

Opening of flowers and time of anthesis in grapevines, *Vitis vinifera* L.

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S u m m a r y : During two years, opening of flowers in *Vitis vinifera*, cvs Müller-Thurgau and Blauer Spätburgunder was investigated. At average weather conditions flowers opened in periods of about 24 h. Opening started about 5:00, reached a maximum between 7:00 and 9:00 and was finished at about 12:00. Within an inflorescence, opening of flowers reached a maximum on the 5th or 6th d and was finished after 7 d, i.e. 7 periods. The diurnal rhythm was probably regulated by the photoperiod. To a certain extent the length of periods depended on temperature. High temperatures caused an advanced rhythm and a decreased length of period and *vice versa*. At the time of opening, anthers in all flowers had already dehisced. About 16–18 % of the flowers of cv. Blauer Spätburgunder and 60–63 % of cv. Müller-Thurgau proved to be pollinated before opening and growth of pollen tubes had already started. The two cultivars were partially cleistogamous. From corresponding data of this trait in both years a genetic basis for the two cultivars can be concluded. From the length of pollen tubes and the temperature during their growth, the time of anthesis was calculated. Within 24 h, anthesis probably followed two periods: the first period, 5:30–10:30 with a maximum between 6:00 and 8:00, included most of the flowers; the second period was observed between 16:30 and 1:30 with a maximum between 18:00 and 1:00.

Das Aufblühen der Blüten und der Zeitpunkt der Anthese bei Reben, *Vitis vinifera* L.

Z u s a m m e n f a s s u n g : Das Aufblühen der Blüten der *Vitis vinifera*-Sorten Müller-Thurgau und Blauer Spätburgunder wurde in zwei Jahren untersucht. Bei mittleren Witterungsbedingungen öffneten sich die Blüten in Perioden von ca. 24 h. Das Öffnen begann um 5:00, erreichte zwischen 7:00 und 9:00 ein Maximum und war gegen 12:00 beendet. In den einzelnen Infloreszenzen erreichte das Aufblühen am 5.–6. Tag sein Maximum und war nach 7 Tagen, d. h. nach 7 Blühperioden, beendet. Der diurnale Rhythmus wird wahrscheinlich durch die Photoperiode reguliert. Die Länge der Perioden hing zum Teil von der Temperatur ab. Hohe Temperaturen nach Ende einer Blühperiode beschleunigen den Blühhhythmus und führen zu einer Verkürzung der nachfolgenden Periode; niedrige Temperaturen wirkten in umgekehrter Weise.

Zum Zeitpunkt des Aufblühens waren die Antheren in allen Blüten bereits dehisziert. Mikroskopische Untersuchungen ergaben, dass 16–18 % aller Blüten von Blauer Spätburgunder und 60–63 % der Blüten von Müller-Thurgau schon vor dem Öffnen bestäubt waren und das Wachstum der Pollenschläuche bereits begonnen hatte. Die beiden Sorten sind also partiell kleistogam. Die übereinstimmenden Werte für die Sorten in beiden Jahren lassen eine genetische Abhängigkeit vermuten. Aus der Länge der Pollenschläuche beim Aufblühen und der Temperatur während ihres Wachstums konnte der Zeitpunkt des Beginns des Wachstums und daraus der Zeitpunkt der Anthese errechnet werden. Innerhalb von 24 h läuft die Anthese wahrscheinlich in zwei Perioden ab. Während der ersten Periode, von 5:30 bis 10:30 mit einem Maximum zwischen 6:00 und 8:00, fand die Anthese vermutlich in den meisten Blüten statt. Die zweite Periode, von 16:30 bis 1:30, hatte ihr Maximum zwischen 18:00 und 1:00.

Key words : *Vitis vinifera*, cv. Müller-Thurgau, cv. Blauer Spätburgunder, reproductive biology, opening of flowers, anthesis, pollen tube growth, cleistogamy, circadian rhythm.

Introduction

The two *Vitis vinifera* L. cultivars Müller-Thurgau and Blauer Spätburgunder (Pinot noir), are hermaphroditic and self-compatible. During earlier investigations of the reproductive biology it had been observed that flowers probably open in definite periods. Therefore, investigations were performed to present exact data on the opening of flowers in definite inflorescences, the time of anthesis and their dependence on environmental conditions.

