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Is Buckwheat (*Fagopyrum esculentum* Moench) Still a Valuable Crop Today?

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ABSTRACT

Cultivation of buckwheat has decreased progressively worldwide over the last 20-30 years because of its low and erratic yield. In this review, we stress out the strengths and weaknesses of this crop. Buckwheat constitutes a multifood-use pseudocereal with nutritional benefits consisting in the absence of gluten in the flour, the richness in water soluble fibres, high quality proteins, unsaturated fatty acids, and appreciable mineral and vitamin content. The anti-oxidative action of buckwheat as a result of the presence of rutin and other phenolic substances is exploited by the pharmaceutical industry. Buckwheat's benefits also include positive cardiovascular effects, regulation of certain types of diabetes, and prevention of gallstones and hormone-dependent cancers. Buckwheat, therefore, offers multiple nutritional advantages and can play a major role in the prophylaxis of several human diseases. From an agronomical point of view, buckwheat represents a good opportunity for environmentally friendly cultivation, with reduced use of chemical fertilisers and pesticides. However, various physiological and ecological characteristics result in low and variable yields: (1) sensitivity to abiotic factors, such as frost, heat, water deficit, long photoperiod for photosensitive varieties, and tendency to lodging; (2) self-incompatibility, distyly and pollen transfer limitation; (3) indeterminate flowering and extended seed maturation over time leading to difficulties in determining the optimal time to harvest; and (4) female organ flower sterility. As a result, improvement in cultivar breeding and crop management is still needed.

Keywords: cultivation requirements, flower sterility, nutritional qualities, reproduction, world production, yield

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INTRODUCTION

The aim of this review is to analyse the reasons why world production of common buckwheat (*Fagopyrum esculentum* Moench) decreased over the last 20-30 years, although this species still has potentials that could justify a place as an agricultural crop in the present world context. In this paper, we thus summarise the strengths and weaknesses of this crop, and put forward some ideas for future improvement.

Domestication and history

Common buckwheat is one of the oldest domesticated crops from Asia. The origin of its domestication dates back about 4000 to 5000 years in South China (Murai and Ohnishi 1996; Gondola and Papp 2010). The wild *Fagopyrum esculentum* subsp. *ancestrale* is considered the ancestor of cultivated buckwheat (Ohnishi 1988, 1995, 1998; Ohnishi and Konishi 2001). From Southern China, cultivated buckwheat was introduced to Asian countries through two main routes (Murai and Ohnishi 1996). The first route crossed the Himalayan region and Tibet and the second ended up in Japan through Northern China. European populations of buckwheat are genetically close to the Pakistani and Chinese populations. The propagation seems to have followed the Silk Road (Ohnishi 1993; Murai and Ohnishi 1996). The first tracks of buckwheat in Europe date back 3500 years (Opperer 1985 in Ohnishi 1993). Nevertheless, cultivation in Europe became popular only in the early Middle Ages. The first historical documents mentioning buckwheat cultivation in Europe date from the 14th and 15th centuries (Ohnishi 1993; Gondola and Papp 2010). Buckwheat would

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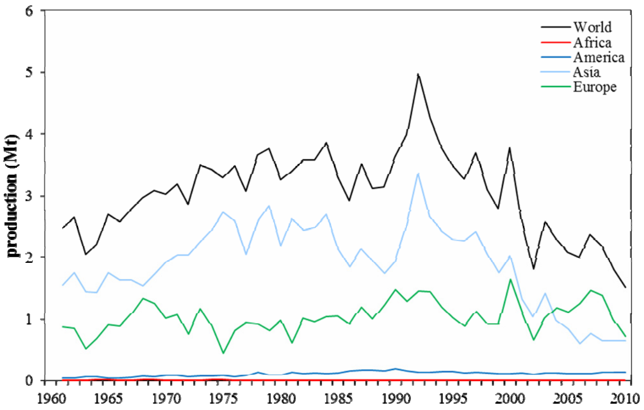

Fig. 1 Evolution of buckwheat production from 1961 to 2010 for the different continents and the World (FAOSTAT 2012).

first have reached southern Europe (Yugoslavia, Italy and southern France) from Germany and then reached northern France and England one century later (Ohnishi 1993). From the 17th century, emigrants imported buckwheat to North America, Argentina, Brazil and South Africa (Kreft 2001). Buckwheat became very popular due to its low requirements in terms of soil fertility and its high relative growth rate. In France, the cultivated area reached a maximum in the middle of the 19th century (Ferault 1984).

