Floral Biology of Common Buckwheat  
*(Fagopyrum esculentum* Moench)*

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**ABSTRACT**

Common buckwheat (*Fagopyrum esculentum* Moench) is widely cultivated but the floral biology of this auto-incompatible distylos species was poorly documented. This review, based on our recent results obtained with the cultivar ‘La Harpe’ and the literature, summarizes main aspects related to its reproduction: morphogenesis, flowering, nectar, pollination and flower functionality. The activity of the reproductive meristems is potentially endless but the morphogenesis is stopped by the abortion processes. When the plant has one unfolded true leaf, the morphogenesis of the reproductive structures occurs at many nodes and this developmental stage is highly sensitive to environmental stress. *Hymenoptera* (*Apis mellifera* L. and *Bombus* spp.) and *Diptera* (*Syrphidae*) are the main visitors. Honeybee appears to be an effective pollinator and the most numerous visitors in Western Europe. At the anthesis, ‘hexoses-dominant’ floral nectar is secreted by unicellular secretory hairs during all the light period even after pollination. Except for the morphology of the reproductive organs, both morphs differ only in the nectar production. Thrum flowers secrete more nectar than pin flowers. Pollinator abundance is an important parameter to secure the yield but even without pollen transfer limitation the seed set is low. Flower fate appears to be dependent on a mechanism internal to the raceme which controls the percentage of flowers able to set a seed. Infertile flowers with an undersized gynoecium and last abortions after fecundation are not frequent. In contrast, flowers with a normal sized gynoecium which do not set seed after compatible pollination are the main contribution to the low seed set. This female organ sterility seems to be the most yield limiting factor throughout the world.

**Keywords:** distyly, morphogenesis, nectar, pollination, resource, seed set

**CONTENTS**

INTRODUCTION ............................................................................................................................. 1
REPRODUCTIVE STRUCTURE INITIATION AND DEVELOPMENT .................................................. 2
FLOWERING AND SEED RIPENING .......................................................................................... 2
DISTYLY AND SELF-INCOMPATIBILITY ................................................................................... 4
NECTAR PRODUCTION ............................................................................................................... 4
POLLINATORS ............................................................................................................................. 5
POLLINATION ............................................................................................................................. 5
FUNCTIONALITY OF FLOWERS .............................................................................................. 6
CONCLUSION ............................................................................................................................ 6
ACKNOWLEDGEMENTS ............................................................................................................. 7
REFERENCES ............................................................................................................................ 7

**INTRODUCTION**

Common buckwheat, *Fagopyrum esculentum* Moench, is one of the oldest domesticated crops of Asia. This crop was very popular food during 17th-19th century and was later abandoned during the 20th century in Western countries because of the competition with wheat. Common buckwheat has a promising future on a worldwide scale due to recent discoveries on its nutritional qualities. It is a multi-food-use pseudocereal with a better nutritional value than many common cereals and a functional food with industrial applications (Hagels 1999; Tomotake et al. 2000; Bonafaccia et al. 2003a, 2003b; Kawa et al. 2003; Kim et al. 2004; Krokósková and Mrážová 2005; Christa and Soral-Śmietana 2008; Liu et al. 2008; Tang et al. 2009). Therefore, buckwheat which is mainly consumed in Asia and in Eastern Europe is an alternative to common cereals in Western countries and receives increasing attention. This situation motivates new breeding programs and further researches to increase productivity of buckwheat achenes.

Up to now, seeds are the most important product and the success of the harvest depends on the flower number, the seed weight and the seed set. The evolution from the wild ancestor, *F. esculentum* ssp. *ancestrale*, towards present-day cultivars drifted from *F. esculentum* ssp. *esculentum*, has considerably modified plant morphology (Lakanov and Napalova 2001). The wild species has a stronger main stem with many axillaries, a more developed root system and higher photosynthetic leaf area than modern cultivars (Lakanov and Napalova 2001; Chen et al. 2004; Logacheva et al. 2008). Successive selections allowed the elimination of the strong seed dormancy and the abscission layer of the pedicel, the limitation of lodging, the increase of seed set and seed weight (Kreft 1989; Campbell 1997;
Funatsuki et al. 2000; Lakhovan and Napolova 2001; Wagatsuma 2004). These numerous improvements turned out to be insufficient to obtain yields allowing buckwheat to compete with the other cereals. Actually, the mean yield in t ha⁻¹ at world scale is for buckwheat 0.86, rye 2.21, wheat 2.80, rice 4.11 and maize 4.81 (FAOSTAT data, 2006).

