

Floral biological investigations of apple cultivars in relation to fire blight

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Summary: Floral activity was studied in two apple cultivars: an *Erwinia*-tolerant ('Freedom') and a sensitive one ('Sampion'). Since more types of protogyny occur in apples, the period of stigma activity is different. Papillae of the exposed stigma in flowers of 'Freedom' function longer (usually more than a week) than in the delayed homogamous 'Sampion'. Despite of this, cv. 'Freedom' is tolerant to *Erwinia amylovora* (Burr.) Winslow et al., suggesting no relationship between the floral biological type (including the exposure and longevity of stigma) and the infection by *E. amylovora*. According to SEM micrographs, nectary stomata in 'Freedom' are already open in the flower bud, where nectar secretion starts and continues until the senescence of the stigma. However, the long period of nectar secretion does not create optimal conditions for bacterial growth, since nectar production is scant in the flowers of 'Freedom'. The surface of the nectary, its nectar-retaining capacity, and the amount and concentration of nectar may influence the susceptibility of apple cultivars. It is manifested well by the smooth nectary surface with nectary stomata rising slightly above the epidermis in flowers of cv. 'Freedom', contrasting the wrinkled, striate nectary surface with slightly sunken stomata in the flowers of 'Sampion'.

Key words: apple, *Erwinia amylovora*, floral biology, nectary, nectar, nectary stomata, stigma

Introduction

Fire blight, caused by *Erwinia amylovora* (Burr.) Winslow et al., continues to be one of the most intensively studied bacterial diseases of pome fruit trees (van der Zwet et al., 1988, Johnson & Stockwell, 1998). Prevention of blossom infection is a key in fire blight management because the bacterial ooze originating from blossom infections provides much of the inoculum for secondary phases of the disease, including the infection of shoots, fruit and rootstocks (Schroth et al., 1974, van der Zwet & Beer, 1991).

For blossom infection *E. amylovora* needs to increase its population size through an epiphytic phase that occurs mainly on stigmatic surfaces, but also on the anthers and the hypanthium. The bacterium first colonises the stigma, which is followed by the external washing of cells from the stigma to the hypanthium. The pathogen gains entry to the plant through nectary stomata (nectarthodes) located on the hypanthial surface (Rosen, 1936, Hattingh et al., 1986, Thomson, 1986, Wilson et al., 1989, 1990, Johnson & Stockwell, 1998).

In the *Rosaceae* family nectar, consisting mainly of sucrose, glucose and fructose, is secreted through nectary stomata. The secretory product acts as an attractant for pollinating insects, but also supports the epiphytic growth of bacteria. Conditions for the pathogen vary greatly, according to the timing of nectar production, sugar concentration, environmental influences, as well as floral age and morphology (Ivanoff & Keitt, 1941, Paulin, 1987, Campbell et al., 1991, Johnson & Stockwell, 1998).

Rosaceae species are characterised by "wet-stigmas" that are covered with club-shaped papillae, with an additional cuticular layer. Stigmas provide a protected, nutrient-rich, hydrated environment for the pathogen to multiply (Hattingh et al., 1986, Wilson et al., 1989). The bacteria penetrate the stigmatic tissues mostly through intercellular spaces or between two adjoining cells by dissolution of the walls (Rosen, 1936).

The development of fire blight is affected by air temperature and relative humidity. Moderately high temperatures are favourable for bacteria, the optimum for rapid development of the infection ranges from 21–27 °C. Rainy weather followed by warm, cloudy weather, especially during blossoming and ultimate shoot growth, is very favourable to outbreaks of fire blight (van der Zwet & Keil, 1979, van der Zwet, 1986).

As for floral biological types, the majority of authors (Maliga, 1956, Porpáczy, 1964, Soltész et al., 1980.) described apples as protogynous. Later on Orosz-Kovács & Scheid-Nagy Tóth (2001) described more floral biological types of apple cultivars:

In the case of **protogyny brachybiostigmata** (Delpino cit. Filarszky, 1911) – traditionally called protogyny – the stigma is fully developed before pollen shedding, but it is becoming senescent and is not receptive at the time of anther opening, thus the stigma phase and the pollen shedding phase are totally separated. This type of protogyny was not found to be typical in apple cultivars. While investigating ten apple cultivars, it was constant only in two of them in each season of study: cvs. 'Jonagold' and 'Summerred'. At this type it was

typical that the balloon-stage and the young, open flower-stage with closed anthers continued for a few days. In the phase of stigma activity nectar secretion may start, for example cv. 'Summerred' secretes nectar, while cv. 'Jonagold' does not (Orosz-Kovács & Scheid-Nagy Tóth, 2001).