Since its domestication, hundreds of local varieties of buckwheat have been created (Campbell 1997; Chauhan *et al.* 2010). A broad diversity exists among these varieties in terms of the ploidy level, the size and shape of seeds, the colour of the pericarp and of the flowers, the size of the plants, and the yield (Campbell 1997; Chauhan *et al.* 2010).

World production and decline in popularity

The evolution of world buckwheat production can be followed from 1961 (FAOSTAT 2012, **Fig. 1**). On a global scale, the cultivated surfaces of wheat were 44 times higher than those of buckwheat in 1961. The difference increased almost two-fold due to a progressive neglect of buckwheat and a reduction in its cultivated surfaces by 59.4% whereas the surface devoted to wheat remained relatively stable. The decrease was most spectacular in China (production decreased by 22% between 1981 and 2010). In the majority of Western European countries, cultivation of buckwheat almost disappeared during the 20th century, but has started to increase again in recent years. The contribution of the European Union was 6.7% of the world production in 2006 and reached 14.7% in 2010 (223 329 tonnes, FAOSTAT 2012).

The area devoted to buckwheat cultivation worldwide covered 3.5 million ha in 2000 and 1.9 million ha in 2010, representing 3.8 and 1.5 million tonnes of seed, respectively (FAOSTAT 2012). The production of China remains the highest, representing 37.6% of the total; Russia and the Ukraine contribute for 22.4% and 9.0%, respectively. Other countries producing more than 10 000 tonnes include France (8.3% of world production), U.S.A. (5.7%), Poland (5.4%), Brazil (3.5%) and Japan (1.0%) (**Table 1**).

STRENGTHS OF BUCKWHEAT

Agronomic advantages

Buckwheat cultivation requires low maintenance and is well adapted to environmentally-compatible agriculture (Radics and Mikóházi 2010; Loch and Lazányi 2010). It tolerates poor and acidic soils (down to pH 5) as well as light soils, although it performs better in drained sandy or silty soils (Marshall and Pomeranz 1982; Olson 2001). Buckwheat does not tolerate heavy, compact or highly calcareous soils (Marshall and Pomeranz 1982). It responds well to fertiliser with limited requirements (Marshall and Pomeranz 1982; Myers and Meinke 1994; Olson 2001; Muzammil and Hoult 2002; Sharma 2005; Loch and Lazányi 2010). Campbell and Gubbels (1978) estimated that an uptake of 47 kg N, 22 kg P_2O_5 and 40 kg K_2O per ha is sufficient to produce 1600 kg seeds.

As a result of its fast germination (that generally takes place within 4-5 days), its fast growth and large above-ground biomass, buckwheat is relatively little affected by competition from weeds (Björkman 2000; Olson 2001). Diseases are rare (Marshall and Pomeranz 1982; Edwardson 1996), most frequently caused by fungi (Brandenburger 1985; Milevoj 1989). The plant can host about 20 viruses, including cucumber and tobacco mosaics, and some bacteria. Aphids, wireworms, coleoptera and even one nematode species (*Ditylenchus dipsaci*) can affect the crop but damage is generally limited and does not require pesticide treatment (Brandenburger 1985; Milevoj 1989; Myers and Meinke 1994; Olson 2001).

As buckwheat plants decrease weed and parasite abundance, they can be used as allelopathic facilitators (Valenzuela and Smith 2002; Xuan and Tsuzuki 2004; Araj *et al.* 2009; Bone *et al.* 2009; Géneau *et al.* 2011). For example, weed density was reduced by 80% and rice yield increased by 20% by applying 2 tonnes per ha of buckwheat pellets 2 days before rice planting. Allelopathic substances include diethylphtalate, gallic acid and catechin (Eom *et al.* 1999; Iqbal *et al.* 2002, 2003).

Buckwheat plants incorporated in the soil constitute a good green manure, increasing soil fertility (Xuan and Tsuzuki 2004). In addition, incorporating or mulching provides protection against pathogens (Wiggins and Kinkel 2005; Géneau *et al.* 2011) or weed seed bank (Gibson *et al.* 2011).

Table 1 Production of buckwheat per country during the past 50 years, expressed in tonnes (FAOSTAT 2012).