Increasing productivity and yield stability, as well as improving the efficiency of breeding programmes, requires to study the parameters that affect the duration of the flowering period, the pollination and the seed set. Concerning the reproductive mechanisms, buckwheat is a complex and exciting crop because of its numerous particularities. It is a hermaphroditic species with an indeterminate growth which produce self-incompatible distylos flowers pollinated by insects (Nagatomo and Adachi 1985). These characteristics make the improvement of buckwheat productivity complex, but their understanding will help to increase yields.

In this paper, we summarize the main aspects related to the reproduction of buckwheat: morphogenesis, flowering, nectar production, pollination and flower functionality. Most recent results reported here (Quinet et al. 2004; Halbecq et al. 2005; Cawoy et al. 2006a, 2006b; Cawoy 2007; Jacquemart et al. 2007; Cawoy et al. 2008) were obtained with the cultivar “La Harpe”. This diploid cultivar, adapted to the climate of temperate Western Europe, was developed and commercialized by INRA (Institut National de la Recherche Agronomique, France).

REPRODUCTIVE STRUCTURE INITIATION AND DEVELOPMENT

Growth of buckwheat is indeterminate and morphogenetic processes implicated in the establishment of the reproductive structures are potentially endless (Marshall and Pomeranz 1982; Quinet et al. 2004). They are dependent on the activity of meristems with an indeterminate mode of functioning which account for the anthesis potentialities of buckwheat to extend its flowering phase for protracted time period until abortion processes end the production of reproductive structures (i.e. inflorescence, cyme and flower; Quinet et al. 2004). These processes are regulated by resource availability. Actually, treatments which alter source/sink organ ratio during inflorescence morphogenesis by excision of selected inflorescences and/or leaves, respectively enhance or reduce the number of inflorescences and the number of flowers per inflorescence. Moreover seed development on a plant affect plant height, number of axillaries and reproductive morphogenesis in inflorescences, limiting the production of inflorescences and flowers (Racys and Montvilleneuve 2005; Cawoy et al. 2007).

Buckwheat initiates flowers over a wide range of day-lengths (Nagatomo and Adachi 1985) and even under continuous light (Hao et al. 1995), but cultivars do not similarly react to photoperiod. Some cultivars, as the Japanese summer cultivars, seem non-sensitive to photoperiod whereas others, as the Japanese autumn cultivars and the European cultivar “La Harpe”, behave as facultative short-day plants (Minami and Namai 1986; Lachman and Adachi 1990; Hagiwara et al. 1998; Michiyama et al. 1998, 2003; Quinet et al. 2004). For photosensitive cultivars, flower initiation is advanced by short days compared to long days (i.e. it occurs at lower nodes) but more inflorescences and more flowers per inflorescence are initiated and the flowering period is longer under long days. The floral transition occurs sequentially at the base of the pedicel of the preceding flower (Fig. 1E, 1F). After the production of 5-30 metamers, the arrest of functioning of the shoot apical meristem is accompanied by the abortion of the last inflorescence produced.

Buckwheat inflorescence is a compound raceme that produces laterally 1-30 uniparous cymes (Fig. 1D; Marshall and Pomeranz 1982; Nagatomo and Adachi 1985; Quinet et al. 2004). Inflorescences are situated at the extremity of the peduncles coming from the axil of the leaves or grouped in a terminal cluster at the extremity of the axes (main stem and axillaries; Fig. 1A). Peduncle sometimes bears two or rarely three inflorescences. The arrest of the morphogenetic activity of the raceme meristem and the abortion of the last formed cymes terminates the construction of the inflorescence (Quinet et al. 2004). Cymes develop in the axil of a bract wrapping 1-20 young flower buds that are initiated sequentially at the base of the pedicel of the preceding flower (Fig. 1D). Morphogenesis of the cymes stops with the abortion of some latest formed flowers.

