Gentile delle Langhe". *Riv. Ortoflorofrutt.* It. 52(3):293-297.
- Barbe, I.P. (1974): Contribution à l'étude des premiers stades de développement du fruit chez le Noisetier (*Corylus sp.*). *Mémoire de fin d'études*, E.N.S.A., Toulouse, 1-69.

Table 6 Relative ranking of hazelnut cultivars to eastern filbert blight susceptibility based on observational field data (Pinkerton et al., 1993; personal communication, J.W. Pscheidt and S.A. Mehlenbacher; cit. Olsen et al., 2000.)

Susceptible	Intermediate	Resistant	Immune
Ennis (+++++)	Barcelona (++++)	Clark (++)	Gasaway (-)
Daviana (+++++)	Butler (++++)	Lewis (++)	VR 4-31 (-)
DuChilly (+++++)	Hall's Giant (+++)	Gem (+)	VR 11-27 (-)
TGdL (+++++)	Willamette (+++)	TdG (+)	VR 20-11 (-)
Tonda Romana (+++++)			VR 23-18 (-)
Casina (++++)			
Negret (++++)			
Newberg (+++++)			
Dundee (+++++)			

TGdL = 'Tonda Gentile delle Langhe'; TdG = 'Tonda di Giffoni'.

+++++ = Highly susceptible, long canker length, low vigor. Cultivar type = 'Ennis'.

++++ = Susceptible, long canker length, medium vigor.

+++ = Intermediate susceptibility, good vigor in the presence of eastern filbert blight. Cultivar type = 'Barcelona'.

++ = Intermediate susceptibility, but with shorter cankers or fewer stromata than 'Barcelona', good vigor in the presence of eastern filbert blight.

+ = Resistant, shorter cankers and with good vigor. Cultivar type = 'Clark'.

- = Highly resistant, shortest cankers, can become infected but only under very high disease pressure. Cultivar types = 'Tonda di Giffoni'.

- = Immune, does not become diseased. Cultivar type = 'Gasaway'