Country	1961	1971	1981	1991	2001	2010
China	1500000	2000000	2600000	2500000	1250000	570000
USSR*	745000	1000000	476000	1217000	-	-
Russian Federation**	-	-	-	-	574360	339290
Ukraine**	-	-	-	-	387600	133700
Republic of Moldova**	-	-	-	-	5001	48
Kazakhstan**	-	-	-	-	44900	26960
France	55660	18990	7200	29700	58872	125900
USA	19596	18000	48000	95000	61653	86347
Poland	59000	49000	130405	39197	58661	81226
Brazil	500	9500	50000	47000	57536	53487
Japan	42800	19500	18000	19700	26000	15300
Canada	26496	54974	52800	23300	16300	2362
Korea	6124	4842	7210	6604	3796	1954
Bhutan	3000	4000	5650	7831	4000	3898
South Africa	11000	6700	2771	221	221	241

*USSR was formally dissolved in December 1991
** was part of the USSR before 1992

The advantages of buckwheat used as green manure are multiple, including high growth rate and biomass of the green manure crop, high nutrient (especially nitrogen) content (1.2% N), high phosphorus mobilisation, high decomposition rate and high litter quality (N'Dayegamiye and Tran 2001; Valenzuela and Smith 2002; Miko *et al.* 2005; Teboh and Franzen 2011).

Used as ground cover in orchards (mainly apple) or vineyards, buckwheat participates in pest control. Indeed, because of the production of pollen and nectar during the long-lasting flowering period, buckwheat attracts insects, including pest predators like syrphids for example (Brown 2001; Pontin *et al.* 2006; Fréchette *et al.* 2008). Due to its attractiveness, buckwheat can also be used to increase pollinator populations in order to maintain pollination services in intensive crop cultivation areas (Carreck and Williams 2002; Pontin *et al.* 2006).

Nutritive qualities

Buckwheat is consumed by humans and animals in different forms corresponding to different types of production: flour, whole seeds, sprouts, shoots and honey.

Buckwheat seeds are of high nutritive value. Bran flour has high concentrations of proteins, fibres, lipids, minerals and vitamins (Steadman *et al.* 2001a, 2001b; Bonafaccia *et al.* 2003a, 2003b; Van Hung *et al.* 2009; Vojtišková *et al.* 2012). Buckwheat flour is richer in proteins than rice, wheat, sorghum or maize (Krkošková and Mrázová 2005; Qin *et al.* 2010). Buckwheat seeds contain 13-15% proteins, half of which are constituted of globulin (Javornik and Kreft 1984; Ikeda *et al.* 1991; Ikeda and Asami 2000). All amino acids are represented equally and the lysine level is higher (5.9 g/100 g of proteins) than in all other cereals (de Francischi *et al.* 1994; Wei *et al.* 1995; Zheng *et al.* 1998; Bonafaccia *et al.* 2003b; Qin *et al.* 2010). Buckwheat is also rich in arginine (Zheng *et al.* 1998). Arginine is an amino acid that is known as a growth hormone releaser, an immune stimulant and a wound-healing agent (Przybylski and Gruczyńska 2009).

The high quality of buckwheat proteins is, however, counterbalanced by their low digestibility because of the presence of protease inhibitors and tannins (Farrell 1978; Javornik *et al.* 1981; Ikeda *et al.* 1986, 1991).

Fibres are mainly present in the pericarp. Bran flour with pericarp fragments contains 40% fibres, including 25% water-soluble fibres (Steadman *et al.* 2001b). This flour is richer in soluble fibres than are wheat and oats (Krkošková and Mrázová 2005; Qin *et al.* 2010).

The embryo concentrates lipids. Buckwheat seeds contain mainly short chain lipids (palmitic acid, oleic acid, linoleic acid) and long chain lipids (as high as 8% in the fibres) in higher concentration than do other cereals (Mazza 1993; Campbell 1997). The ratio between unsaturated and saturated fatty acids averages 3.8 (Bonafaccia *et al.* 2003b). The high proportion of unsaturated fatty acids increases the nutritional value of buckwheat, compared to all other cereals (Steadman *et al.* 2001b).

Mineral content (P, K, Mg, Ca, Fe, Zn, Mn, B and Cu) is considerable (Steadman *et al.* 2001a). Buckwheat is richer in Zn, Cu and Mn than are other cereals (Ikeda *et al.* 1998; Steadman *et al.* 2001a). Seeds are also rich in Se, an oligoelement frequently deficient in human nutrition (Kitaguchi *et al.* 2008; Cuderman *et al.* 2010). Vitamins include B1, B2, B3, B6 and C (Bonafaccia *et al.* 2003b; Lebiedzińska and Szefer 2006).