Flowers are white to pink and the perianth is planar (perpendicular to the pedicel) at anthesis with a diameter about 6-7 mm (Fig. 1E; Campbell 1997; Cawoy et al. 2006a). It is formed of five petaloid tepals (not joined together; Fig. 1G). The androecium is formed of two whorls of stamens (Fig. 1G). Five stamens with introrse dehiscence form the external cycle and three stamens with extrorse dehiscence form the internal cycle (Campbell 1997). The stamens of the internal cycle are about 1.2 times longer than those of the external cycle and they contain about 7.5% more pollen grains (Namai and Fujita 1995). The gynoecium is formed of a superior unilocular ovule containing an orthotropous ovule and is surrounded by three styles (Campbell 1997). At the base of the ovary and alternating with the stamens, eight glands secrete nectar (Fig. 1G).

FLOWERING AND SEED RIpenING

Flowering starts 4 to 6 weeks after sowing and goes on during 4 to 15 weeks (Hedike 1996; Naumkin 1998; Alekseyeva and Bureyko 2000; Halbecq et al. 2005; Cawoy et al. 2006a). Flowers are usually in anthesis only one day (Nagatomo and Adachi 1985; Quinet et al. 2004). The first anthesis occurs on the lowest inflorescence appearing on the 3rd to 5th node above the cotyledons of the main stem and the flowering progresses acropetally (from the base towards the top) along this axis (Fig. 1A; Quinet et al. 2004). Under this inflorescence, the flowering of axillaries progresses basipetally (from the top towards the base) along the main stem whereas along the axillaries flowering progresses acropetally (Fig. 1A). The inflorescence scale, flowering starts with the anthesis of the first flower formed in the first cyme (Nagatomo and Adachi 1985; Quinet et al. 2004). Flowering continues from the base towards the top of the inflorescence (Fig. 1E), and within the cymes few days after anthesis of the first flower, another flower enters in anthesis (Nagatomo and Adachi 1985; Quinet et al. 2004). A peak of flowering which corresponds to anthesis of the last cyme (Quinet et al. 2004) occurs about 8 weeks after the first anthesis, and at this time plant growth stops (Naumkin 1998; Murakami et al. 2002; Halbecq et al. 2005; Cawoy et al. 2006a).

After pollination, about 10 days are required before the embryo reaches its maximal size and two more weeks are needed for grain maturity (Obendorf et al. 1993). Guan and Adachi (1992) reported differences in growth rate of embryo according to seasons. The zygote divides more actively in summer than in autumn, and three days after pollination its
Size is 1.7 times larger under autumn conditions. The fruit (the seed) is a triangular achene that measures about 5 mm long. Under the pericarp, the endosperm is covered by a fine testa and the embryo is situated at the centre of the endosperm (Marshall and Pomeranz 1982). Pericarp which is green during seed filling becomes brown then grey when the seed is mature (Fig. 1F). Due to the profusion of flowers (tens in anthesis per plant and per day), the long flowering period and consequently the long ripening period (seeds at all stages of ripening coexist within plants and inflorescences; Fig. 1F), choice of appropriate harvesting time is difficult (Marshall and Pomeranz 1982; Funatsuki et al. 2000). Moreover, there is no abscission layer but the pedicels are delicate and wind may cause scattering of grains on the soil (Campbell 1997; Funatsuki et al. 2000).

