5 Grain Legumes: an Overview

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Abstract

The grain legumes are important sources of protein in animal and human diets. This chapter provides an overview of some basic aspects of their biology and production in Europe. All early agricultural societies apparently domesticated a grain legume at much the same time as a cereal, perhaps indicating that their nutritional value was noticed. The cool-season grain legumes came to Europe from the Middle East with arable agriculture, followed in historical times by common bean from the Americas and soybean from China. The basic growth habit is indeterminate, with simultaneous flowering and pod filling. Most species are self-pollinating but produce more flowers than can mature as pods. The cool-season starchy species (pea, faba bean, lentil and chickpea) have many attributes in common, including parallel diseases. The lupins (white, narrow-leafed and yellow) form a closer cluster, and have an unusual seed composition where the main energy store for germination is cell wall material. The number of warm-season legume species is large, but only two, common bean and soybean, are important in Europe. Seed size is highly variable in the cool-season species and common bean, and seed colour in all species. Many cultures prefer specific sizes and colours for food use. A wide range of antinutritional substances has evolved to protect legume seeds from predators, and humans have developed methods to remove or denature them, or reduce them through breeding, in order to improve quality for food and feed.

Introduction

The legume family (*Fabaceae*) is one of the largest families of flowering plants. The unifying feature of the family is the characteristic legume pod with a double row of ovules. The family is also characterized by flowers with five fused sepals and five petals. The wide diversity of about 20,000 species comes from adaptability, particularly to nutritionally poor environments, helped by the ability of most

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species to biologically fix nitrogen in symbiosis with bacteria of the *Rhizobiaceae*. According to the current model, early in the evolution of the legumes, a copy of the basic plant–mycorrhizal fungus recognition system was harnessed (neofunctionalized, in evolutionary jargon) to recognize nitrogen-fixing bacteria. Another co-evolutionary process occurred above ground, as the flowers and bees became adapted to each other for pollination.

In agriculture, the legume family is second in importance only to the cereals (*Poaceae*), based on area harvested and total world production, with more than 650 million t of grain legumes produced on 240 million ha in 2011 (FAOSTAT, 2016). Several roles attributed to the legumes are often overlooked. Grain legumes provide one-third of the plant protein and a similar proportion of the vegetable oil used for human consumption (Graham and Vance, 2003). The amino acid composition of legumes complements that of cereals and root crops (Wang *et al*., 2003), perhaps explaining why the two groups were domesticated together (Gepts, 2004). Legumes are also important forage crops in temperate and tropical regions.

Legumes provide essential minerals for the consumer (Grusak, 2002). In addition, the secondary metabolites that protect the plant against pathogens and pests (e.g. see Ndakidemi and Dakora, 2003) may also protect the human consumer against certain cancers (Madar and Stark, 2002) and have some benefit in the treatment of diabetes (Jenkins *et al*., 2003). The consumption of grain legumes can reduce cholesterol in blood, and shows a hypoglycaemic effect. Other secondary compounds include antinutritional factors, such as trypsin inhibitors (Gupta, 1987) and allergens (Spergel and Fiedler, 2001).

The family has been traditionally divided into three subfamilies: *Caesalpinioideae*, *Mimosoideae* and *Papilionoideae*, the latter comprising 28 tribes and including the grain legumes along with the important forage legumes (Fig. 5.1). The cool-season legumes (tribes *Fabeae*, *Cicereae* and *Trifolieae*) are closely related and highly similar at the genome level, and slightly removed from the *Genisteae* (Wojciechowski *et al*., 2004), and the warm-season legumes (tribe *Phaseoleae*) are similarly closely related (Lee *et al*., 2001) (Fig. 5.1).

The *Fabaceae*, together with a range of less important plants, play a vital role in biological nitrogen fixation (BNF), which is tens of times more effective taking place in symbiosis than in free-living bacteria. It was only in the final quarter of the 20th century that more nitrogen was fixed in the manufacture of synthetic fertilizer than by BNF. Although ancient farmers would not have known how the legumes worked, they certainly noticed the effect of the legume on the following crop, as was made clear by Columella in ancient Rome (Evans, 1998).

Since legume crops can fix their own nitrogen, the question of 'starter nitrogen' is often raised: should the farmer apply some N fertilizer to assist with crop establishment until symbiotic nitrogen fixation is active, and if so, how much? Hence, agronomists in many countries recommend the application of 20–40 kg/ha of N fertilizer at sowing time.

Origin and Spread in Europe

The movement of early Neolithic agriculture into south-west Asia and then the Mediterranean Basin is fairly well documented from the archaeological record.