Material and Methods

Investigations were carried out in 1975 and 1976 with *Vitis vinifera* cvs Müller-Thurgau and Blauer Spätburgunder in a vineyard near the State Institute for Viticulture in Freiburg, Germany.

Sixteen inflorescences of each cultivar, developing in the middle part of the vines, were investigated. On 23 June 1975 and 11 June 1976 one to three flowers had opened in these inflorescences and further opening could be expected

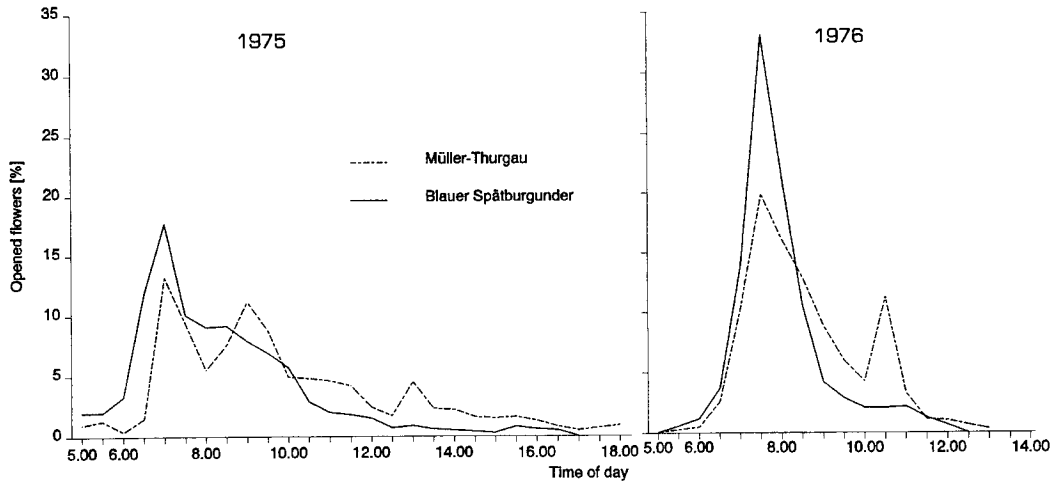


Fig. 3: Percentage of opened flowers during the day, 1975 and 1976.

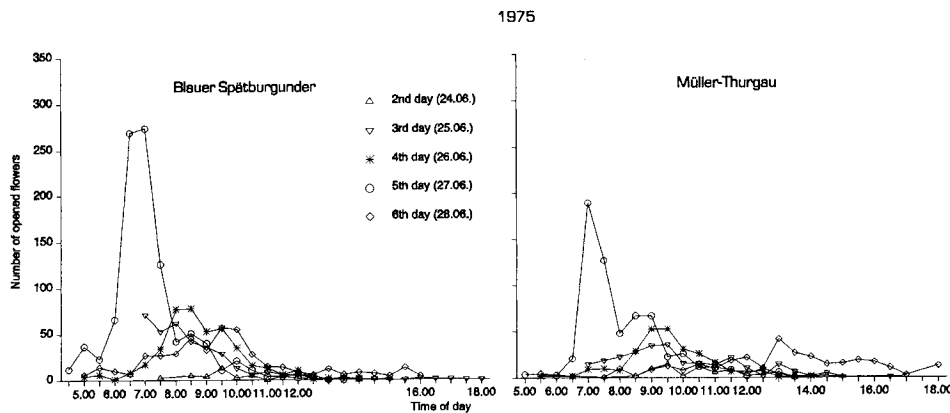


Fig. 4: Number of opened flowers during the day on each day of flowering, cvs Blauer Spätburgunder and Müller-Thurgau, 1975.

following day (the day of opening) the difference becomes more evident: The average temperature reached only 16.5 °C before the 4th day, however, 20.5 °C before the 5th day of opening. Likewise, the sum of temperatures during the relevant time and the mean relative air humidity showed remarkable differences.

Time of anthesis: In all flower buds fixed at opening or immediately thereafter, anthers had already dehisced and stigmata were pollinated. Anthesis, therefore, must have taken place before opening or during the opening process. From microscopical investigations it can be concluded that both assumptions proved correct.