During flowering, temperature influences yields through impacts on development and fertility of the reproductive structures (Marshall and Pomeranz 1982; Adachi et al. 1983; Björkman 2000). Due to its frost sensitivity, buckwheat culture is restricted to low altitudes in temperate areas and harvest must be done before early frosts (Marshall and Pomeranz 1982; Björkman 2000). The optimal temperature for its growing is between 18 and 23°C. The flowering is inhibited below 15°C (delayed initiation and reduction of flower number) and flowers wither early at 10°C (Tahir and Farooq 1988; Lachman and Adachi 1990; Jessop et al. 1998; Gang and Yu 1998; Slawinska and Obendorf 2001). High temperatures (≥ 25°C) and dry winds cause flower withering, abortion of reproductive structures in development, malformations of embryo sac and fruit desiccation (Krotov 1963 in Campbell 1997; Nagatomo and Adachi 1985; Guan and Adachi 1992, 1994; Gang and Yu...
1998; Slawinska and Obendorf 2001). During flowering and seed maturation, limiting water supply and flooding are damaging to endosperm development. They may cause embryo abortion and lighter mature seeds (Marshall and Pomeranz 1982; Lakanov 1991; Kalinová et al. 2002; Sugimoto and Sato 2000). In order to stay viable, pollen needs humidity. Viability is lost in 1h when pollen is placed at 23°C in dry atmosphere (Adhikari and Campbell 1998). Slawinska and et al (2001) mention a reduction of 45% of fertilization events when pollen comes from plants grown at 25°C instead of 18°C.

DISTYLY AND SELF-INCOMPATIBILITY

Buckwheat possesses a sexual dimorphism: each population is composed of plants with pin (long pistil and short stamens) and thrum (short pistil and long stamens) styles reach about the level of the middle of the filaments of the anthers) flowers (Nagatomo and Adachi 1985; Campbell 1997; Quinet et al. 2004). As in most distylos species (Lewis and Jones 1992), the action of the genes which control heterostyly in buckwheat is confined to the floral parts of the plants affecting mainly gynoecium and stamens. Actually, buckwheat morphology (proportion of different biomass: nectar, stamens, petioles, in full flowering, mature plants) and seed weight differences between morphs (Komenda 1989b). Authors mention that the perianth size of buckwheat shows a strict self-incompatibility (Nagatomo and Adachi 1985; Amen and Fujita 1995; Cawoy et al. 2006a), and pollen grains of the thrum flowers are 1.4 times larger than those of the pin flowers (thrum: 50-55 μm; pin: 34-40 μm; Marshall and Pomeranz 1982; Samborska-Cianna et al. 1989b; Namai and Fujita 1995; Cawoy et al. 2006a). The exine sculpturing and the size of the stigmatic cells differ also between the two morphs (Bahadur et al. 1984; Samborska-Cianna et al. 1989b). Authors mention that the perianth size of buckwheat is generally larger in thrum than in pin flowers and report seed weight differences between morphs (Komena et al. 1986; Lee 1986; Namai 1990b). However, Cawoy et al. (2006a) do not confirm these observations but find differences in nectar production (see below).

Loci controlling heteromorphism of the distylos species are closely related to loci controlling sporophytic incompatibility reactions. They are inherited together like one diallelic gene, called supergene S, which segregates as a simple Mendelian character (Ganders 1979). Sharma and Bogue (1961) postulated that supergene S is composed of three genes: G (style length); F (staminal incompatibility); P (pollen incompatibility); A (anthor height, i.e. filament length). According to Matsui et al. (2003), S contains tightly linked to pleiotropic G, and F is tightly linked or pleiotropic with A. Common buckwheat is therefore strictly self-incompatible (Nagatomo and Adachi 1985; Adachi 1990). The genetic model represents thrum genotype as (S^G/F/P/a) and S^G/F/P/a as compatible (Sad of 3.5 per flower). This implies that a 1:1 ratio between the two morphs is conserved from generation to generation. Studies on Fagopyrum homotropicum, a homostylous and self-compatible species discovered ten years ago, and on hybrids between F. esculentum and F. homotropicum, revealed that the genetic control of the floral morphology and compatibility is not limited to the super gene S. This allele controls the flower morphology and has been designated as S' (Woo et al. 1999). At a second locus would be located a diallelic gene (S), responsible for the morphology of the reproductive organs (Matsui et al. 2004; Wang et al. 2005). The two complementary dominant genotypes S and S' control self-compatibility in F. homotropicum. To map S' allele in buckwheat, RAPD (Random Amplified Length Polymorphism) and AFLP (Amplified Fragment Length Polymorphism) markers are presently available (Aii et al. 1998; Nagano et al. 2001; Yasui et al. 2004)

Following incompatible self-pollination (intra-morph pollination), pollen tube growth is inhibited at two-third of the style length in the long styles of pin flowers, and at the junction between the stigma and the style in the short styles of thrum flowers (Schoch-Bodmer 1934). In consequence, the pollen tubes stop at nearly the same distance from the ovary in both morphs. Miljuš-Đukić et al. (2003, 2004) detected some proteins in the styles 2 h after compatible and incompatible pollinations. The proteins responsible for the self-incompatibility response are not the same in the long and the short styles. These authors assume that some of the proteins have probably a role in pollen adhesion to the stigma surface or and in the inhibition of the pollen tube elongation.

