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Pollen tube growth in sweet cherry (*Prunus avium* L.) styles following fully compatible, half compatible and incompatible pollinations

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Summary: *In vivo* as well as in *vitro* pollen tube growth studies along the style were performed, each with two pairs of sweet cherry cultivar combinations by means of fluorescence microscopy. *In vivo* studies showed that the percentage of pollen tubes penetrating the middle and basal section of the style was higher in the fully compatible 'Margit' x 'Alex' combination than in the half compatible 'Germersdorfi 3' x 'Alex' cross. The year effect was significant at P=0.1 probability level. All pollen tubes *in vitro* stopped at the upper third of the style in the incompatible 'Vera' x 'Van' cross, whereas in the half compatible 'Alex' x 'Van' 50% of the pollen tubes penetrated to the lower third of the style. By *in vitro* fluorescence microscopy, it was possible to distinguish half compatible combinations from incompatible ones. Results obtained by in vivo technique only were much ambiguous.

Key words: pollen tube growth, sweet cherry, incompatibility

Introduction

In Angiosperms, sperm cells of the pollen grain that lands upon the stigma surface must reach the embryo sac where double fertilisation occurs. It is the pollen tube that is responsible for transporting sperm cells in the pistil.

Pollen tube growth in genus *Prunus* was first studied by *Stösser* (1980) in sweet cherry, sour cherry and plum flowers. According to his observations the pollen tube first grows through the swollen papillary cells, then penetrates into the transmitting tissue of the style where it travels intercellular. Leaving the style, the transmitting tissue narrows and the pollen tube grows along the ventral suture of the ovary but considerably slower than in the style. In sweet cherry, *Stösser & Anvari* (1981) reported that although several pollen tubes start from the stigma surface, only 1–6 can reach the ovary. The same was observed in other fruit taxa such as *Eucerasus, Pseudocerasus* (*Schmidt,* 1976); blackberry (*Engelhardt & Stösser,* 1979). The explanation for the reducing number of pollen tubes is their competition for nutrients (*Herrero,* 1992). In the loculus, pollen tubes leave their well-defined route and their ramification, distortion occurs (*Stösser & Anvari,* 1981). The characteristics of pollen tube growth of *Prunus* in the ovary were described by *Herrero* (2000) in peach, as an example. After recognition of the viable ovule, the pollen tube enters the nucellus with the guidance of the secretion of micropyle and external integument cells.

Pollen tube growth can be characterised by its rate and expressed as the time needed from pollination until the first pollen tube reaches the base of style or fertilisation occurs. In sweet- and sour cherry, pollen tubes *in vivo* arrive to the base of style in 2–3 days, whereas pollen tubes travel 6–8 days until the first reaches the ovule (*Stösser & Anvari,* 1981). The time observed from pollination until fertilisation in sweet cherry is 3–4 days (*Bradbury,* 1929; *Tukey,* 1933, 1934), but according to *Popatov & Dutova* (1973, cit. in *Nyéki,* 1974) it is only 1–3 days.

Factors affecting pollen tube growth:

Temperature has strong influence on pollen tube growth. *Lewis* (1942, 1954) pointed out that in the genera *Oenothera, Primula* and *Prunus* high temperature accelerates compatible pollen tube growth but slows down incompatible tubes since inhibitory reactions are speeded up at a higher temperature.

Nagy (1965) examined pollen tube growth of Hungarian sour cherry cultivars at three different temperatures. For pollen tubes of 'Paraszt meggy', 27–29°C was optimal in every cultivar combination tested. However, pollen tubes of 'Egri fürtös' preferred 20–22°C in 'Eugénia' and 'Királyi Amarella' pistils, whereas in 'Pándy' flowers the optimal temperature was 27–29°C. *Kerékné* (1981) studied the effect of temperature on pollen tube growth after pollinating some self-fertile sour cherry cultivars. The optimum temperature was 20°C (68–83% of flowers contained pollen tube). At

30°C self- and cross pollen germinations were equally weak. In sour cherry cultivars *Cerovia & Ružia* (1992) found parabolic interaction between temperature and the number of pollen tubes in the style. The most pollen tubes in the pistils were observed at 15–20°C.