Every 30 min 20 flowers were investigated for pollination and germination of pollen grains. In case pollen grains had germinated, the longest pollen tube per flower was measured. In 1976, 28 % of the Müller-Thurgau flowers opened on the 2nd day showed already germinated pollen grains. Towards the 7th day the percentage increased up to about 95 %. Similar results were observed in 1975. In Blauer Spätburgunder flowers the number with prefloral anthesis was distinctly lower. The number of those flowers increased similarly from the 2nd towards the 7th day but only from 6 to 40 % (Fig. 5). In both years the frequency of flowers with

prefloral anthesis was similar: 18 % in 1975 and 16 % in 1976 in Blauer Spätburgunder, on the other hand, in Müller-Thurgau 60 % in 1975 and 63 % in 1976.

Table

Meteorological data for the day/time preceding the 4th and 5th day of opening, 1975

	Preceding day	Time span between 12:00 at the preceding day to 5:00 at the day of opening
4th day of opening (*)		
Average temperature (°C)	17.5	16.5
Rel. air humidity (%)	90.9	90.3
5th day of opening (o)		
Average temperature (°C)	19.9	20.5
Rel. air humidity (%)	81.7	75.6

(*), (o): see Fig. 4.

during the following days. Starting at 4:30 on the second day of flowering, inflorescences were inspected for opened flowers every half hour till 20:00. In order to record the course of opening within the inflorescences, flowers were removed at each time of inspection and subsequently fixed in alcohol:acetic acid (3:1) for further investigations. About 3,000-4,000 flowers of each cultivar were investigated each year.

Stigmas, styles and ovules of flowers were prepared after STAUDT (1982) and germination of pollen grains, pollen tube growth and length of pollen tubes were investigated. At each time of inspection 20 flowers were studied. From these data the number of flowers with germinated pollen grains was calculated referring to the absolute number of flowers. According to former results on the velocity of pollen tube growth and its dependence on temperature (STAUDT 1981), the approximate time of starting of pollen germination was calculated from the length of pollen tubes and the temperatures during their growth. From these data the time of anthesis was calculated. The longest pollen tube of each flower was investigated.

Results

Opening of flowers: According to Fig. 1, weather conditions differed considerably during flowering time in both years. In 1975, the average daily temperature varied between 9 and 19 °C with a minimum of ca. 8 °C on the 6th, 7th and 8th day of opening. On the 2nd, 5th, 6th, and 8th day precipitation was more than 10 mm. In 1976, weather conditions were more favourable; during opening the average temperature varied between 15 and 23 °C, although the minimum temperature reached 8-9 °C on June 16 and 17. No precipitation was observed in this period.

Considering the number of flowers that opened each day, only small differences can be noticed between the two years. In 1975, the maximum of opening took place in both cultivars on the 5th day and it was almost finished on the 7th day. Only a few flowers opened later, till the 11th day, probably due to unfavourable weather conditions. In 1976, maximum opening took place on the 5th and 6th day and came to an end at the 7th day (Fig. 2).

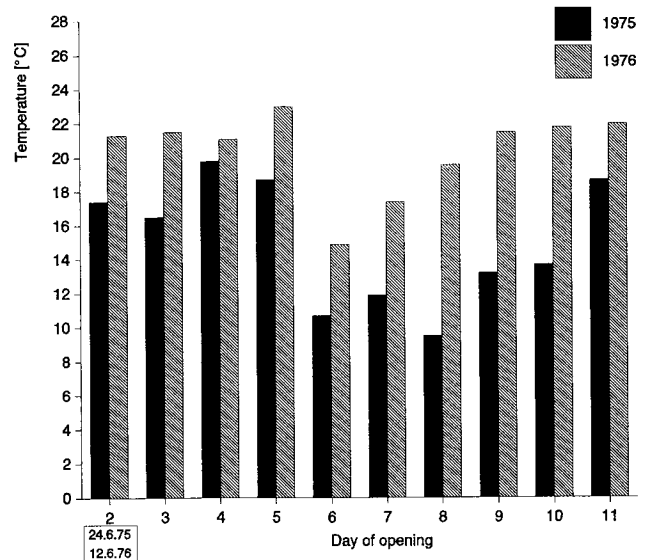


Fig. 1: Mean daily temperatures during the time of opening of flowers, 1975 and 1976. The second day of opening was June 24, 1975 and June 12, 1976, respectively.

In 1975, flower buds opened for the first time at 5:00, the maximum was between 7:00 and 9:00, and it decreased towards 12:30. In both cultivars, a few buds, about 2 %, opened between 12:30 and 18:00. In 1976, opening started at 5:30; the maximum was between 7:00 and 8:30 and it was finished almost completely at 12:30. No opening was observed after 13:00, although some of the inflorescences were exposed to sunshine during the whole afternoon and temperatures at the inflorescences reached about 30 °C (Fig. 3).