In the case of **protogyny macrobiostigmata** (*Delpino cit. Filarszky*, 1911) the stigma is also functioning before pollen shed, however, it is still receptive at the time of anther dehiscence. In this case dichogamy changes to homogamy. There is no autogamy in autosterile apples, that is why – opposing delayed autogamy in other plants described by Cruden & Lyon (1989) – the term **delayed homogamy** was introduced, like in some sour cherry cultivars (Orosz-Kovács, 1991). This type is frequent in apples, as for instance in cvs. 'Idared', 'Smoothee', 'G.243', 'Burgundy', 'Lysgolden', 'Red Rome Van Well' and 'Ozark Gold' (Orosz-Kovács & Scheid-Nagy Tóth, 2001).

The third type, which may occur in apple cultivars, is **homogamy**, where pollen shedding and stigma secretion start at the same time in the open flower and these activities remain synchronous during the life of the flower. This type occurred in cvs. 'G. 243', 'Smoothee' and 'Burgundy'. Different floral biological types may change in different seasons, or in a season both or all three types may occur in a single tree (Orosz-Kovács & Scheid-Nagy Tóth, 2001).

Among the investigated cultivars mentioned above, full protogyny, as described by Gottsberger (1977) in *Prunus*, *Pyrus* and *Malus* taxa, was not found. This paper, however, presents the floral activity of such an apple cultivar (see cv. 'Freedom' later on).

Studying the effect of rootstocks on floral biological types Scheid-Nagy Tóth (2000) pointed out that in some cultivars partial protogyny is a cultivar characteristic (e.g. 'Mutsu'), while in other cultivars this floral biological type occurred most frequently in trees grown on rootstock M.26. The delayed homogamous flowers of 'Idared' can also be considered as a cultivar specific trait, since it was constant on all rootstocks.

Soltész *et al.* (1980) stated that the degree of dichogamy is the smaller, the shorter the blossom period or the later a cultivar blooms. According to them stigmas in apple function for 2–5 days. From cultivars studied by them the longevity of stigmas in apple cv. 'Starkrimson' was the shortest.

Apple stigmas belong to the wet type (*Heslop-Harrison & Shivanna*, 1977). According to Stösser (1983) stigma papillae are turgid for 1–2 days after the flower has opened. The author considers the short time following anthesis as the most optimal period for fertilisation. Stigma papillae lose their turgidity 2–3 days after anthesis (*Braun & Stösser*, 1985). *Davary-Nejad et al.* (1993) reported that stigma activity lasts 1.5–2 days in hot, sunny weather, and 4–5 days in cool, cloudy weather.

Orosz-Kovács *et al.* (2001a) claimed that longevity of stigmas in apple flowers depends on floral biological type. In protogynous flowers the stigma phase may last from one to a few days. The stigma of delayed homogamous flowers usually functions for a longer time, because in this case it is receptive in the phase of pollen shedding, as well. The

longevity of stigma in homogamous flowers is the shortest. Here the flower becomes old 1–2 days after anthesis, having shed its pollen and also the stigma becomes senescent.

The epiphytic populations of *E. amylovora* grow predominantly on the pistils of apple flowers (*Hattingh et al.*, 1986). The period during which the stigma provides a suitable place for bacterial multiplication decreases with the increase of temperature, and also if apple flowers have already been pollinated (*Pusey*, 2002)

The primary entry site for the pathogen is provided by the open stomata on the nectary surface (reviewed by *Bubán et al.*, 2003). The nectary structure of some *Maloideae* taxa was described by *Kartashova* (1965) and *Orosz-Kovács et al.* (2001b, 2002). *Nagy Tóth* (1991) and *Orosz-Kovács et al.* (1991) described the nectary structure of apple cultivars.