The amount of pollen on the stigma and pollinator cultivar affects pollen tube growth and so control fruit set. In apple, a large quantity of pollen on the stigma stimulates pollen tube growth. On the other hand, in walnut, too much pollen reduces fruit set (*Szentiványi*, 1990).

Several factors have an indirect effect on pollen tube growth such as plant nutrition, water- and light supply (*Preil*, 1970), pesticides, environmental pollution, etc. For instance, several pesticides (such as azoxystrobin and captan) was shown to reduce pollen germination and tube growth of *Prunus* spp. as well as similar growth inhibition could be observed when pollen infected by flower pathogens such as *Monilinia* spp. (*Yi* et. al, 2003ab; *Holb*, 2003). *Moreover, Bayer & Stösser* (2001) pointed out that tolerance to extreme weather conditions (such as frost) secures pollen tube growth.

Pollen tube growth and its relation to incompatibility:

Host incompatibility systems of stigma and style in flowering plants mean inhibition of pollen germination and pollen tube growth. In gametophytic incompatibility systems, rejection is manifested in the style where incompatible pollen tubes are arrested. The end of these pollen tubes is usually swollen, fluorescing intensely due to callose accumulation. The papillae are small with intensive secretion (*Bubán*, 1996). According to *Herrero* (2000) and *Sage* et al., (1994) the ovary may also be a site for incompatibility.

As arrested or abnormal pollen tubes are signs of incompatibility, pollen tube growth studies are suitable for selecting self-and cross-incompatible cultivar pairs. *Schmadlak* (1965, cit. in *Brózik & Nyéki*, 1980) developed the so called "affinity coefficient" that is the ratio of the number of pollen tubes penetrating the stigma and the number of pollen tubes at the base of the style. However, there are different opinions about the site of incompatibility reactions in cherry. After crossing 'Eaeanski Rubin' with other sour cherry cultivars, *Cerovia & Ružia* (1992) reported incompatibility in the upper third of the style. *Stösser* (1980) also found this pistil section to be responsible for incompatibility reactions in sweet cherry. *Schmidt & Timmann* (1997) regarded a cultivar combination compatible when pollen tubes reached the ovary. By *in vitro* pollen tube growth studies and test-crosses, they have determined the S-genotype of some German sweet cherry cultivars, however, pollen tube growth differences between half- and fully compatible combinations were not observed.

Ortega et al. (2002) reported differences in the number of pollen tubes between fully- and half compatible almond pollinations. Incompatible pollen tubes in half compatible crosses stopped in the first (upper) and second third section of the style. However, the number of pollen tubes in the third section of the style was similar in both types of pollination.

In apple, *Petropoulou & Alston* (1998) found no differences in pollen tube growth between fully- and half compatible pollinations at low temperatures (5 °C, 10 °C and 15 °C). In their opinion, a good receptivity of the stigma can overcome incompatibility in half compatible crosses. The number of pollen tubes correlated well with fruit set. *Anvari & Stösser* (1981) reported pollen tube growth inhibition in the first and second section of the style when selfing apple flowers.

In our work, *in vivo* pollen tube growth of fully- and half-incompatible pollinations was compared. The *in vitro* method was used to test whether pollen tube growth of half compatible and incompatible combinations corresponds to their S-alleles.

Material and method

In vivo pollen tube growth experiments were conducted in three years (2000, 2001 and 2002). The trial included 'Margit'(S_4S_{12}) x 'Alex'(S_3S_3') (fully compatible) and 'Germersdorfi 3' (S_3S_{12}) x 'Alex' (S_3S_3') (half compatible) combinations. 'Margit' and 'Germersdorfi 3' flowers were isolated with parchment bags in their balloon stage. When stigmas became receptive, they were hand-pollinated by using toothpicks (appr. 1500 flowers per combination). A sample of 2 x 10 flowers per cultivar was collected 24, 48, 72, 96 and 120h (1–5 days) after pollination and fixed in FPA (a fixing solution containing 70% ethanol, propionic acid and formaldehyde at a ratio of 8:1:1).