- Barbeau, G. (1972):** Contribution a l'étude de la biologie florale et certains aspects de la physiologie du Noisetier. Mémoire de fin d'études, E.N.S.A., Montpellier, 1-92.
- Barbeau, G. (1973):** Contribution a l'étude du Noisetier. La Pomologie française 15(4):79-83.
- Barbeau, G. (1973a):** Contribution a l'étude du Noisetier. I. La Pomologie française 1:3-17.
- Baron, L. & Painter, J.M. (1965):** Progress report on heavy pruning Herman Schoen filbert orchard, Washington County. Proc. Nut Grow. Soc. Ore. and Wash., 51:55-56.
- Bergamini, A. & Ramina, A. (1968):** Contributo allo studio del "fabbisogno in freddo" del nocciuolo (*Corylus avellana* L.) Atti. Conv. Naz. Studi Nocciuolo 18:1-16.
- Bergougnoux, F., Germain, E. & Sarraquigne J.P. (1978):** Le noisetier production et culture. "Invuflec" Malemort, 1-164.
- Beyhan, N. & Odabas, F. (1997):** The investigation of compatibility relationships of some hazelnut cultivars. Acta Hort. 445:173-175.
- Dimoulas, I. (1978):** Étude de quelques aspects de la reproduction chez le Noisetier, *Corylus avellana* L., D.E.A. Phys. Vég. Univ. Bordeaux II, 1-32.
- Dimoulas, I. (1979):** Étude de divers aspects de la reproduction sexuée chez le Noisetier (*Corylus avellana* L.). These présentée a l'Université de Bordeaux II.
- Everinoff, V.A. (1958):** Le choix des variétés des noisetiers a cultivar dans les sud-ouest. Elm. ec. hat. sup. agr. 6:21-78.
- Ferrán, X., Tous, J., Romero, A., Lloveras, J. & Pericón, J.R. (1997):** Boron Does Not Increase Hazelnut Fruit Set and Production. HortScience 32(6):1053-1055.
- Geraci, G. (1974):** Prove di biologia fiorale su tre cultivar di nocciuolo. Tecnica agricola 26(4):1047-1063.
- Germain, E. (1983):** Physiology of reproduction in filbert (*Corylus avellana* L.) flowering and fruiting. Conv. Inter. sul Nocciuolo, Avellino, 47-53.
- Germain, E. & Leglise, P. (1973):** Le Noisetier. INVUFLEX ed. Paris, 1-89.
- Germain, E., Leglise, P. & Delort, F. (1976):** Pollinización del avellano (*C. avellana* L.) I^{er} Congr. Inter. de Almendra y Avellana, REUS: 143-153.
- Germain, E., Leglise, P. & Delort, F. (1976a):** Analyse du system d'incompatibilité pollinique observé chez le noisetier *Corylus avellana* L. I^{er} Coll. Rech. fruit, Bordeaux, 197-216.
- Germain, E., Leglise, P. & Delort, F. (1981):** Analyse du système d'incompatibilité pollinique observé chez le noisetier *Corylus avellana* L. I^{er} Coll. sur les Réch. Fruit, Bordeaux, 197-216.
- Giulivo, C. & Pisani, P.L. (1973):** Ulteriori ricerche sull'attitudine produttiva dei diversi tipi di infiorescenze femminili nel nocciuolo. L'Informatore Agrario, 43.
- GRIGGS, W.H. (1953):** Pollination Requirements of Fruits and Nuts. Univ. Calif. Ext. Circ., 424.
- Hampson, G.R., Azarenko, A.N. & Soeldner, A. (1993):** Pollen-stigma interactions following compatible and incompatible pollinations in hazelnut. J. Amer. Soc. Hort. Sci. 118:814-819.
- Heitz, A. (1973):** Contribution a l'étude de quelques aspects de la formation de fruit chez le Noisetier (*Corylus sp.*). Mémoire fin d'études, E.N.S.A. Montpellier, 166.
- Jacoboni, N., Tombesi, A. & Cartechini, A. (1968):** L'autosterilità della "Tonda Romana" e la compatibilità con il "Nocchione". Atti Conv. Naz. Studi Nocciuolo 10-11(10):221-240.
- Jannaccone, A. (1937):** Ricerche sull'aborto seminale del Nocciuolo in rapporto alla nutrizione. Atti Conv. del Nocciuolo, Napoli, 47-61.
