Floral biology of medicinal plants I. *Apiaceae* species

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Summary: The Apiaceae family consists of several species which are well known for their therapeutical use and also as spice plants. Although fennel (*Foeniculum vulgare* Mill.), caraway (*Carum carvi* L.), anise (*Pimpinella anisum* L.), coriander (*Coriandrum sativum* L.), dill (*Anethum graveolens* L.), angelica (*Angelica archangelica* L.) and lovage (*Levisticum officinale* Koch.) are also economically considerable cultures, data on their flowering biology are rather scarce. This review supports data on the characteristic constitution of flowers and inflorescences, flowering dynamics, pollination mechanism and crossability of some of the most significant medicinal and spice species.

The inflorescence is a compound umbel. Flowers are hermaphrodite, however also monoeceous, mainly male flowers are turning up too. In blooming of a plant individual, a strict sequence is observed. The main umbel is the first to bloom, followed by the different range umbels in order of their range. In their pollination, both wind and insects are considered to be active. For each species, proterandry is characteristic. Although autogamy is considered to be almost unpossible, and geintonogamy as well as xenogamy to be the most characteristic ways of fertilization, several cases of self-fertilization proved to be also successful. Crossability among cultivars or species is depending on the genotype combination and usually produces less seed set than the above forms of fertilization.

Introduction

The species being declared as medicinal and aromatic plant are most diverse, taxonomically. In Hungary, about 180 plant species are supplying the drug demand. Nevertheless, trying to group the species, we find that a considerable proportion of them belong to some plant families, such as *Apiaceae*, *Lamiaceae* and *Asteraceae*. Among them, the former two include closely related taxa concerning therapeutical use, effective material accumulation and cultivation aspects.

The majority of medicinal plant species belonging to these families originates from the Mediterranean region. Their value as aromatic plant is based on the a considerable level of essential oil accumulation, however, the composition of the essential oil is characteristic for each species.

The umbelliferous species provide first of all seed-drugs, such as anise, caraway, fennel or coriander, rarely roots (angelica, lovage) being widely used also as condiments for conserves, bakery products, salads. Their main therapeutic application is based on carminative, spasmolytic, choleretic effects. As such, the drugs are used first of all in tea mixtures, digestive herbal preparations. The drug production in these cases is a large scale agricultural production – with some exceptions e.g. fennel, lovage – in annual culture.

Because of the growing demand and widening utilization areas, breeding of varieties, which may assure desired quality is spreading all over the world. After a starting period of selection breeding, recently, also more hyphenated methods are considered to bring further results. However, in the practice, selfing and crossing can rarely be carried out succefully. A severe need arised to gain more accurate data on the flowering and pollination mechanism, and on compatibility aspects. Based on own results and literature references, this summary provides information of floral biology of the most important cultivated *Apiaceae* species.

Morpology of inflorescences

The inflorescence of the *Apiaceae* species is a compound umbel. The main umbel is at the top of the shoot, while the shoot produces several lateral side branches. Regularly, they are numbered from the first (the oldest) till the fourth or rarely the fifth (the youngest) side branches. Each umbel consists of several umbellets, which are composed by individual flowers. The form of the umbels is different, from the compact globe type (angelica – *Angelica archangelica* L.) till the almost flat umbel (fennel – *Foeniculum vulgare* L.). The number of the umbels is characteristic for the species, however, it may vary at a large scale. For caraway (*Carum carvi* L.), *Smolyanov & Ksenzba* (1976) mention 3–12 umbellets within one umbel, and 14–21 flowers within one umbellet. According *Sváb* (1993), 5–10 umbellets form one umbel. Own investigations in 8 different caraway populations in different years showed, that the number of umbels varies between 5 and 31 in case of annual strains,

while it is always higher in the biennial varieties, even up to 60 umbels/plant (unpublished results). The number of umbellets is generally the highest in the first range side umbels and it is less both in the main as well as in the higher range umbels: in 4 populations we measured as an average 9 umbellets (main umbel), 12 (first range umbel), 10 (second range umbel), 5 (third range umbels). In fennel, differences among the main and the next range umbel are not pronounced in this respect, we measured 19–25 umbellets in each of them. In anise (*Pimpinella anisum* L.) 12–15 or even more rays (umbellets) form one umbel (*Szujkóné,* 1976), while its quantity is less in coriander (*Coriandrum sativum* L.), reaching only 3–5 (*Heeger,* 1956). *Dános* (1998) mentions 7–15 umbellets for anise, coriander and lovage, but considers angelica to have more than 30 rays in the compound umbels.