The flowers were handled according to *Preil* (1970). The flowers were washed under water for 1h, then the tissues were softened in a 8M NaOH solution for 18h. After rinsing under water for 1h, the flowers were kept in a 0.1% aniline blue - 0.1M K_3PO_4 solution for at least 1h.

For pollen tube growth studies styles, with stigmas were separated from the other parts of the flowers and put onto a microscope slide with a drop of glycerol. The styles were then covered with a slip and slightly pressed (squash preparations). For each pistil, the number of germinated pollen grains on the stigma and pollen tube number in the first, second and third sections of the style were recorded by fluorescence microscopy (Fluoval microscope). For each sample average numbers were calculated. For data analysis, the number of pollen tubes in each part of the style were expressed as a percentage of the number of germinated pollen grains on the stigma.

For determining differences among pollinations and years, analyses of variance were performed (one-way analysis by Welch-test of Ministat 3.2. software, Vargha, 2000; multifactor analysis by Statgraphics 5.1).

In vitro pollen tube growth studies were carried out in 2002 in 'Vera' (S_1S_3) x 'Van' (S_1S_3) (incompatible) and 'Alex' (S_3S_3') x 'Van' (S_1S_3) (half compatible) combinations. Artificial pollination was performed

according to *Schmidt & Timmann* (1997) as follows. Flowers of 'Vera' and 'Alex' in their balloon stage were collected, and inserted into 1% agar dishes. The 'Alex' flowers were emasculated beforehand (as they are self-fertile). The Petri dishes were kept at room temperature. Next day, when the stigmas became sticky the flowers were hand-pollinated with 'Van' pollen and left for 48 h. In compatible pollen tubes, this time is sufficient for reaching the ovary. The flowers then were put into FPA fixing solution and later prepared for fluorescent microscopy as described at *in vivo* pollen tube growth experiments. In each flower the style section penetrated by the longest pollen tube was determined. Flowers then were distributed according to this style section.

Table 1. Differences in pollen tube growth in the styles of 'Germersdorfi 3' and 'Margit' (multifactor analysis of variance for percentage of pollen tubes in the style)

Source of variation	d.f.	Sum of squares	F-ratio	Probability*
Cultivar	1	0.003	0.30	0.589
Style section	2	0.730	80.69	0.000
Cultivar x Style section	2	0.047	5.17	0.0077
Error	84	0.009		

* significance of the probability at P<0.05

Results:

In vivo pollen tube growth:

Pollen tube growth differences between fully- and half compatible combinations as well as style sections were first tested by using all data of all samples (every year and every day after pollination). Results obtained by multifactor-

Table 2. Differences in pollen tube growth in the 1st, 2nd and 3rd sections of the styles of 'Germersdorfi 3' and 'Margit' (one-way analysis of variance for percentage of pollen tubes in the style)

Style section	Cultivar	Pollen tubes in the style as the percentage of germinated pollen grains on the stigma		Welch-test (d ratio)
		Mean	Standard deviation	
1st (upper) third	Germersdorfi 3	0.365	0.153	1.911+
	Margit	0.265	0.133	
2nd (middle) third	Germersdorfi 3	0.0591	0.0716	-1.808+
	Margit	0.109	0.0794	
3rd (lower) third	Germersdorfi 3	0.0093	0.0248	-1.688
	Margit	0.0267	0.0313	

+significance of the probability at P<0.1

Table 3. Number of germinated pollen grains on the style and percentage of pollen tubes in the styles of 'Germersdorfi 3' and 'Margit'*