Flour is the best known product obtained from buckwheat and the absence of gluten constitutes a nutritional advantage (Van Hung *et al.* 2009). The flour is not suitable for making bread and is thus traditionally used in mixtures with other flours (up to 30% with wheat flour for example, Bojňanská *et al.* 2009). Buckwheat flour is mixed with wheat flour to make noodles, pancakes, girdle cakes, cakes, biscuits, cracknels, etc. (Levent and Bilgiçli 2011). In North America, the flour is used in chocolate and candy. The nutrient composition differs according to the degree of seed crushing and depends on the relative abundance of the different tissues (**Table 2**; Skrabanja *et al.* 2001; Steadman *et al.* 2001a, 2001b; Skrabanja *et al.* 2004; Vojtišková *et al.* 2012). Without pericarp (dehulled), buckwheat seeds can be consumed whole or crushed into grits. Grits are used to decorate pastries or are incorporated into soups, sauces and salads. Seeds are also used as a substitute for meat or meat dressing and as stuffing for meat and vegetables. Whole seeds can be used fresh or roasted ("Kasha") or stewed as a side dish, in soups or in salads. They are also incorporated in beers or other local alcoholic beverages, or even in gluten-free ice creams (Campbell 1982, 1997).

Table 2 Average nutritional composition of buckwheat groats, light-coloured flour and bran. (cited from Krkošková and Mrázová 2005).

Buckwheat product	Groats (%)	Flour (%)	Bran with endosperm (%)
Starch	55	75	18
Proteins	12	6	36
Lipids	4	1	11
Soluble carbohydrates	2	1	6
Total dietary fibres	7	3	15
Ash	2	1	7

Sprouts can be consumed in salads 2 days after germination, and young shoots can be eaten 10 days later. Young plantlets may still be harvested to make juice three weeks after germination. Sprouts are rich in amino acids, minerals and fibres (Kim *et al.* 2001). They are more digestible and more valuable than seeds from a nutritional point of view, as the lysine content is seven times higher and vitamin C content 30 times higher (Kim *et al.* 2001, 2004).

Honey is a major by-product of buckwheat cultivation with a dark colour and strong taste. It is used to sweeten foods, chiefly pastries. One ha of buckwheat produces on average 125 kg honey and the best cultivars produce 150 to 300 kg/ha (Naumkin 1998; Olson 2001). Tetraploid cultivars generally produce more nectar than do diploid cultivars (Jablonski and Sklanowska 1990; Alekseyeva and Bureyko 2000). Buckwheat is of interest to beekeepers because flowering lasts generally until the first frosts, at a period when there are few other melliferous plants (Marshall and Pomeranz 1982).

Medicinal properties

Several buckwheat extracts are produced for pharmacological and dietetics purposes (Przybylski and Gruczyńska 2009). The anti-oxidative potential is high, mainly in buckwheat leaves, because of the presence of tocopherols and phenolic substances, such as 3-flavonols, flavonol, rutin, phenolic acids and flavonoids (Oomah *et al.* 1996; Watanabe *et al.* 1997; Holasova *et al.* 2002; Kalinová *et al.* 2011; Shao *et al.* 2011). Buckwheat is the only crop that contains rutin (quercetin-3-rutinosid), and in high quantities (Fabjan 2003; Sun and Ho 2005; Brunori *et al.* 2009; Vojtišková *et al.* 2012). This compound has anti-oxidative and anti-inflammatory actions and reduces blood vessel weakness (Pisha and Pezzuto 1994; Hagels 1999). Rutin content in buckwheat represents 2-10% of the dry weight of the plant. Inflorescences and aerial organs contain 100 times more rutin than do seeds. In the seeds, the pericarp is richer in rutin than the albumen (Hagels 1999; Park *et al.* 2000; Kreft *et al.* 2003; Baumgertel *et al.* 2010; Gulpinar *et al.* 2012; Vojtišková *et al.* 2012). A further role of rutin would be to limit blood platelet coagulation, protecting LDL against oxidation and increasing angiotensin I activity, which controls the blood pressure (Kawakami *et al.* 1995; Pereira *et al.* 2003).

Buckwheat honey also has high anti-oxidative activity, mainly from enzymes, vitamin C and phenolic substances (Nagai *et al.* 2001; Gheldof *et al.* 2003; Schramm *et al.* 2003).

One great benefit of buckwheat is related to its positive cardiovascular effects. Cholesterol level (LDL) remains low and blood pressure is regulated with a diet including buckwheat (He *et al.* 1995; Kayashita *et al.* 1995, 1996, 1997; Tomotake *et al.* 2000, 2001). Partly because of low digestibility, sterols seem to be excreted and consequently could contribute to the reduced blood cholesterol level (Kayashita *et al.* 1997). The absence of gluten in buckwheat flour is highly advantageous in particular diets such as those for patients with coeliac disease (de Francishi *et al.* 1994; Aubrecht and Biacs 2001; Alvarez-Jubete *et al.* 2010). Moreover buckwheat flour has a higher content of proteins, vitamins and minerals than have other flours without gluten (Kunachowicz *et al.* 1996; Léder *et al.* 2010).