The number of umbels is influenced also by the intraspecific taxon (cultivar) and by the condition of the plant in connection with ecological factors. It was proved, that biennial caraway develops less inflorescences if vernalization is not satisfactory or the plant density is high in the stand (*Németh,* 1998).

The flowers of these species are usually complete. The sepals are reduced (*Mihalik,* 1998), hardly recognised or united with the fruit wall (*Szujkóné,* 1992). The number both of petals and stamens is five. Especially in coriander, petals are bigger in the external flowers than in the internal ones (*Bernáth,* 1993). The corolla has different colour. It is white with greenish or pink (caraway, anise, *Pimpinella anisum* L.), or even violet shade (coriander), while it is yellow in case of fennel, dill (*Anethum graveolens* L.), lovage (*Levisticum officinale* KOCH) and green in angelica. The pistil is composed of two carpels, from which the twin fruits develop and will be separated each other during ripening (except coriander). Beside the majority of hermaphrodite flowers, male flowers are often described (andromonoecy). The proportion of male flowers is increasing with the umbel order (*Bouwmeester & Smid,* 1995, *Heeger,* 1956) and in the second half of vegetation (*Mihalik,* 1998).

A symptom of abnormal development of flowers represent also male sterility. In caraway, *Keulen* (1988) mentions former observations for this trait, but she could not prove it in own materials.

Blooming dynamics

Szujkóné (1976) describes 9 onthogenetical phases in anise from closed bud stadium till dehiscence of anthers. Considering to literature data and own observations, the main phases seem to be similar in case of the other species in topic, too. Opening of the buds begins with separation of the petals during which phases the stamina and the pistil start to elongate. At the time of petal opening the anthers become ripe and produce pollen. According to relevant data, each species discussed here exhibit proterandry: the stigmata become receptive only after the anthers having dehisced and split. Ripeness of the stigmata is shown by the erect styles standing in V form, and the wet surface of the stigmata. At this time the corolla usually has been shed. After fertilization, the styles dry out, turn down but remain on the mericarp.

In blooming of a plant, a strict sequence can be observed. The main umbel is the first to bloom, while it is followed by the different range umbels in order of their range. Within an umbel the order of umbellets' flowering is the following: the outside flowers in the outside umbellets, the outside flowers in the internal umbellets, after which the inside flowers of the outside umbellets, followed by the inside flowers of the inside umbellets (*Keulen,* 1988).

Duration of the described onthogenetical phases has a basic importance in both spontaneous and artificial fertilization processes. In this respect, data include first of all information on caraway. Time shift among flowering of different range umbels of biennial caraway plant usually takes 5–7 days (*Smolyanov & Ksenzba,* 1976). In Hungary, in annual caraway we registered 1–3 weeks for flowering of a single umbel, where the later opening (higher range) umbels developed more slowly (*Németh* et al., 1999).

As for individual flowers, *Van Roon & Bleijenberg* (1964) observed in open field experiments with biennial caraway a period of 5–7 days between the emergence of pollen and the receptivity of stigmata. In annual caraway we measured 3–8 days for this phases (*Németh* et al., 1999). The length of these periods is highly depending on temperature, in warm weather the flowering phases take place more quickly (*Toxopeus & Lubbert,* 1998). Therefore, differences between biennial and annual ecotypes (flowering in April and June, respectively) or even vegetation years may be considerable.