Cultivar**	G	M	G	M	G	M	G	M	G	M	G	M
Days after pollination	**1**		**2**		**3**		**4**		**5**		**Average (days 1–5)**	
2000												
Number of germinated pollen grains	26.1	31.9	23.7	36.6	18.5	24.6	11.8	31.8	10.5	28	18.1	30.6
Pollen tubes in the 1st third of style (%)	**52.5**	24.1	**54.0**	39.1	49.7	43.1	39.8	38.1	37.1	36.6	**46.6**	36.2
Pollen tubes in the 2nd third of style (%)	20.3	17.9	16.9	22.4	0.0	26.4	0.0	17.6	0.0	15.1	7.4	19.9
Pollen tubes in the 3rd third of style (%)	**7.7**	0.0	6.3	8.5	0.0	6.5	0.0	5.7	0.0	4.2	2.8	5.0
2001												
Number of germinated pollen grains	18.6	21.6	40.3	16.5	44.7	16.8	39.1	20.9	49.9	17.2	**38.5**	18.6
Pollen tubes in the 1st third of style (%)	**10.8**	0.0	39.0	37.6	28.0	33.9	35.5	29.2	**48.3**	33.1	32.3	26.8
Pollen tubes in the 2nd third of style (%)	0.0	0.0	**8.2**	0.0	3.6	6.0	0.0	9.6	9.0	10.5	4.2	5.2
Pollen tubes in the 3rd third of style (%)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.8	0.0	1.2
2002												
Number of germinated pollen grains	25.9	37.8	35.3	30	35.6	35.6	23.6	27.2	34.5	35	31.0	33.1
Pollen tubes in the 1st third of style (%)	0.0	0.0	**25.5**	14.7	**34.8**	22.2	**47.0**	23.5	**45.8**	22.3	**30.6**	16.5
Pollen tubes in the 2nd third of style (%)	0.0	0.0	0.0	7.7	5.6	11.8	**16.9**	9.9	8.1	8.6	6.1	7.6
Pollen tubes in the 3rd third of style (%)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.7	0.0	5.7	0.0	1.9
Average 2000–2002												
Number of germinated pollen grains	23.5	30.4	33.1	27.7	32.9	25.7	24.8	26.6	31.6	26.7	29.2	27.4
Pollen tubes in the 1st third of style (%)	**21.1**	8.0	**39.5**	30.5	**37.5**	33.1	**40.8**	30.3	**43.7**	30.7	**36.5**	26.5
Pollen tubes in the 2nd third of style (%)	6.8	6.0	8.4	10.0	3.1	14.7	5.6	12.4	5.7	11.4	5.9	10.9
Pollen tubes in the 3rd third of style (%)	**2.6**	0.0	2.1	2.8	0.0	2.2	0.0	3.1	0.0	5.2	0.9	2.7

***Bold** figures: the percentage of pollen tubes in a given year. style section and day is at least 25% higher at 'Germersdorfi 3'.
Underlined figures: the percentage of pollen tubes in a given year. style section and day is at least 25% higher at 'Margit'
**G= Germersdorfi 3. M=Margit

analysis of variance are presented in *Table 1*. Significant differences in the number of pollen tubes between 'Germersdorfi 3' x 'Alex' and 'Margit' x 'Alex' combinations were not detected. The three style sections (thirds) differed from each other in the number of pollen tubes. There was no significant interaction between combination and style section. Then data of each section of the style were separated and differences in the percentage of pollen tubes were studied individually *(Table 2)*. According to our results, fully- and half compatible pollinations showed slight differences in the upper and mid part of the style at a P=0.1 probability level.

In *Table 3*, percentage of pollen tubes in each style section as well as the number of germinated pollen grains (for completeness) are presented 1–5 days after pollination.