Seeds, mainly embryos, contain substances that decrease glucose and insulin levels in blood and can thus prevent or regulate some types of diabetes (mainly type I diabetes). The active substances include fagopyritols, D-*chiro*-inositol - an uncommon product in nature - and *myo*-inositol (Horbowicz *et al.* 1998; Kawa *et al.* 2003; Ueda *et al.* 2005). The first two are present in large amounts (Berlin *et al.* 1990; Ueda *et al.* 2005).

Because of its high fibre content and its poorly digestible proteins, buckwheat also contributes to prevent gallstones (Kayashita *et al.* 1997; Tomotake *et al.* 2000; Tsai *et al.* 2004) and decreases constipation and risks of colon cancer (Cassidy *et al.* 1994; Liu *et al.* 2001). It is also used in obesity treatments as satiety appears more rapidly than with other cereals (Škranbanja *et al.* 2001, 2004).

Buckwheat seeds contain high levels of lignans (phenylpropanoids, matairesinol and secoisolariciresinol diglycoside), which can prevent some hormone-dependent cancers and heart diseases (Setchell 1995; Manach *et al.* 2004).

WEAKNESSES AND CULTIVATION LIMITATIONS

Low and variable yield

Compared to classical cereal crops, common buckwheat has a low seed yield and productivity remains poor (Sangma and Chrungoo 2010). In 1961, the mean yield of wheat/ha worldwide was two-fold higher than that of buckwheat. In 2010, wheat yield was 2.6 times higher than in 1961 while the increase in buckwheat yield was only 1.6 over the same period (FAOSTAT 2012). On average, buckwheat mean seed yield is 1.0 t ha^{-1} but large differences are recorded among countries and varieties. For example, in 2010, the average yield ranged from 0.4 t ha^{-1} in South Africa and 0.8 t ha^{-1} in China to 3.4 t ha^{-1} in France (FAOSTAT 2012). These differences in yield among countries highlight that progress in cultivar breeding and crop management is still feasible (Hara *et al.* 2009). Over a period of 15 years (1996-2011), large annual variations in buckwheat yield of up 30 to 50% occurred worldwide because of climatic factors, whereas wheat production remained rather stable.

Seed set remains low, compared to the number of flowers produced (several hundreds to thousands per plant). Seed set varies widely from plant to plant and over different years. Seed set is rarely higher than 30% and averages 15-20% (Ren and Liu 1986; Campbell 1997; Gang and Yu 1998; Woo *et al.* 1999; Bavec *et al.* 2002; Halbrecq *et al.* 2005). Deficient or inadequate pollination, sterility of the female organs, failure of fertilisation and embryo abortion are the main factors explaining this low seed set (Adachi 1990). Sensitivity to climatic conditions and dependence on insect pollination can induce variations in yield in different seasons, years and locations (Kalinová *et al.* 2005; Kalinová and Vrchotova 2011). Nevertheless, these factors are insufficient to account for the maximum 30% seed set recorded. Moreover, hand pollination in growth chambers under optimal and controlled conditions suggest the occurrence of endogenous problems since 40% seed set remained a maximum whatever the experimental conditions (Cawoy *et al*. 2007a).

Sensitivity to climatic factors

Annual yield differences in the same location reveal the sensitivity of buckwheat to climatic factors (Michalova *et al.* 1998; Morishita and Tetsuka 2001; Kalinová *et al.* 2002; Kalinová *et al.* 2005). More than just the often unpredictable meteorological conditions, sowing date strongly influences yield (Inoue *et al.* 1998; Jessop *et al.* 1998; Halbrecq *et al.* 2005; Japhet *et al.* 2009). Phenology and yield of common buckwheat mainly respond to three climatic factors: temperature, water and photoperiod.

1. Temperature

Buckwheat cultivation is only feasible under temperate climates. Because of its sensitivity to frost, the crop is limited to low altitudes. In the Himalayas, cultivation is no longer possible beyond approximately 2500 m a.s.l. (Ohnishi 1988; Tahir and Farooq 1988). Sowing takes place when there are no more risks of late spring frosts, usually in May or June in Western Europe (Halbrecq *et al.* 2005) and harvest has to be completed before the first autumn frosts (Marshall and Pomeranz 1982; Björkman 2000; Olson 2001). Seed maturity is reached after an average of 3 months of cultivation in temperate regions. Under less favourable climatic conditions, the cycle of development extends to more than 5 months (Michiyama *et al.* 1998a, 1998b).