NECTAR PRODUCTION

Efficiency of pollination depends on a plant’s capacity to attract pollinators by flower morphology, and by pollen and nectar productions. In buckwheat, nectar production can be influenced by heteromorphy, ploidy level, plant age, flowering time, and abiotic factors (Tahir and Farooq 1988; Namai 1990a, 1990b; Alekseyeva and Bureyko 2000; Cawoy et al. 2006a; Jacquemart et al. 2007; Cawoy et al. 2008).

On the receptacle, at the base of the ovary and alternating with the filament of the stamens, 8 yellow protruding nectaries with the shape of a hook and organised in a circle secrete non-protected nectar (Fig. 1G). Nectar secretion begins after the opening of the perianth and nectar drops accumulate on the receptacle against the nectaries (Cawoy et al. 2008). The nectaries are made of a modified monolayered epidermis covering a multilayered nectary parenchyma (Fig. 1H). The nectar parenchyma is supplied in water and nutrients by vascular bundles consisting in phloem and xylem connected to the vascular system of the other floral organs. A parenchyma with some chloroplasts constitutes the underlying tissue: the sub-nectary parenchyma.

The nectar is composed of sucrose, fructose and glucose (Kirillenko and Bochkareva 1983; Alekseyeva and Bureyko 2000; Cawoy et al. 2006a). The two hexoses (fructose and glucose) are the major components of buckwheat nectar (85%; nectar ‘hexoses-dominant’; Cawoy et al. 2006a). Fructose becomes the main sugar with more than 50% at the flowering peak (Lee and Heimpel 2003). In the field, the average nectar production is estimated at 0.08-0.10 mg sugar per flower during the period of full flowering (Alekseyeva and Bureyko 2000). In controlled conditions, a flower products about 0.16 μl of nectar after 10 hours of secretion (Cawoy et al. 2006a). According to Lee and Heimpel (2003) sugar concentration in the field varies along the day: from 34% early morning to less than 10% at mid-day. However, other total sugar concentrations are reported in the literature, fluctuating from 36 to 51% under field conditions and up to 55% under controlled conditions (Jablonski and Szklanowska 1990; Lee and Heimpel 2003; Racys and Montiviene 2005; Cawoy et al. 2006a). Differences in air moisture and secretion rate could be responsible for these fluctuations.

The biological characteristics of buckwheat cultivars influence nectar production (Naumkin 1998; Alekseyeva and Bureyko 2000). Tetraploid cultivars produce more nectar and pollen than diploids (30-40% more) and are thus more attractive for insects (Kirillenko 1984; Jablonski and Szklanowska 1990; Alekseyeva and Bureyko 2000). Although at the exception of the flowers both morphs are morphologically identical, thrum flowers produce until 30% more nectar than pin flowers during the first half part of the flowering (Cawoy et al. 2006a). Nevertheless, no differences in nec-
taries histology or in the nectar supply to inflorescences were observed between the two floral morphs (Cawoy et al. 2008). The observed differences in nectar production between morphs in distyloid species are unusual (Omnelas et al. 2004; Teixeira and Machado 2004). Total sugar concentration is similar in both morphs, but sucrose concentration is significantly higher in thrum flowers (16.8 versus 12.9%). Sucrose/hexose ratio is therefore higher for thrum plants (Cawoy et al. 2008).

Nectar production does not significantly differ between pollinated and unpollinated flowers and no nectar reabsorption was observed (Cawoy et al. 2006a, 2008). Nectar production of flowers is positively related to the number of open flowers per plant which fluctuates with the plant age (Cawoy et al. 2006a). The amount of nectar per flower and per plant is the highest during the flowering peak. Inflorescences of the terminal cluster have the maximum nectar production per flower (Cawoy et al. 2008).