In 1976, except on the 7th day, maximum opening took place between 7:00 and 8:30. In 1975, maximum opening of flower buds was delayed on many days, for instance the fourth day. On the other hand, in both cultivars flower buds opened extremely early on the 5th day: the maximum was reached already between 6:30 and 7:00 (Fig. 4). In the Table, meteorological data are given for the preceding day/time of the 4th and 5th day of opening.

The average temperature on the day preceding the 4th day was 17.5 °C, but 19.9 °C on the day preceding the 5th day. If the relevant time is taken into consideration, i.e. the time between 12:00 of the preceding day and 5:00 of the

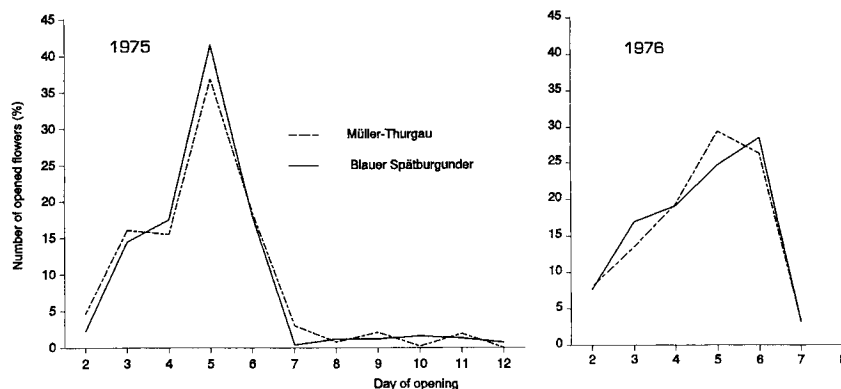


Fig. 2: Percentage of flowers opened per day, 1975 and 1976.

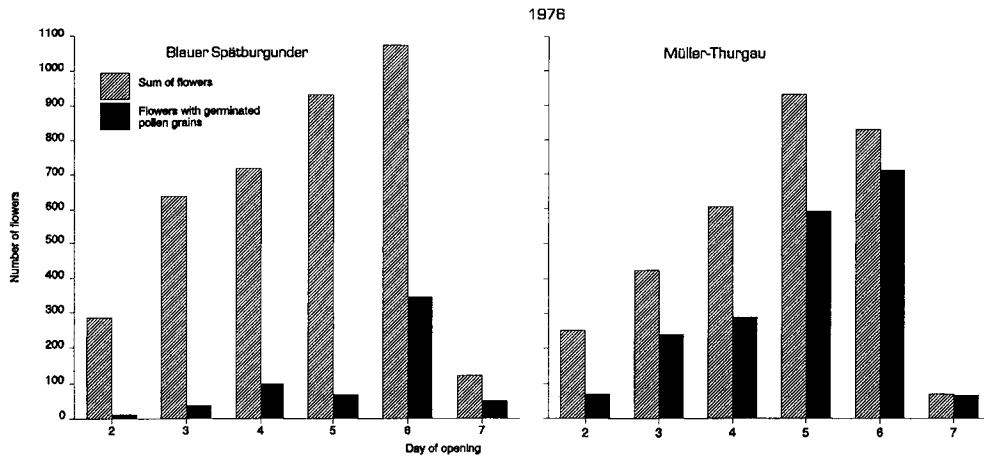


Fig. 5: Number of flowers with germinated pollen grains at the time of opening, cvs Blauer Spätburgunder and Müller-Thurgau, 1976.

From investigations of STAUDT (1981), the velocity of growth of pollen tubes at various temperatures is known. From the length of pollen tubes at the time of opening and the temperature during their growth, the time of onset of pollen tube growth was calculated. From these results the time of anthesis was deduced.

Irrespective of the time of opening, in about 20-25 % of the flowers with prefloral anthesis growth of pollen tubes had started in 1975 ca. 1 h before opening. In 1976 this happened in about 35 % of those flowers. At average temperatures, pollen grains need about 0.5 h on the stigma to become ready for germination. Consequently, anthesis may have happened at the earliest 1.5 h before opening. In both years, in about 45-55 % of the flowers anthesis had taken place about 2.5-1.5 h before opening. In about 35-55 % of the flowers, pollen tubes had probably grown already for three or more hours, and in 5-10 % for about 13-24 h. Except for slight differences at the beginning of germination, the cultivars showed nearly conformity in both years (Fig. 6).