The optimal temperature for germination is 10°C (Jakimenko 1982 in Kalinová and Moudrý 2003). The developmental stage most sensitive to frost is one to two expanded leaves. At this stage, exposure for 4 to 6 h to temperatures between –1 to –3°C is lethal (Kalinová and Moudrý 2003).

During the flowering period, temperatures influence both development and fertility of the reproductive structures (Marshall and Pomeranz 1982; Adachi *et al.* 1983; Oplinger *et al.* 1989; Björkman 2000). The optimal temperature is between 18 and 23°C. Flowering is inhibited below 15°C with delayed initiation and reduction in flower numbers. A temperature of 10°C induces early withering of flowers (Tahir and Farooq 1988; Lachman and Adachi 1990; Jessop *et al.* 1998; Gang and Yu 1998; Slawinska and Obendorf 2001). However, high temperatures (30°C) and dry winds are also detrimental, causing flower withering, abortion of developing reproductive structures and embryo sac malformations (Krotov 1963 in Campbell 1997; Nagatomo and Adachi 1985; Guan and Adachi 1992, 1994; Gang and Yu 1998). Pollen viability is similarly dependent on temperature and on relative humidity. Pollen placed at 23°C under dry air lost viability within 1 h (Adhikari and Campbell 1998). Slawinska and Obendorf (2001) reported a 45% reduction in fertilisation events when pollen originated from plants grown at 25°C compared to plants at 18°C. Pollen tubes stop growth in the style before fertilisation at 30°C (Sugarawa 1956 in Marshall and Pomeranz 1982; Namai 1990). Finally, high temperatures (30°C) also increase lodging as a result of a reduction of the stem diameter (Michiyama and Sakurai 1999).

2. Water

Water requirements of buckwheat are high (Tahir and Farooq 1988; Lakhanov 1991; Gang and Yu 1998). A quantity of 225-315 kg of water is needed to produce 1 kg of seeds (Gang and Yu 1998). Plants quickly wither under drought conditions because of their shallow root system (Marshall and Pomeranz 1982; Myers and Meinke 1994; Berglund 1997; Campbell 1997). However, rehydratation quickly takes place when normal water conditions are restored and growth resumes (Lakhanov 1991; Campbell 1997; Delpérée *et al.* 2003). Water constraints applied during the vegetative phase are less detrimental than when imposed to plants engaged in the reproductive phase (Cawoy *et al.* 2006a). During flowering and seed set, limited water supply is prejudicial to endosperm development and may induce embryo abortion (Marshall and Pomeranz 1982; Lakhanov 1991; Kalinová *et al.* 2002). The fertility loss can cause a 50% yield decrease.

Risks of lodging under abundant precipitation and strong winds are substantial in soils with high nitrogen levels (Marshall and Pomeranz 1982; Berglund 1997; Schulte *et al.* 2005). When plants are lodged, the apex stands up again but the main stem often remains in contact with the soil and is prone to disease and rotting (Campbell 1997; Sangma and Chrungoo 2010). Water excess, either through surface flooding or saturation at a few cm below the surface, is also prejudicial for buckwheat yield (Marshall and Pomeranz 1982; Björkman 2000; Sugimoto and Sato 2000; Sakata and Ohsawa 2005). Flooding is more damaging than saturation in terms of stress duration. When occurring at the first leaf stage or at the flowering stage, flooding reduces yield by lowering flower production. Flooding for more than 10 days at the flowering stage or more than 3 days during the maturation stage affects seed weight (Sugimoto and Sato 2000).

3. Photoperiod

Buckwheat initiates flowers over a wide range of day lengths (Nagatomo and Adachi 1985) and even under continuous light (Hao *et al.* 1995), but the different varieties do not react similarly to photoperiod (Romanova and Koshkin 2010; Hara *et al.* 2011). For example, Russian varieties are less photosensitive than Asian varieties (Romanova and Koshkin 2010). Some cultivars, such as Japanese summer cultivars, seem non-sensitive to photoperiod, whereas other cultivars, such as autumn Japanese cultivars and the European variety “La Harpe”, behave as facultative short day plants (Minami and Namai 1986a, 1986b; Hagiwara *et al.* 1998; Lachman and Adachi 1990; Michiyama *et al.* 1998a, 1998b; Kachonpadungkitti *et al.* 2001; Michiyama *et al.* 2003; Quinet *et al*. 2004). Photosensitive varieties initiate flowers at lower node and produce more inflorescences and more flowers per inflorescence under short days compared to long days. Moreover, long days decrease the percentage of fertilised flowers, but do not affect seed weight (Inoue *et al.* 1998; Michiyama *et al.* 2003). These results could be explained by an alteration in source-sink relationships causing an increased competition for resources between vegetative and generative organs (Hagiwara *et al.* 1998). Although buckwheat can grow under all photoperiod regimes, photosensitive varieties should preferentially be cultivated under short photoperiods in order to gain larger yields.