Environmental conditions influence strongly nectar production and relative concentration of sugars (Naumkin 1998; Alekseyeva and Bureyko 2000). Light is required to induce nectar secretion. Transferring plants or inflorescences from light to darkness stops the nectar production. Under controlled conditions, nectar secretion is stable along the light period (Cawoy et al. 2008).

Volume of nectar per flower is light dependent as shown by the increasing of nectar secretion of 41% when the light irradiance doubles (Cawoy 2007). Nectar secretion appears thus linked to photosynthesis but, after a whole defoliation, despite the absence of the photosynthetic leaf area, the nectar secretion persists and the nectar is still highly sugared (defoliation: minimum 34%; control: 50%). Therefore, the photosynthesis may take place in other parts of the plant as the inflorescence pedicels, the cyme bracts and the main stem (Cawoy et al. 2008).

Low temperatures reduce sucrose production and modify consequently the relative concentration of sugars in buckwheat nectar (Alekseyeva and Bureyko 2000). With a cool and wet weather, sugar production per flower can be 15 times higher than during droughty periods (Racys and Montviliene 2005). Optimal soil humidity for nectar production averages 60% and water stress decreases sugar production (Alekseyeva and Bureyko 2000). Therefore sowing dates could affect nectar production (Naumkin 1998; Alekseyeva and Bureyko 2000). High soil fertility could also have a positive influence (Munitsa 1978).

POLLINATORS

Self-incompatibility of buckwheat requires cross-pollination between pin and thrum flowers (Nagatomo and Adachi 1985; Adachi 1990). Ren and Liu (1986) showed that pollen dispersal can reach 600 m if wind speed is lower than 3 m s\(^{-1}\) and 1000 m when wind speed is higher than 6 m s\(^{-1}\). However, 1% of flowers are wind pollinated (Björkman 1995a, 1995c; Lee and Choi 1997). Some syrphids (Syrphidae, Hymenoptera (Bombus, Andrena, Osmia and Megachile) represent 25% and Syrphidae 27% of the floral visitors (Wang and Li 1998). Variation in the visitor guild occurs in Belgium between the beginning and the end of the flowering period, as the proportion of honeybee was higher in July (50%) than in September (21%; Jacquemart et al. 2007). This decrease in honeybee abundance at the end of the summer could be linked to the decrease of nectar production observed after the flowering peak (Naumkin 1998; Alekseyeva and Bureyko 2000; Cawoy et al. 2006a). Variations of buckwheat visitor guild between months have already been reported elsewhere (Lee and Choi 1997; Carreck and Williams 2002). Bumblebees (Bombus) and honeybees visit buckwheat predominantly between 09:00-12.00 h daily whereas syrphids are still active in the afternoon (McGregor 1976; Free 1993; Hedtke and Pritsch 1993; Limonta and Antignati 1994; Naumkin 1998; Alekseyeva and Bureyko 2000; Goodman et al. 2001; Jacquemart et al. 2007).

POLLINATION

Pollination efficiency depends on the insect abundance and on the insect ability to collect, transport and deposit pollen on a compatible stigma.

Honeybee foraging activity (time spent per inflorescence and plant) is not affected by day period, although fewer flowers are visited per trip after mid-day, whereas syrphid foraging activity decreases in the course of the day (Jacquemart et al. 2007). Honeybees are more active during warm and sunny days as well as during the flowering peak (Alekseyeva and Bureyko 2000). A single honeybee visits an average of 14-20 flowers min\(^{-1}\), and works on buckwheat for 4.5 h d\(^{-1}\)(Free 1993; Hedtke and Pritsch 1993; Jacquemart et al. 2007). This insect appears to be the most effective pollinator of buckwheat because it collects both types of pollen (pin and thrum) on a same trip and its foraging and prospecting behaviour, collecting nectar and pollen, and the length of its foraging period (Namai 1990a, syrphid; Björkman 1995b, 1995c; Nagatomo and Adachi 1997; Lee and Choi 1997; Carreck and Williams 2002). Some syrphids (Eristalis spp.) and perhaps other Diptera species could act as co-pollinators due to their high relative frequency and activity during the entire flowering period (Namai 1990a; Alekseyeva and Bureyko 2000; Jacquemart et al. 2007).