Parallel to stigma activity, the commencement of nectar secretion was also studied by *Orosz-Kovács et al.* (2001b). Based on SEM studies of the nectary surface six types were described:

- 1–2. Nectary stomata of the protogynous cv. 'Summerred' are open already in the balloon stage. Stomata are still functioning in the young flower, opening and closing, according to which nectar secretion becomes rhythmic. In the similarly protogynous cv. 'Jonagold' nectar production begins only in the open flowers.
- 3–4. In the delayed homogamous flowers of apple cv. 'Ozark Gold' secretion cannot be detected in balloon stage, it commences only after the opening of the flower. On the other hand, the flowers of another delayed homogamous cultivar, 'Idared', begin nectar production already in the balloon stage.
- 5–6. In the homogamous flowers of 'G.243' nectar secretion starts in the balloon stage, whereas in the also homogamous 'Smoothee' it begins only in the opened young flower (*Orosz-Kovács et al.*, 2001b).

The surface of the nectary was characterised in several apple cultivars by *Nagy Tóth* (1991) and *Orosz-Kovács et al.* (1991). According to their studies secretory surfaces were highly variable in apple, the majority of them was strongly divided by grooves and wrinkles. This kind of nectary surface possesses a good nectar retaining capacity.

There is great variability in nectar sugar composition of apple cultivars, although in most of them about 50% of the total sugar amount is sucrose, while the rest is glucose and fructose (*Davary-Nejad et al.*, 1993). *Orosz-Kovács et al.* (1997) stated that there are significant differences between apple cultivars in the ratio of mono- and disaccharides. On the basis of the quotient S/G+F, introduced by *Baker and Baker* (1990), the majority of the studied cultivars belong to the sucrose-rich group.

Nectar amount and refraction of apples are affected by the environment and cultivar characteristics. *Soltész et al.* (1980) and *Benedek et al.* (1990) measured 2–5 mg nectar with 23–29% refraction in flowers of apple cultivars grown in Hungary. Based on investigations of 10 apple cultivars

Orosz-Kovács et al. (2001c) reported that during the ontogenesis of apple flowers the amount of nectar and refraction values change. Young flowers with undehiscent anthers produce 1.5–4.5 μl nectar, pollen shedding flowers 2–6 μl , senescent flowers that have finished pollen shedding 2.5–8 μl in the average of three years. Nectar refraction was the highest in the phase of pollen shedding in most apple cultivars. According to nectar refraction values, apple cultivars were classified into five groups. When planting cultivars with protogynous flowers, attention should be paid to the fact that besides matching the stigma phase of the cultivar to be pollinated to the blooming time of the pollen donor, their nectar refractions should also be similar.

The aim of this study was to determine the period of stigma receptivity in different floral biological types and to decide whether there is a correlation between *Erwinia* sensitivity and stigma longevity. A further aim was to find an answer to the question: is there a relationship between the

surface of the nectary, the period of nectar secretion, the volume and refraction of the secretory product and blossom infection by *Erwinia amylovora*?

Material and methods

The activity of reproductive organs was studied in the flowers of an *Erwinia*-tolerant ('Freedom') and an *Erwinia*-sensitive ('Sampion') apple cultivar from 2000 to 2004.

Flowers of the two apple cultivars originated from the cultivar collection and a high density experimental orchard of the Research and Extension Center for Fruit Growing in Újfehértó.

In the daylight hours the following reproductive functions of the flowers were studied in the field: the appearance of stigmatic exudate, the beginning of stigma senescence, duration and hourly amount of nectar secretion.