Furthermore, it was investigated whether the flowers which opened at a definite time of day showed differences in the percentage of prefloral anthesis. In both years prefloral anthesis was observed in all flowers of Müller-Thurgau which opened between 5:00 and 6:30. In flowers which opened after 7:00 the percentage decreased and finally reached ca. 50 %. In flowers of Blauer Spätburgunder that opened after 7:00, the frequency was distinctly lower, it varied from about 30 to 10 % (Fig. 7).

In Fig. 8 the frequency of the beginning of pollen tube growth in the course of 24 h is presented. Only those flowers are included in which pollen tubes were already observed at the time of opening. In about 45-50 % of the flowers pollen tube growth had started between 6:00 and 11:00. Consequently, anthesis must have occurred about 0.5 h earlier, i.e. between 5:30 and 10:30. Only in about 5 % of the flowers anthesis occurred between 12:30 and 15:30. Thereafter, flowers with anthesis increased to about 25-45 % between 16:30 and 1:30 the following day. Concerning the flowers of the second maximum in Fig. 8, it seems unlikely to suppose that the anthers of these flowers had dehisced in the morning and the pollen grains remained on the stigmata for more than 4 h without germination. From earlier studies it is known that stigmata can be pollinated already before opening and

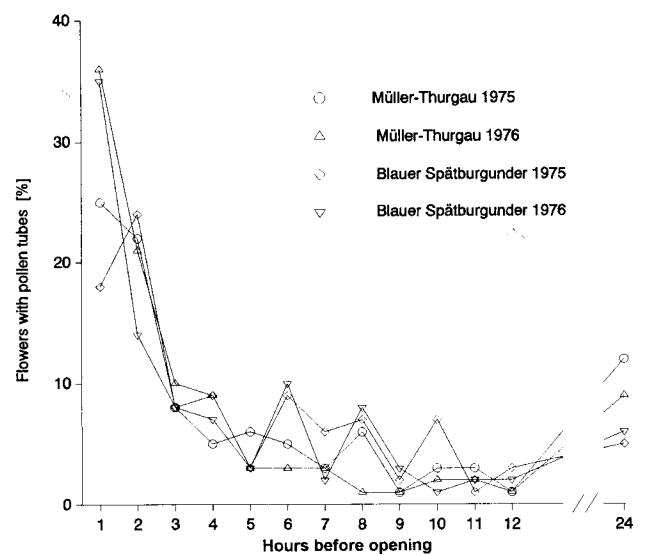


Fig. 6: Percentage of flowers with pollen tubes prior to opening as related to the time before opening, cvs Müller-Thurgau and Blauer Spätburgunder, 1975 and 1976.

pollen tube growth is able to start after a definite time. Therefore, these flower buds can be assumed to belong to a second period of anthesis occurring between 16:30 and 1:30.

In nearly all flowers that opened between 5:00 and 7:30 maximum pollen tube length was 1,400-2,200 μm . This leads to assume that anthesis must have occurred during the second period. In a few of these flowers anthesis may be traced back even to the end of the first period of the preceding day, 13:00-15:00. These flowers were probably prevented to open due to an expiring of the opening period.

Discussion

Circadian rhythms in flowers have been reported either concerning the movement of petals of open flowers or the opening and closing of flowers itself (BÜNSOW 1953; OLTMANN 1960; ENGELMANN 1960; OVERLAND 1960). In *Vitis vinifera* the rhythm of opening of flowers within an inflorescence followed periods of 24 h. Within a short time the period could be increased by lower temperatures and decreased by