Under experimental cages, the efficiency of honeybee pollination (introduced colony) is good since this insect deposits compatible pollen on most flowers (>90%) without discrimination between floral morphs (Jacquemart et al. 2007). On the other hand, Cawoy et al. (2006a) reported that honeybee spends more time on thrum (higher producer of nectar) than on pin flowers, particularly in the morning, visiting more thrum inflorescences and more thrum flowers per inflorescence. Despite its better pollinator attraction, thrum flower stigmas capture fewer pollen grains than those of pin flowers (Namai 1990a, syrphid; Björkman 1995b, Aphis mellifera; Cawoy et al. 2006a, Aphis mellifera). Nevertheless, according to Björkman (1995b), thrum flowers receive three times more compatible pollen grains than pin flowers. However, Cawoy et al. (2006b) observed a similar number of pollen tubes in the style of both morphs.
Along the day, pollen deposition on stigmas and pollen tube growth increase. The saturating pollen load for fruit initiation occurs at about 10 pollen grains per flower allowing a high fruit set (80-90%; Namai and Ohsawa 1986; Björkman 1995c). Seed weight and progeny vigor increase if pollen number is higher than 10 grains due to gametophytic competition (Skerbotosova et al. 1974 in Namai 1990a; Björkman 1995c). A single insect visit delivers only an average of 5 pollen grains (Namai 1990a; Björkman 1995c). Two or more honeybee visits are therefore required for an optimal fruit set, similar to hand cross-pollination (Björkman 1995a). However, the most flowers mainly pollinated by honeybees in the Belgian fields present less than 10 pollen grains at the end of their life (one single day; Cawoy et al. 2006a). Moreover, more than one hour usually separated two successive insect visits. This delay limits gametophytic competition as pollen tube growth is very fast; only 5-10 min are necessary to reach the ovules in thrum styles and 15-20 min in pin styles (Schock-Bodmer 1930; Tatebe 1956; Campbell 1997). These facts could be seemed as a pollen limitation transfer, but although seed set is low (about 15%) under field conditions in Belgium, it does not increase after hand cross-pollination, suggesting an absence of pollen limitation (Cawoy et al. 2006a). These results show that factors other than pollenization events are leading fertility in buckwheat. Nevertheless, in order to avoid insufficient pollination, the availability of pollinators, such as honeybees which are the main pollinators of buckwheat in Western Europe, should be considered before choosing field location or to add hives.

FUNCTIONALITY OF FLOWERS

Even when possible effect of an inadequate pollination by insects is eliminated through hand pollination with exclusively compatible pollen, a variable proportion (35-97%) of the flowers does not set seed (Björkman 1995c; Taylor and Obendorf 2001; Cawoy et al. 2007). In experiment without pollen limitations, Taylor and Obendorf (2001) showed that 76 to 91% of the pollinated flowers did not show any sign of fertilization. Three causes can explain the seed production failure: male or female sterility or/and embryo abortion.

Male sterility seems a marginal event since studies on pollen germination show a good viability (>90%; Hirose et al. 1994; Adhikari and Campbell 1998; Cawoy et al. 2006b; Chen et al. 2007). Björkman (1995c) estimates that flowers pollinated with at least 90 grains of pollen and that are not producing seed have a deficiency of female reproductive structures.