- Johansson, E. (1935):** Pollineringsförsök med Hassel vid. Alnarp. 1927-1933. Sver. Pom. Fören. Arss., 262.
- Johnson, K.B., Mehlenbacher, S.A., Stone, J.K., Pscheidt, J.W. & Pinkerton, J.N. (1996):** Eastern filbert blight of European hazelnut: it's becoming a manageable disease. Plant Dis. 80(12):1308-1316.
- Jona, R. (1986):** Hazelnut. In: Monselise, S.P. (ed.), CRC Handbook of Fruit Set and Development. CRC Press, Boca Raton, FL. 193-216.
- Kavardzhikov, L. (1980):** Effect of air temperature on phenophases of flowering in Hazel. I. Effect of some temperature parameters on flowering. Grad. Lozar. Nauka 17(6):3-10.
- Kolesnikov, V.A. (1953):** Plodovodstvo, Moskva.
- Lagerstedt, H.B. (1977):** The occurrence of blanks in the filbert *Corylus avellana* L. and possible causes. Economic Botany 31(2):153-159.
- Latorse, M.P. (1981):** Étude de facteur limitant la productivité du noisetier *Corylus avellana* L. Université de Bordeaux II.
- Limongelli, F. (1983):** Auto ed interfertilità della cultivar di nocciuolo "Tonda di Giffoni" Conv. Inter. Sul Nocciuolo, Avellino, 327-329.
- McKay, J.W. (1966):** Sterility in Filbert (*Corylus*). Proc. Amer. Soc. Hort. Sci. 88:319-324.
- Me, G. & Radicati, L. (1983):** Studies on pollen incompatibility in some filbert (*Corylus avellana* L.) cultivars and selections. In: Mulcahy, L. and Ottaviano, E. (eds.), Biology and Implication for Plant Breeding. Elsevier Sci. Publ. Co. Inc., 237-242.
- Me, G., Sacerdote, S. & Vallania, R. (1983):** Osservazioni sul comportamento dei nuclei del polline di nocciuolo germinato in vitro. Conv. Inter. sul Nocciuolo, Avellino, 309-312.
- Mehlenbacher, S.A. (1997a):** Revised dominance hierarchy for S-alleles in *Corylus avellana* L. Theor. Appl. Genet. 94:360-366.
- Mehlenbacher, S.A. (1997b):** Testing compatibility of hazelnut crosses using fluorescence microscopy. Acta Hort. 445:167-171.
- Mehlenbacher, S.A. & Thompson, M.M. (1988):** Dominance relationships among S-alleles in *Corylus avellana* L. Theor. Appl. Genet. 76:669-672.
- Modic, D. (1971):** Prispevek k preucevanju oplodbe pri leskah (*Corylus avellana*, *Corylus maxima*) in njihovih krizancev. Zbornik BF Ljubljana 18:120-126.
- Modic, D. (1974):** Ra ziskave cvetenja in interfertilnosti med sartami leske v predalpskem obmoju SR Slovenije. Izv. razis. delo, 83-93.
- Mussano, L., Radicati, L., Me, G. & Sacerdote, S. (1983):** Influence on the pollen quality in differentiating the hazelnut ovary. Conv. Inter. sul Nocciuolo, Avellino, 321-325.
- Ninot, J. & Mena, J. (1983):** Pollinisation et productivité de noisetier au "Camp de Tarragona". Conv. Inter. sul Nocciuolo, Avellino, 341-344.
- Olsen, J. L., Mehlenbacher, S. A. & Azarenko, A. N. (2000)** Hazelnut Pollination. Hort Technology 10 (1): 113-115.
- Paglietta, R. (1970):** Importanza dell'impollinazione incrociata nell' nocciuolo. II. colt. e giorn. vinicolo Italiano, Cas. Monferato, 1-20.
- Painter, J.H. (1965):** Project report on the Wilsonville Filbert Project. Nut Grow. Soc. of Ore. and Wash., Proc. 51th Ann. Meet., 23-25.
- Pinkerton, J.N., Johnson, K.B., Mehlenbacher, S.A. & Pscheidt, J.W. (1993):** Susceptibility of European hazelnut clones to eastern filbert blight. Plant Dis. 77:261-266.
- Pinkerton, J.N., Johnson, K.B., Theiling, K.M. & Griesbach, J.A. (1992):** Distribution and characteristics of the eastern filbert blight epidemic in western Oregon. Plant Dis. 76:1179-1182.