In case of fennel, results are similar. Indian researchers measured a complete separation of male and female phases both at flower and at umbel level in wild as well as cultivated forms of *Foeniculum vulgare* (*Koul* et al., 1996). Within an umbel, *Reichardt & Pank* (1993) observed a 4–6 days interval between anthers and stigma ripening. In flowering dynamical experiments carried out with cultivar 'Soroksári', in its big umbels a significant time shift was registered even among flowers of a single umbel (*Németh* et al., 1999). Between the outside and inside umbellets of the same umbel we found 1–4 days difference in appearance of the equivalent phases, depending also on the range of umbel.

The phenomenon is similar in coriander, where according *Szujkóné* (1992) the outside flowers of umbels of coriander are always earlier in blooming than the others; however no data about exact time interval are published.

Pollination

For effective pollination of the species studied, both wind and insects are considered to be involved. It is not quite clear yet which is the more important one. In different crossing experiments of Dutch researchers (*Van Roon & Bleijenberg,* 1964; *Keulen,* 1988) seed set of caraway was only appropriate if flies were put under the isolation bags. Air

circulation in greenhouse also increased pollination success of non-isolated flowers (*Toxopeus & Lubberts,* 1998), however, application of insects multiplied the result. In open field, the situation may be somewhat different. *D'Albore* (1986), cit. by *Bouwmeester & Smid,* 1985) stated, that wild insects belonging to the families of *Syrphidae, Muscidae, Calliphoridae* etc. are responsible for 99% of the pollination of caraway. *Bouwmeester & Smid* (1995) found, that preventing insect pollination by placing gauze cages on the plots, reduced seed yield by 15–20%, but they supposed that wind transfer in addition to insects also plays a role in fertilization of caraway.

For coriander, the effect of wind was practically excluded, as almost no amount of pollen grains was detected in the air above the crop (*Koul* et al., 1989). Besides, the role of several insects was proved in pollination, such as species of the *Isoptera, Hymenoptera, Orthoptera, Diptera, Hemiptera and Lepidoptera* families.

In comparison trial of caraway, cumin (*Cuminum cyminum* L.) and anise it was found, that maximum seed yield occurred in each plantations in open-pollination plots, followed by bee pollination and insect exclusion (*Hussein* et al., 1991). Anise attracted the maximum numbers of bees and *Diptera*. This latter finding supports the assumption, that *Apiaceae* species have different floral scents, showing various degrees of specialization in pollination biology (*Tollsten* et al., 1994). According *Ricciardelli* (1986), observations revealed, that angelica, caraway, anise and fennel as well as other related species showed significant differences concerning their pollinators. While *Apis mellifera* was one of the most common visitors of angelica, wild bees occurred at higher proportions on caraway and anise. The author states, that *Apiaceae* species are particularly attractive to *Apoidea* and other insects. Data of *Heeger* (1956) confirm, that honey-bees and other *Hymenoptera* are important pollinators of angelica and lovage, although the colour of their petals is not especially attractive. On the contrary, fennel and dill were not visited by honey-bees, which might mean, that they are not appropriate honey-bearing plants, although in Hungary there are also other observations (*Boros & Szujkóné*, 1970). *Heeger* (1956) describes several further insect species as visitors of the medicinal plants of *Apiaceae* family, however, proof about their role in pollination is not always clear.

Beside scent of the flowers, colour and form of the flowers may attract insects. According to the assumptions of *Bouwmeester & Smid* (1985) even the male flowers of caraway may have its importance in attracting the pollinators. In *Daucus carota* no effect of different flower colours on the pollination was registered (*Westemoreland & Muntan,* 1996), but in the mentioned medicinal plant species, cultivars do not differ in flower (petal) colour.

Fertilization properties

Based on the flower constitution and flowering sequence, in the mentioned species of *Apiaceae* family, autogamy is considered to be almost unpossible, and geintonogamy as well as xenogamy to be the most characteristic ways of fertilization. Although this behaviour is generally accepted (*Heeger,* 1956), special experiments to clear the fertilization mechanism of the species were carried out in some cases only.