Female deficiencies of flowers depend on their location on the plant and on the plant age (Halbrecq et al. 2005; Cawoy et al. 2007). Flowers have not the same probability to initiate a seed within an inflorescence. Seed set decreases from the basis to the summit where seed set becomes null (Halbrecq et al. 2005; Cawoy et al. 2007). First flowers in anthesis are also more likely to produce a seed than the following ones (Asako et al. 1980; Björkman et al. 1995c; Taylor and Obendorf 2001). Samboroborska-Ciana et al. (1989a) observed a decrease in the size of gynoecium through time and Nagatomo and Adachi (1985) mentioned the presence of numerous flowers with pistil of abnormal small size. According to Cawoy et al. (2007), occurrence of undersized and sterile gynoecia is dependent on the position of the flower in the raceme – being more frequent in distal than in proximal cymes (until 49% of flowers in the last third of an inflorescence) – and developing in the inflorescence (increase of 26%). In controlled conditions, among the morphologically normal hand pollinated flowers, less than 10% of the flowers exhibited a later abortion of seed (i.e. ovary expended) and about 60% did not develop seed (Cawoy et al. 2007). “Early abortion” (i.e. wilted flower) observed just after flowering mainly accounts for the low final yield in buckwheat (Taylor and Obendorf 2001; Halbrecq et al. 2005; Cawoy et al. 2007). Taylor and Obendorf (2001) attempted to make the difference between early abortion of embryo and sterility of female organs. Early abortion of embryo (24 h after pollination) involved on average 10% of pollinated flowers and therefore was not the most important limiting factor for yield. Flowers presenting a non-viable mega-gametophyte at anthesis represented 20% and their proportion remained constant during the flowering period. Nevertheless, 30% of flowers at the beginning and 60% at the end of flowering presented a normal embryo sac without further signs of abortion 24 h after pollination. According to Taylor and Obendorf (2001), this could be explained by a wrong alignment of the canal of the style and the micropyle. The occurrence of this aberration, which is dependent of the flower position in the raceme similarly as the occurrence of undersized gynoecia, suggests that it could result from an alteration of flower morphogenesis, in response to a limitation of resource availability (Gang and Yu 1998; Halbrecq et al. 2005; Cawoy et al. 2007). These variations in the female reproductive success in an inflorescence could be induced by a resource competition among structures (vegetative organs, meristems producing flowers, young reproducing organs and fruits in formation) and/or a limited resource supply inherent to the inflorescence and resulting of this structure (i.e. distal flower are lesser supplied in resource than proximal ones because the diameter of the sieve-tube cells decreases; see review in Cawoy et al. 2007). However, a mechanism own to the raceme seems to regulate flower fate in an inflorescence independently of assimilate availability (Cawoy et al. 2007). When applied during the inflorescence morphogenesis, treatments altering source/sink organ ratio by excision of selected inflorescences enhances the number of flowers. Compensation for the loss of racemes is partial; the inflorescences that are kept produced an increased number of flowers that are insufficient to balance the loss due to the excisions. Despite the increase of resource availability, treatments do not change the final distribution between wilted pollinated flowers with a normal sized gynoecium, flowers with an undersized gynoecium, aborted seeds and ripe seeds (Cawoy et al. 2007). The fate of flowers appears therefore to be dependent on a mechanism internal to the raceme which controls the percentage of flowers able to set a seed (Cawoy et al. 2007). This mechanism may be disturbed by drastic reductions of resource supply (e.g. a large defoliation).

CONCLUSION

Due to the sensitivity of buckwheat to climatic factors, sow- ing date strongly influences the yield of this crop (Baumgärtner et al. 1998; Inoue et al. 1998; Jessop et al. 1998; Halbrecq et al. 2005; Cawoy et al. 2006b). Pollinator abundance, mainly honeybees, is also an important factor that guarantees the achene yield (Ren and Liu 1986; Jablonski and Szklanowska 1990; Björkman 1995a; Lee and Choi 1997; Wang and Li 1998; Goodman et al. 2001; Cawoy et al. 2006b; Jacquemart et al. 2007). Therefore, agronomical practices could be locally improved to optimise seed set of buckwheat.

Resource availability influences the reproductive morphogenesis and consequently the number of flowers produced by plants and the duration of the flowering period. On the other hand, the fate of flowers appears to be dependent on a mechanism internal to the raceme which controls the percentage of flowers able to set a seed (Cawoy et al. 2007). Flowers with a normal sized gynoecium which do not set seed after compatible pollination are the main contribution to the low seed set in buckwheat. This female organ sterility seems to be the main yield limiting factor of common buckwheat throughout the world. However, its origin still remains unknown. Understanding of mechanisms which control this sterility may help to improve significantly yields.
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