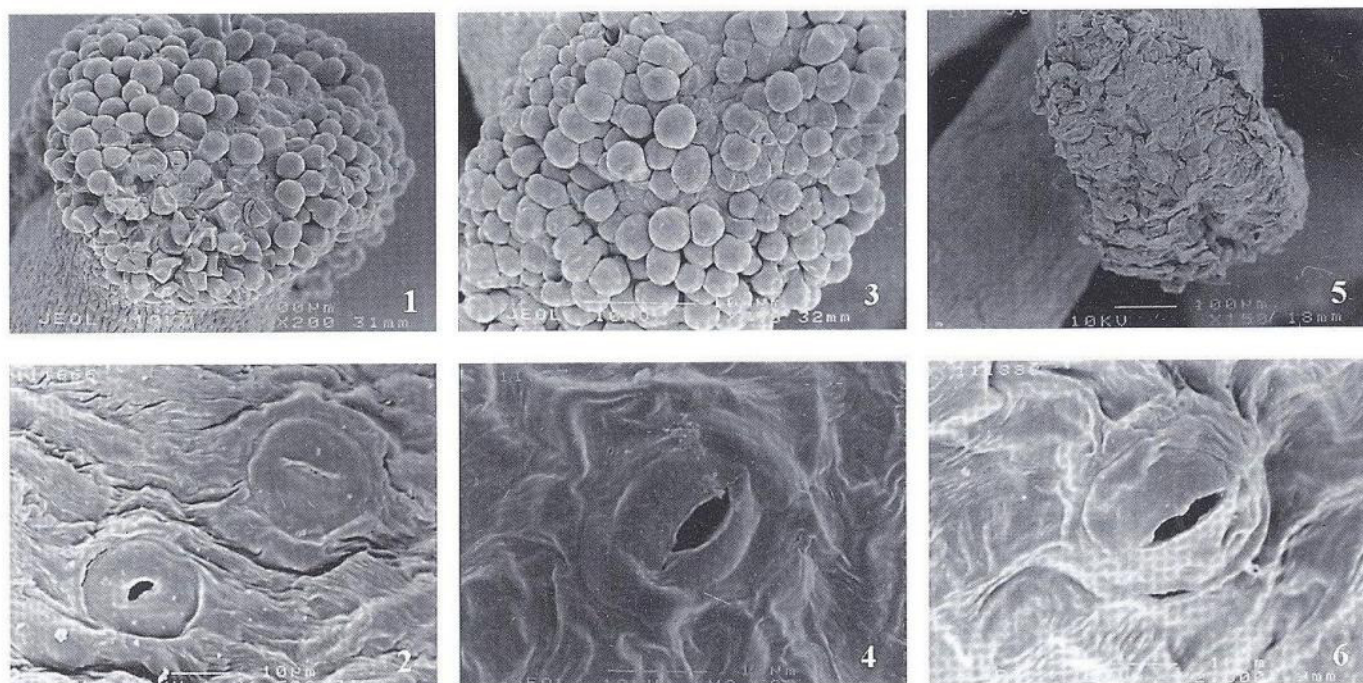


Figure 1–6. Stigma and nectary surface of apple cultivar 'Freedom' (1–2: in the flower bud with exposed stigma; 3–4: in the stage of pollination chamber (balloon stage); 5–6: in the stage of anther dehiscence)

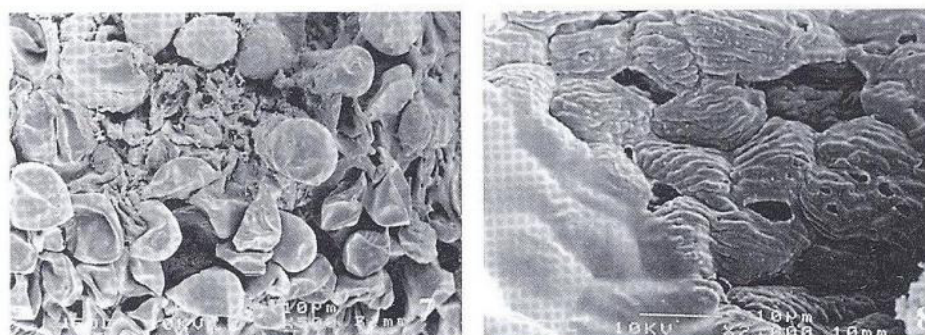


Figure 7–8. Stigma and nectary surface of apple cultivar 'Sampion' in the young flower, before pollen shedding

Nectar production was measured after 24 hour isolation of at least 20 flowers per year and also hourly in 15–20 marked flowers. Nectar volume was determined with calibrated microcapillaries, refraction was measured by a hand-held refractometer (type OG-101/A).

Stoma opening on the nectary surface and intactness of stigma papillae in the course of bloom was investigated by scanning electron microscopy (SEM) in 2003. For SEM studies 3 flowers per cultivar were fixed in 0.2 mol glutaraldehyde, and washed in 0.1 mol Na-cacodilate-buffer, then dehydrated in ascending ethylene-series. After critical point drying, the material was gold sputter coated. SEM-micrographs were executed by an ASID-4 SEM adapted to a Yeol 100 C equipment.