In 2000, pollen tube growth was more rapid in 'Germersdorfi 3' pistils than in 'Margit' as in 'Germersdorfi 3' the most tubes were observed on the first day after pollination but in 'Margit' it was on the third day. The first pollen tubes in the third section of the style appeared on the first day in 'Germersdorfi 3' x 'Alex' combination but were missing from the third day, moreover, the number of pollen tubes in every section decreased in time. Although in 'Margit' pistils pollen tubes reached the lower third of the style on the second day only, since then they were present every day. In 2001 and 2002, pollen tubes in 'Germersdorfi 3' styles did not reach the third section of the style at all, in contrast to 'Margit' styles.

According to our data the first section of the style was penetrated by more pollen tubes in 'Germersdorfi 3' than in 'Margit' pistils. In the second and third sections, however, there are more tubes in 'Margit' than in 'Germersdorfi 3' styles.

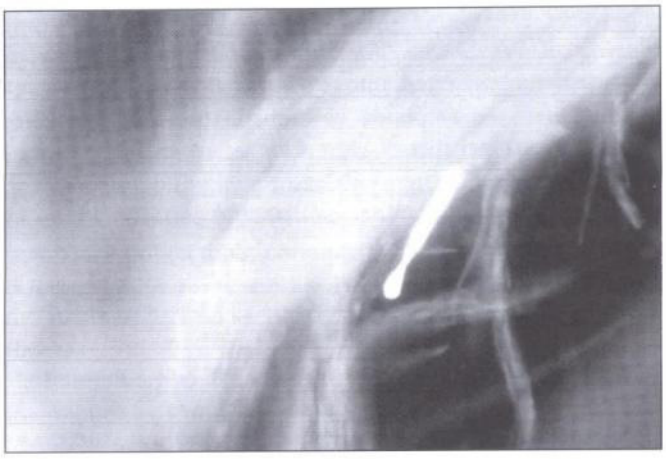

Figure 1. A swollen pollen tube end in 'Vera' (S_1S_3) x 'Van' (S_1S_3) combination

Figure 2. Pollen tubes in the upper third of 'Margit' style

Pollen tube growth related to temperature:

Pollen tube growth is highly affected by weather conditions – especially by temperature. Daily mean, maximum and minimum temperature data of the years studied on five consecutive days after pollination are given in *Table 4*.

The percentage of pollen tubes in the whole style and days after pollination were taken for testing the year effect *(Table 5)*. The largest percentage of pollen tubes was observed in the warmest year, 2000. Then was a significant difference between years studied only at P=0.1 level.

In vitro pollen tube growth:

Percentage of flowers belonging to each style section are shown in Table 6. In the half compatible combination, pollen tubes penetrated the bottom section of the style in 50% of the flowers. Here the number of tubes varied from 1 to 8.

On the contrary, in all 'Vera' flowers pollen tubes reached only the upper third section of the styles only. The pollen tube end was often swollen and intensively fluorescent *(Figure 1)*.

Discussion

In our data, percentage of pollen tubes was calculated instead of using their absolute number as the number of pollen tubes in the style is highly affected by the number of germinated pollen grains on the stigma.

Statistical analysis showed no significant differences between the pollen tube growth of compatible and half compatible combinations in the style as a whole and in separate style sections. However, when looking at raw data, there are differences between them as described in the Results chapter, especially in the third section of the style as in 2001 and 2002 no pollen tubes were found here in 'Germersdorfi 3' flowers in contrast to 'Germersdorfi 3' x 'Alex'. As using all data recorded, statistical analysis was performed, large standard deviations resulted. In this case, we accepted the hypothesis and did not consider the statistical results. We concluded that 'Germersdorfi 3' x 'Alex' (half compatible) and 'Margit' x 'Alex' (compatible) combinations showed differences in pollen tube growth. Thus it does not correspond with the results observed by *Schmidt & Timmann* (1997) as no differences between compatible and half compatible pollinations were found by

Table 4. Daily mean. maximum and minimum temperature after pollination in 2000–2002