Profuse and extended flowering

The morphogenetic processes involved in the establishment of the reproductive structures of buckwheat are potentially endless. They are dependent on the activity of meristems with an indeterminate mode of functioning that accounts for the plant potentiality to flower over a protracted time period (Quinet *et al*. 2004; Cawoy *et al*. 2009). These characteristics lead to several traits that negatively affect yield, including the presence of high numbers of simultaneously open flowers per plant and per day, the spreading over 1-3 months of the flowering period and consequently the coexistence of seeds at all stages of ripening within plants and inflorescences. The appropriate time for harvesting is thus difficult to determine (Marshall and Pomeranz 1982; Funatsuki *et al.* 2000). There is no flower abscission layer but the pedicels are brittle and wind may cause scattering of seeds on the soil and therefore yield losses in late harvests (Campbell 1997; Sangma and Chrungoo 2010). Harvest is optimally performed when about 75% of seeds are physiologically ripe (Oplinger *et al*. 1989; Björkman 2000; Olson 2001). Seed shedding can occur during mechanical harvesting further enhancing losses (Campbell and Gubbels 1978; Radics and Mikóházi 2010).

Seeds have to be dried before storage (at a maximum temperature of 45°C) to reduce their water content below 16% (Campbell and Gubbels 1978; Marshall and Pomeranz 1982; Olson 2001).

Limitations in pollination events

Buckwheat is a distylous species: A population is composed of plants with pin flowers (long style and short stamens) and plants with thrum flowers (short style and long stamens) (Nagatomo and Adachi 1985; Björkman 1995b; Campbell 1997; Quinet *et al.* 2004). Because of this heteromorphy linked to sporophytic self-incompatibility, the strict outcrossing requires pollination vectors. Buckwheat is mainly pollinated by insects. Quantification of local pollinator guild efficiency is thus essential. Buckwheat is visited by a diverse fauna, including Hymenoptera such as honeybees (*Apis mellifera* in Europe and North America, and *A. cerana* in Asia), bumblebees, solitary bees and wasps; Diptera including Syrphidae and Calliphoridae; Lepidoptera, Hemiptera, Nevroptera and other orders (Ren and Liu 1986; Hedtke and Pritsch 1993; Ogasahara *et al.* 1995; Lee and Choi 1997; Wang and Li 1998; Michiyama *et al.* 2000; Goodman *et al*. 2001; Carreck and Williams 2002; Jacquemart *et al.* 2007; Taki *et al.* 2009, 2010). The most common visitors belong to Apoidae (Hymenoptera, *Apis* spp. and *Bombus* spp.) and Syrphidae (Diptera, *Eristalis* spp.).

Honeybees (*Apis mellifera*) are commonly considered as the main pollinators (McGregor 1976; Namai 1990; Hedtke and Pritsch 1993; Björkman 1995a, 1995c; Lee and Choi 1997; Goodman *et al.* 2001; Jacquemart *et al.* 2007). Accordingly, agronomists recommend the introduction of beehives to ensure satisfactory seed yield (McGregor 1976; Wang and Li 1998; Dalby 2000; Goodman *et al.* 2001). Out of the total number of floral visitors, however, honeybees represent only 2-5% in Japan, 35% in China and 37% in Russia (McGregor 1976; Ogasahara *et al.* 1995; Wang and Li 1998; Sasaki and Wagatsuma 2007; Taki *et al.* 2010). Near its area of origin (China), other Hymenoptera (*Apis cerana*, *Bombus* spp., *Andrena* spp., *Osmia* spp. and *Megachile* spp.) represent 25% and Syrphidae account for 27% of the insect visitors (Wang and Li 1998). Bumblebees and honeybees visit predominantly between 09.00 - 12.00 h, whereas syrphids are still active in the afternoon (Hedtke and Pritsch 1993, Limonta and Antignati 1994; Alekseyeva and Bureyko 2000; Goodman *et al.* 2001; Jacquemart *et al.* 2007). An individual honeybee, *Apis mellifera*, visits an average of 14-20 flowers/min and works buckwheat for 4-5 h/day (Hedtke and Pritsch 1993; Jacquemart *et al.* 2007). In Europe, this insect species appears to be the most effective pollinator of buckwheat since it collects both types of pollen (pin and thrum) on a single trip and its foraging and prospecting behaviour, collecting both nectar and pollen, promotes frequent contact with stigmas (Jacquemart *et al.* 2007). Some syrphids (*Eristalis* spp.) and perhaps other Diptera species may act as co-pollinators because of their high relative frequency and activity during the entire flowering period (Namai 1990; Alekseyeva and Bureyko 2000; Jacquemart *et al.* 2007; Taki *et al.* 2009).