Results and discussion

Stigmas of apple cv. 'Freedom' frequently stick out of the 4–12 mm long flower buds surprisingly early, i.e. already 7–10 days before anthesis. The deep purple styles and stigmas rise above the flower bud through a small gap among the purple petals. This stage corresponds to the exposed stigma position, described by *Gottsberger* (1977). So flower opening begins with protogyny. The secretion of stigmatic exudate starts before anthesis, enabling the stigma to receive pollen. Thus the stigma is receptive already about a week before flower opening. In the exposed stigma stage, there is no other food source for insects besides the stigma exudate, since the flower buds are almost totally closed. Therefore insects do not visit the flowers, thus pollination can take place exclusively by wind. According to SEM studies the stigma is perfectly developed in this stage, and open stomata can already be seen on the nectary surface (*Fig. 1, 2*). Nectar secretion commences already in the tiny, few mm large flower bud, however, secretion is so scarce that a measurable amount of nectar cannot be found in the flowers until anther dehiscence in the course of hourly measurements.

This stage may continue for some days in cv. 'Freedom', during which time bud size is increasing, petals elongate and, reaching the stigmas, close around them. In the next stage of flower development stigmas can be seen in the small circle-shaped gap formed by the petals. This stage may last for some days, corresponding to the pollination chamber defined by *Gottsberger* (1977). However, the odour reminding of rotting fruits, mentioned by the author, cannot be smelled in the case of this apple cultivar. Smallish insects can gain entrance into the flower, searching for pollen and nectar. Stigma papillae are fully turgid in this stage, and stomata are open on the nectary surface (*Fig. 3, 4*). Nectar is still scant and therefore cannot be measured.

The above two stages of protogyny belong to stigmatic activity, which continues in the balloon stage and the open young flower, too, but comes to an end when anthers start to dehisce. Thus the stigma is usually receptive for more than five days, in cool weather even more than a week. At the time

of pollen shedding the surface of the stigma is getting brown, gradually becoming senescent, which can be followed on SEM micrographs, as well (*Fig. 5*).

The majority of flowers in cv. 'Freedom' showed this type of perfect protogyny, but in the five years of study some flowers were found where the browning of stigma started only during anther dehiscence. These flowers can be considered as delayed homogamous. In 2004 more flowers were delayed homogamous than dichogamous. In some seasons the first stage of flower development is not protogyny with exposed stigma, but pollination chamber.

According to SEM micrographs, the nectary stomata of cv. 'Freedom' rise slightly above the epidermis, and the cuticle covering the epidermis is almost totally smooth (*Fig. 2, 4, 6*). This structure refers to higomorphy. Nectar evaporates more easily from this less divided surface, it cannot remain in the flower for a long time, thus ensuring no continuous source of nutrients for *E. amylovora*.

The other studied apple cultivar is the *Erwinia*-sensitive 'Sampion'. During the ontogenesis of the flower the stigma does not stick out of the flower bud, but it is also protogynous at first. In the balloon stage the stigma is already secreting. This stage may last for more than 1 day depending on weather conditions. In this cultivar two floral biological types can be observed. In protogynous flowers the stigma becomes senescent already in the open, young flowers with undehisced anthers (*Fig. 7*). However, in the majority of flowers, the secretion of stigmatic exudate goes on and the stigma does not become brown in the young flower, but only when most of the anthers have dehisced. In the latter case the floral biological type is delayed homogamy, because the initial dichogamy shifts to homogamy later on. The stigma is receptive for 1–3 days in this cultivar, i.e. for a shorter time than in 'Freedom'.

In the flowers of 'Sampion' nectary stomata indicate mesomorphy or meso-xeromorphy, being slightly sunken and the cuticle is striate (*Fig. 8*). Nectar may stay in the grooves of the wrinkled surface of the nectary, because the creases act as a sponge, retaining the secretory product. This sugar solution may be enough for multiplication of bacteria.

In contrast, in flowers of the tolerant cv. 'Freedom' nectar production is scant, a measurable amount of the secretory product is either not present or only at the time of nectar secretion peaks.

Hourly nectar production of the susceptible cv. 'Sampion' is also little, but it is more than that of the tolerant cultivar. It is sufficient to keep the surface of the nectary continuously wet, ensuring nutrients for bacterial growth.

According to data of 2001, nectar refraction may also influence the increase of *E. amylovora* population. The nectar of 'Sampion' is dilute, refraction ranges between 12–18%, 15.33% as an average. The nectar of 'Freedom' is more concentrated: 21–46%, the mean value being 24.5%, which is less favourable for bacterial growth. Nectar refraction above 30% is supposed to be a restricting factor for development of fire blight (*Thomson, 1986*).

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