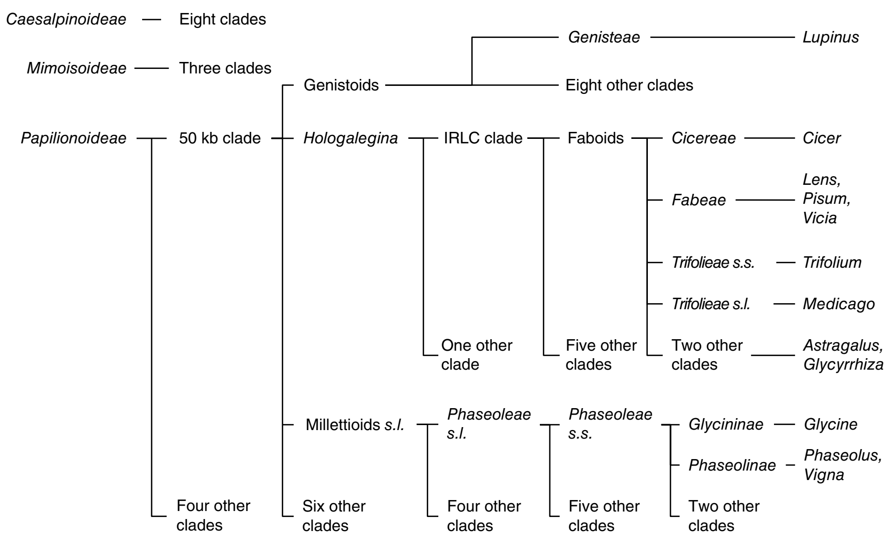

Fig. 5.1. Phylogeny of the legumes, arranged to highlight the genera that include important crops in Europe. IRLC, Invert repeat lacking clade; *s.s.*, *sensu stricto*; *s.l.*, *sensu lato*. (Adapted from LOWO, 2013.)

The most numerous grain remains found in early farming villages come from three cereals: (i) emmer wheat (*Triticum turgidum* subsp. *dicoccum* Schrank ex Schulber); (ii) einkorn wheat (*Triticum monococcum* subsp. *monococcum* L.); and (iii) barley (*Hordeum vulgare* L.). Several grain legumes appear as companions of the cereals, as far back as 10,000 BC, and the most frequent of these in the Fertile Crescent are lentil (*Lens culinaris* Medik.), common pea (*Pisum sativum* L.) and bitter vetch (*Vicia ervilia* (L.) Willd.) (Zohary and Hopf, 2000), the latter now hardly cultivated. Faba bean (*Vicia faba* L.) and chickpea (*Cicer aretinum* L.) are now understood to be part of that initial round of domestication, and their apparent rarity is attributed to the fragility of the carbonized seeds (Tanno and Willcox, 2006). As agriculture started in other parts of the world, a grain legume was always among the early domesticates, with common bean (*Phaseolus vulgaris* L.) having been brought into cultivation in Central and South America, and soybean (*Glycine max* L.) in China. Lupins, with their adaptation to acid, sandy soils, were brought into cultivation much later, in the first millennium BC. Lucerne (alfalfa) (*Medicago sativa* L.) was taken into use for horse feed in Bronze Age Anatolia. The records of the exploitation of clovers and other forage legumes, in contrast, began in Spain around AD 1000 and spread beyond the Pyrenees after about AD 1500 (Kjaergaard, 2003). Vetches (*Vicia* spp. other than faba bean) sit on the boundary between forages and grain legumes, being primarily grown for forage purposes but having sufficiently large seeds to be developed for grain use, if certain antinutritional factors can be overcome.

Grain legumes have been used for food for thousands of years and their history is tightly linked with the evolution of human civilization. They remain vital in the nutrition of many societies, although they have been replaced as protein sources by meat, sometimes excessively in many other countries where they retain importance as animal feed. Furthermore, most are also consumed as green vegetables when the seeds and/or pods are immature.

The Cool-season Starchy Legumes

The grain legumes in the *Faboid* clade have many characteristics in common. Germination is hypogeal, meaning that the cotyledons and cotyledonary buds remain under the soil surface, and if the emergent shoot is damaged, it can be replaced by new shoots from the axils of the cotyledons. The seedlings are generally tolerant of mild frosts, from –4°C in lentil to –10°C in some spring-sown cultivars of faba bean and pea. The leaves are pinnately compound, with oval leaflets generally ending in tendrils (reduced to a point in faba bean). A pair of stipules clasps the stem at the node. After a certain number of nodes of vegetative growth, racemes of flowers are produced in the leaf axils (Fig. 5.2). The induction of flowering is either day-neutral (not affected by day length) or long-day (promoted by increasing day length above a certain minimum value). Flowers and developing seeds are

(A) (B)