Flower sterility and abortion

Even after removing the possible effect of an inadequate pollination by insect visitors through hand cross-pollination, a proportion of flowers do not set seeds (Björkman 1995c; Taylor and Obendorf 2001; Cawoy *et al*. 2007a, 2007b). This suggests that internal defects are responsible for seed production failure, namely male or female sterility or/and embryo abortion.

Male sterility seems marginal since pollen viability is high (>90%) at moderate temperatures (Hirose *et al.* 1994; Adhikari and Campbell 1998; Cawoy *et al*. 2006b); thus pollen is not considered to be a limiting factor (Taylor and Obendorf 2001). Björkman (1995c) estimated that flowers pollinated with at least 90 pollen grains and not producing seeds were deficient at the level of the female reproductive structures. In experiments without any pollen limitation, Taylor and Obendorf (2001) reported that 76-91% of pollinated flowers did not reveal any signs of fertilisation.

Female deficiencies of flowers depend on their location on the plant and on the plant age (Halbrecq *et al.* 2005; Cawoy *et al*. 2007a). Consequently, flowers within an inflorescence do not have equal chances for seed set which decreases from the proximal to the distal position in the reproductive structure (Halbrecq *et al.* 2005; Cawoy *et al.* 2007a, 2007b). The first flowers in anthesis are also more likely to produce seed than are later ones (Asako *et al.* 1980; Björkman 1995c; Taylor and Obendorf 2001). Samborborska-Ciana *et al.* (1989) observed a decrease in the size of gynoecia over time and Nagatomo and Adachi (1985) reported the presence of numerous flowers with an abnormal undersized pistil. Taylor and Obendorf (2001) also observed an inadequate alignment of the canal of the style with the micropyle. The occurrence of these aberrations is dependent on the position of the flower in a raceme suggesting that it could be an alteration of flower morphogenesis in response to a limitation of resources (Cawoy *et al*. 2007a). However, during inflorescence morphogenesis, treatments that alter the source-sink organ ratio do not affect the final distribution of flowers with a normal sized gynoecium, flowers with an undersized gynoecium, aborted seeds and ripe seeds (Cawoy *et al.* 2007a). Therefore, an internal mechanism, acting at the raceme level, regulates flower development in an inflorescence, independently of assimilate availability.

Late organ excision occurring after inflorescence development, shows that competition for assimilates between reproductive sink organs occurs during seed development. Seed set increased from 3 to 10% after removing all inflorescences except the terminal one (Michiyama *et al.* 1999). In plants where half the inflorescences are removed, compensation mechanisms are set up at the level of the meristems with a 25% increase in flower number and a 10-15% increase in seed set (Halbrecq *et al.* 2005). Conversely, seeds developing on a plant affect reproductive morphogenesis and limit flower production (Cawoy *et al.* 2007a, 2007b).

Pollinated flowers with a normal sized gynoecium that do not set seeds after pollination are the main contribution to the low seed set in buckwheat.

CONCLUSIONS

Buckwheat is receiving increased attention (Léder *et al.* 2009). Nevertheless, progress in cultivar breeding and crop management is still needed (Hara *et al.* 2009; Woo *et al.* 2010; Sangma and Chrungoo 2010). The International Plant Genetic Resources Institute (IPGRI) and Consultative Group on International Agriculture (CGIAR) have identified buckwheat as an important but underutilized nutraceutical crop, which has tremendous potential for use in crop improvement programs (Chrungoo *et al.* 2011). Molecular markers and cytogenetic variations have been successfully used for analysing the diversity in buckwheat (Chauhan *et al.* 2010). Efforts towards collection and documentation of buckwheat genetic resources will help to identify agronomically intended traits, such as low shattering, increased nutritive quality, self-compatibility and homostyly in varieties under development (Ölschläger *et al.* 2010; Chrungoo *et al*. 2011).

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