Experimental research of *Keulen* (1988) on caraway revealed, that a small amount of seed set may happen also inside an umbel or even inside a single flower. In isolated umbels she got 0.68–5.78% seed set, depending on cultivar. If only the outside flowers of the outside umbellets were left in isolated umbels, these proportions became lower, but self-pollination was not fully excluded even in these cases (0.0–3.62% seed set). Irregular behaviour of the flowers as well as spontaneous selection of some cultivars for this trait were proposed by the authors as explanation. The most simple statement, that autogamy or fertilization within one umbel is impossible, was refused also by own data. In isolated umbels of different range of annual caraway plants we found 0–12% seed set (*Németh* et al., 1999).

In the same experiments, for fennel, the results showed even higher possibility of self-fertilization. Inside an umbel 25–61% seed set was measured by us. Although without mentioning the probability of fertilization inside an umbel, *Reichardt & Pank* (1993) found castration practically necessary before artificial crossings of fennel cultivars.

Similar data exist for coriander. While in isolated flowers no seeds were produced, isolation of umbels assured 55–68% seed set (*Koul* et al., 1989).

These findings may serve also as proofs, that there does not exist any genetical self-incompatibility in those species, and eventual low seed set might have caused by disturbances of flowering-synchronisation, lack of pollinators or other problems. Fertilization properties are namely influenced by several factors. As the most often mentioned ones, the presence and percentage of irregular or not complete (male) flowers may play a significant role in seed set. According to investigations of *Bouwmeester & Smid* (1995), some regularities could be established in seed formation of caraway umbels. In a plant individual, seed sett was significantly higher in lower range umbels than in higher range ones and within an umbel, it was higher in peripheral umbellets, than in the central ones. The authors succeeded to prove the connection between seed set and the presence of male flowers. In the mentioned cases, where fewer seeds developed, also the proportion of male flowers was significantly higher. Thus, every factor, which influences formation of male flowers, (e.g. plant density) may affect seed production and yield. As described in other vegetable *Apiaceae* species, the propensity for male flower formation may be connected to intraspecific differences (*Somos*, 1975), however in respect of our species there are hardly any reliable data about it. Variety differences in this respect were only proved by *Bouwmeester & Smid* (1995), who got a lower ratio of male flowers in the biennial variety Bleija, than in annual accessions. Under certain limits, several

Apiaceae are able to assure a constant number of hermaphrodite flowers. In the above experiments, removing the 2nd range umbels stimulated the number of perfect flowers also in the 3rd and 4th range umbels.

Beside genetical features, ecological circumstances also determine the yield. *Bouwmeester & Smid* (1995) describe the significance of light supply. They suppose that under reduced light circumstances (in shade) the plant is not able to mobilize enough assimilates for seed development or indirectly, the fertility of flowers is influenced. At the same time, no reduction in seed yield was measured when flowers were kept regularly wet.

In view of the above mentioned data, self-pollination may occur in our plants, however the majority of seed production originates from geintonogamy (pollination between the umbels of the same individual, in this case pollination of older umbels by the younger ones) and xenogamy (pollination between different plant individuals of the same population). Pollination and fertilization has a high probability among the umbels of different range of the same plant, but also among different plant individuals too. Studying the probability of bastardogamy (fertilization between different cultivars), we got seed set up to 84% (average 44%) in caraway and 41–63% (average 50%) in fennel. In the combinations studied, no difference could be proved in seed-set rate of xenogamy and bastardogamy, however, both of them were somewhat higher than the rate after geintonogamy.

Compatibility among different cultivars have not been studied directly, however evaluating four reciprocal combinations in crossings between annual and biennial caraway cultivars, *Keulen* (1988) did not find any significant difference among them concerning seed set.

Under average field circumstances *Bouwmeester & Smid* (1995) found, that abortion of seeds in fertile (hermaphrodite) flowers was 10–15% independent from the examined factors. From biological side, flowering dynamics and optimal formation of flowers seem to be the most important factors in successful fertilization.

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