- Pisani, P.L. (1968):** Contributo allo studio dell'attitudine produttiva dei diversi tipi di infiorescenze femminili nel nocciuolo (cv. "Tonda Gentile delle Langhe"). Atti Conv. Naz. Studi Nocciuolo 20:1-10.
- Pisani, P.L. & Giulivio, C. (1968):** Osservazioni sulla morfologia fiorale e sul trasporto del polline del nocciuolo. Atti Conv. Naz. Studi Nocciuolo 19:1-11.
- Pomper, K.W., Azarenko, A.N., Bassil, N., Davis, J.W. & Mehlenbacher, S.A. (1998):** Identification of random amplified polymorphic DNA (RAPD) markers for self-incompatibility alleles in *Corylus avellana* L. Theor. Appl. Genet. 97:479-487.
- Riera, F. (1958):** L'impollinazione e la fecondazione del nocciuolo. Riv. Ortoflorofrutt. It. 11-12:604-605.
- Rivals, P. & Everinoff, V.A. (1955):** Sur les moyens susceptibles de remédier a la sterilité du noisetier a la Reunion. Rev. Agric. 55:207-212.
- Romisondo, P. (1963):** L'impollinazione incrociata del nocciuolo "Tonda Gentile delle Langhe" II. Frutticoltura 11-12:1-9.
- Romisondo, P. (1963a):** L'impollinazione incrociata del nocciuolo "Tonda Gentile delle Langhe" I. Riv. Ortoflorofrutt. It. 88(3):202-215.
- Romisondo, P. (1963b):** Indagini sull'interdipendenza fra la lunghezza dei rami di un anno e l'attività vegetativa e produttiva del nocciuolo. I. Riv. Ortoflorofrutt. It. 6:594-609.
- Romisondo, P. (1963c):** Indagini sull'interdipendenza fra la lunghezza dei rami di un anno e l'attività vegetativa e produttiva del nocciuolo. II. Annali della Facoltà di Scienze Agrarie della Università degli Studi di Torino, 127-160.
- Romisondo, P. (1965a):** Indagini sull'interdipendenza fra la lunghezza dei rami di un anno e l'attività vegetativa e produttiva del nocciuolo. III. Annali dell'Accademia di Agricoltura di Torino, 16-21.
- Romisondo, P. (1965b):** Alcuni aspetti della biologia fiorale del nocciuolo cv. "Tonda Gentile delle Langhe". Annali dell'Accademia di Agricoltura di Torino, 1-60.
- Romisondo, P. (1966):** Indagini sull'interdipendenza fra la lunghezza dei rami di un anno e l'attività vegetativa e produttiva del nocciuolo. IV. Annali della Facoltà di Scienze Agrarie della Università degli Studi di Torino, 163-186.
- Romisondo, P. (1966a):** Recenti acquisizioni sulla biologia fiorale del nocciuolo. Coltiv. e Giorn. Vin. Ital. 112(2):50-54.
- Romisondo, P. (1968):** Aspetti e problemi della coltura del nocciuolo con particolare riferimento alla biologia fiorale. Riv. Ortoflorofrutt. It. 61(5): 277-302.
- Romisondo, P. (1977):** Aspetti e problemi della coltura del nocciuolo, con particolare riferimento alla biologia fiorale. Riv. Ortoflorofrutt. It. 61(5):277-302.
- Romisondo, P. (1978):** La fertilità nel nocciuolo. Riv. Ortoflorofrutt. It. 62(4):423-429.
- Romisondo, P., Me, G., Limongelli, F. & Radicati, L. (1977):** Aspetti e problemi della coltura del nocciuolo, con particolare riferimento alla biologia fiorale. Riv. Ortoflorofrutt. It. 60(5):277-302.
- Romisondo, P., Limongelli, F., Me, G. & Radicati, L. (1978):** Indagini sulla recettività al polline degli still del nocciuolo "Tonda Gentile delle Langhe" in diversi stadi della fioritura femminile. Riv. Ortoflorofrutt. It. 62(6):655-661.
- Romisondo, P., Me, G., Limongelli, F. & Radicati, L. (1978a):** Indagini sull'impollinazione del nocciuolo cv. Tonda Gentile delle Langhe. Seminario Progetto Finalizzato C.N.R. "Biologia della riproduzione", Bologna.
- Schuster, C.E. (1922):** Pollination of filbert. The Oregon Grower, 3.
- Schuster, C.E. (1936):** Relation of shoot growth to setting and weight of fruit in the filbert. Proc. Amer. Hort. Sci. 12(34):61-65.
- Schuster, C.E. (1944):** Filberts. Ore. Ext. Bul., 628.
- Soltész M. (1996):** Requirements for Successful Fruit Set in Orchards. In: Nyéki J. & Soltész M. (eds.), Floral Biology of Temperate Zone Fruit Trees and Small Fruits. Akadémiai Kiadó, Budapest, 257-286.
- Stritzke, S. (1962):** Untersuchungen über die befruchtungsbiologischen Verhältnisse bei Haselnuss-Sorten unter besonderer Berücksichtigung ökologischer Verhältnisse. Arch. Gartenbau 10(8):603-605.
- Szentiványi P. (1980):** A mogyoró. In: Nyéki J. (ed.), Gyümölcsfajták virágzásbiológiája és termékenyülése. Mezőgazdasági Kiadó, Budapest, 298-300.
- Thompson, M.M. (1965):** A progress report of pollination studies in filbert. Nut Grow. Soc. of Ore. and Wash., Proc. 51th Ann. Meet., 49-54.
- Thompson, M.M. (1967):** Role of Pollination in Nut Development. Proc. Nut Growers Soc. Ore. and Wash. 53:31-36.
- Thompson, M.M. (1971):** Pollen incompatibility in filbert varieties. "Nut Grow. Soc. of Ore. and Wash. Proc.", 56th Ann. Meet., 73-79.
- Thompson, M.M. (1979a):** Growth and development of the pistillate flower and nut in 'Barcelona' filbert. J. Amer. Soc. Hort. Sci. 104(3):427-432.
- Thompson, M.M. (1979b):** Genetics of incompatibility in *Corylus avellana* L. Theor. Appl. Genet. 54:113-116.
- Thompson, M.M. (1979c):** Incompatibility alleles in *Corylus avellana* L. Theor. Appl. Genet. 55:29-33.
- Tombesi, A. (1980):** Impollinazione e fertilizzazione della cv. "Tonda Romana". Atti VI^o Conv. Pomol. Inc. frutt. su: "Frutta secca" e mostra pomologica. Caserta 24(10):313-326.
- Tombesi, A. - Cartechini, A. (1970):** Le esigenze di impollinatori delle principali cultivar di nocciuolo. Tuscia Economia 9-10:3-18.
- Trotter, A. (1930):** Botanica del nocciuolo nei suoi rapporti con la tecnica culturale. Amer. Ist. Super. Agr. di Portici, III:266-240.
- Trotter, A. (1951):** Il nocciuolo (*Corylus*). "Soc. Ed. Dante Alighieri" Roma, Napoli, Citta di Castello.
- Vidal-Barraquer, R. (1974):** La pollinización del avellano. Unión 146:6-7.
- Zannini, P., Me, G. - Radicati, L., Sacerdote, S. & Vallania, R. (1983):** New acquisitions on the gamic compatibility among the hazelnut cultivars. Their influence in relation to the pollinizers choice. Conv. Inter. sul Nocciuolo, Avellino, 313-319.
- Zielinski, Q.B. & Thompson, M.M. (1967):** Self- and cross-pollination experimente in filberts evaluating potencial pollinators. Proc. Amer. Soc. Hort. Sci. 91:187-191.