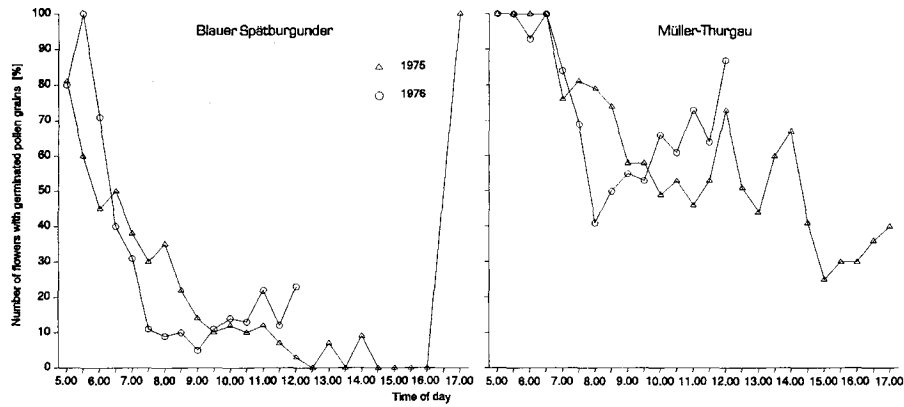


Fig. 7: Percentage of flowers with pollen tube growth as related to the time of day, cvs Blauer Spätburgunder and Müller-Thurgau, 1975 and 1976.

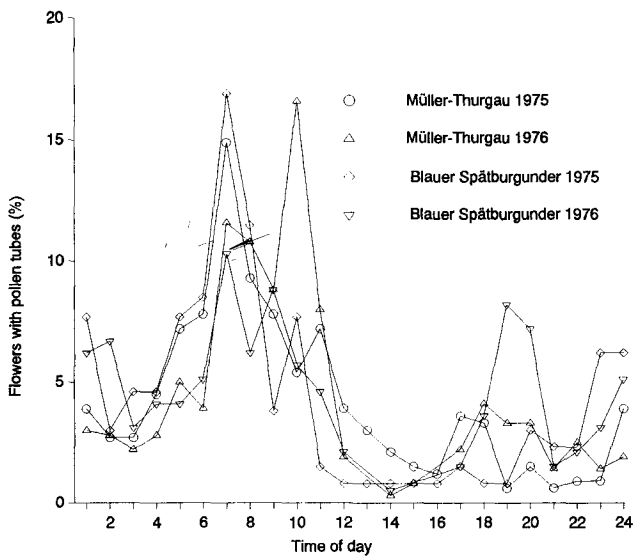


Fig. 8: Percentage of flowers with pollen tubes related to the time of day, Müller-Thurgau and Blauer Spätburgunder, 1975 and 1976.

higher temperatures similar to the results described by OVERLAND (1960) and ENGELMANN *et al.* (1974). At average weather conditions, maximum opening within an inflorescence can be expected at the 5th or 6th d and flowering will not last longer than 7 d. Flower buds opened at a definite time of the day. Opening followed a rhythm which started at about 5:00 and ended at about 12:00. The temperature of the preceding day, or more precisely, the temperature at the preceding non-flowering phase, probably influenced the onset of opening and the time of its maximum. This temperature probably effected the buds to reach the stage of development necessary for opening during the following flowering period. Only adverse circumstances, i.e. very low temperatures, would probably hinder the developmental processes which finally result in the opening of flowers. If the first bud had opened during the first flowering period, the other buds of the inflorescence followed in a diurnal rhythm. The sequence of opening depends probably on the time of initiation of the primordia of the flower buds, the position within the inflorescence, and consequently, the supply with nutrients. In any case

those flowers opened during a certain period which were probably the oldest in development. Neighbouring inflorescences displayed the same rhythm of opening but they may start at different days.

The diurnal rhythm was regulated by photoperiod and was most likely endogenous. In preliminary studies, the circadian rhythm could be verified also in darkness. At constant environmental conditions oscillating continued in subsequent darkness in a 24 h rhythm. The temperature prevailing at the time of opening had no or only a small effect on the opening of flowers.

Flowers of both cultivars of *Vitis vinifera* tended to prefloral anthesis, they were partially cleistogamous. The extent depends upon the cultivar. Anthesis probably followed an endogenous rhythm. Within the diurnal cycle two periods were observed. The first period started in the morning shortly before the onset of opening of the flowers. During 5:30 to 11:00, in most of the flowers which were supposed to open the same day anthers dehiscid. Those flowers must be included to the period in which germination of pollen grains was not observed because anthesis had occurred less than 0.5 h before or directly at the opening of the flowers. A synchronisation with the rhythm of opening can be supposed. The second period occurred at late afternoon to midnight, between 18:00 and 1:30. These flowers opened during the following flowering period. Because of the considerable number of flowers which showed anthesis during that period, an interpretation as a consequence of accidental effects or delay can be excluded.

No essential differences were observed between the cultivars and years. It can be assumed that the course of anthesis is endogenous. From the second period of anthesis it can be concluded that opening of flowers and anthesis are probably two independent processes of which the first is mainly controlled by the photoperiod.

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