Days after pollination*	Daily mean temperature (°C)			Daily minimum temperature (°C)			Daily maximum temperature (°C)		
	2000	2001	2002	2000	2001	2002	2000	2001	2002
1	15.3	7.2	12.8	12.5	1.0	4.3	25.0	14.8	20.8
2	15.9	8.7	12.8	12.7	-0.7	8.8	25.4	16.0	20.5
3	16.2	9.7	13.2	11.0	4.5	7.5	24.9	13.5	20.3
4	17.4	9.7	12.5	9.0	5.8	5.5	25.6	14.0	22.5
5	17.3	7.5	13.1	10.0	4.8	7.5	24.0	12.0	23.5
Average	**16.4**	**8.6**	**12.9**	**11.0**	**3.1**	**6.7**	**25.0**	**14.1**	**21.5**

*Time of pollination in 2000: 18 April; in 2001: 19 April; in 2002: 20 April

Table 5. Year effect on pollen tube growth (one-way analysis of variance for percentage of pollen tube growth)

Year	Pollen tubes in the style as the percentage germinated pollen grains on the stigma of		Welch-test (d ratio)
	Mean	Standard deviation	
2000	0.197	0.179	2.677+
2001	0.116	0.154	
2002	0.105	0.137	

+ significance of the probability at P<0.1

Table 6. Distribution of the flowers according to the style section reached by the longest pollen tube

	Half compatible pollination 'Alex' (S_3S_3') x 'Van' (S_1S_3)	Incompatible pollination 'Vera' (S_1S_3) x 'Van' (S_1S_3)
1st (upper) third	in 20% of flowers	in 100% of flowers
2nd (middle) third	in 30% of flowers	in 0% of flowers
3rd (lower) third	in 50% of flowers	in 0% of flowers

these authors. The 'Germersdorfi 3' x 'Alex' combination had a rapid pollen tube growth on the first days at the top of the styles, then pollen tubes were arrested somewhere in the second section that corresponds to the findings in almond (*Ortega* et al., 2002).

Two phenomena were not expected in the pollen tube growth of a half compatible cross. First of all, in 2000, there was a decreasing tendency in pollen tube number in the styles of cv. 'Germersdorfi 3'. Indeed, 2000 was the warmest among the years studied. However, in spite of the same conditions such rapid pollen tube growth was not observed in 'Margit' styles so the abnormality in pollen tube growth in 'Germersdorfi 3' flowers could unlikely be attributed to the year effect.

Secondly, apart from the year 2000, no pollen tubes had reached the base of the style. Usually, both in fully compatible and half compatible pollinations, more or less the same number of pollen tubes reach the third section of the style (*Schmidt & Timmann*, 1997); *Ortega* et al., 2002). Moreover, in a test pollination in the same 'Germersdorfi 3' x 'Alex' cultivar combination fruit set occurred (data not shown). It might be that this slow pollen tube growth is a property of cv. 'Germersdorfi 3' and pollen tubes may reach the base of style later. To clear up this question, it would be worth extending the sample collection for 7–10 days after pollination.

It was not our aim to describe the effect of the temperature on pollen tube growth. However, our data roughly demonstrate how pollen tube growth relates to temperature. The warmer the weather was, the higher percentage of pollen tube growth was observed.

By *in vitro* pollination and pollen tube growth it was possible to distinguish between incompatible and half compatible pollinations. In the incompatible cultivar combination ('Vera' x 'Van'), all pollen tubes arrested in the upper third of the style, similarly to the observations of *Cerovia & Ružia* (1992) and *Stösser* (1980) who found the same style section to be the place of inhibition. Our results confirm that 'Vera' and 'Van' indeed have the same incompatibility genotype. In the half compatible 'Alex' x 'Van' combination pollen tubes reached the third section. It confirms the fact that these cultivars have a different S-genotype. It was demonstrated that in vitro pollen tube growth correlates with S-allele interactions.

Results of *in vitro* pollen tube growth showed less deviation than those of in vivo experiments. The in vitro method appears to be more useful in pollen tube growth studies as controlled temperature is ensured. The artificial medium and emasculation had no negative effect on pollen tube growth.

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