Fig. 5.2. (A) Faba bean at flowering stage, showing axillary racemes of four to six flowers, and the stipules clasping the stem at the node. (B) White lupin at flowering stage, showing palmately compound leaves and long, terminal inflorescence.

not tolerant of frost. The basic growth habit is indeterminate, with flowering and podding continuing as long as conditions allow. Heat and water deficit are the stresses most likely to halt growth, and moderate stress late in the growing season is often desirable in order to bring the crop to a harvestable state. The number of flowers per raceme is generally determined by genotype, and the number of seeds per pod (on which pod length depends) is strongly determined in that way, while the number of flowering nodes is substantially affected by environment. Sowing is usually in the spring in continental, oceanic and boreal climates, and in the autumn in Mediterranean climates. Autumn-sown faba bean and pea have been developed in oceanic climates and efforts continue to increase their frost tolerance so they can be grown in some continental climates.

Seed size is determined by the size of the pod (Patrick and Stoddard, 2010), which is maternal tissue and determined primarily by the genotype of the mother plant. Severely restricting growing conditions late in the grain-filling period may reduce seed size, but most legumes in such conditions abort pods as a first measure to reduce sink strength, thereby preserving seed size and hence seedling vigour in the next generation. Within a pod, individual ovules may not get fertilized, or individual developing seeds may abort due to some nutritional or mutational cause, but these losses are minor.

None of these species is considered particularly tolerant of drought, flooding, heat or salinity, although there are marginal differences between them, and considerable genetic variation within each one that can be harnessed through plant breeding (Stoddard *et al.*, 2006). Chickpea is considered the most heat-tolerant, both chickpea and lentil are relatively drought-tolerant, and faba bean is the most tolerant of waterlogging.

Rhizobium leguminosarum is the nitrogen-fixing symbiont for most of these species, with several biovars having been selected for optimum performance on individual hosts. Chickpea requires *Rhizobium ciceri*.

The protein concentration in the seeds is 20–25% (higher in faba bean). Their main energy store is starch, in ovoid granules about 15 μm × 25 μm, comprising 40–50% of the seed's dry matter. The amylose (long-chain, essentially unbranched molecules) content of the starch is 30–35%, which is higher than in most cereals, contributing to the slow digestibility of legume starch, which is valuable for lowering the glycemic index and maintaining satiety of the consumer (Stoddard, 2004). The oil concentration is low, around 1% of dry matter except for chickpea which is 3–6% oil, and its main fatty acid is linoleic (Lizarazo *et al.*, 2015).

The most important and widespread insect pests are aphids (*Aphis fabae*, the black bean aphid, and *Acyrthosiphon pisum*, the green pea aphid), leaf weevils (*Sitona lineatus* and other species), seed weevils or bruchids (*Bruchus pisorum* on pea, *Bruchus rufimanus* on faba bean and *Bruchus lentis* on lentil), and the pea moth (*Cydia nigricana*). The aphids are important not only because of the direct damage they do but also for their role as virus vectors. The adult leaf weevils reduce the photosynthetic area of young seedlings, and their larvae do worse damage by consuming root nodules. Bruchids are the hardest to control, as the larvae develop within the seed and are protected from contact insecticides.

The main pathogens are sets of closely related fungi (Tivoli *et al.*, 2006). Each has a leaf, pod and stem blight of the genus *Ascochyta*: (i) *Ascochyta fabae* on faba bean and lentil; (ii) *Ascochyta rabiei* on chickpea; and (iii) *Ascochyta pisi* together with *Mycosphaerella pinodes* and *Phoma medicaginis* var. *pinodella* on pea. These diseases are splash-dispersed and have a low optimum temperature for growth, so are most prevalent on autumn-sown crops in Mediterranean and oceanic climates. The sclerotia of the perfect stage can last up to 3 years in the soil, so a minimum 4-year rotation is recommended. Each has a rust: (i) *Uromyces viciae-fabae* on faba bean and lentil; (ii) *Uromyces pisi* on pea; and (iii) *Uromyces ciceris-arietini* on chickpea. The rusts grow best in warm, relatively humid weather, such as late summer in a continental climate. In other climates, they often arrive so late in the growing season that they help to desiccate the nearly mature crop. Chocolate spot disease, caused by *Botrytis fabae*, is exclusive to and important on faba bean and some vetches, while *Botrytis cinerea*, grey mould, is occasionally found on pea, lentil and chickpea, and is sometimes considered to contribute to chocolate spot disease on faba bean. These fungi can cause catastrophic crop losses when plant surfaces remain wet for a prolonged period and temperatures are close to 20°C, but are seldom problematic in other conditions (Stoddard *et al.*, 2010). *Peronospora viciae* causes downy mildew on pea, faba bean, lentil and some vetches. The literature on its interaction with pea is larger than that on the rest of its hosts combined, suggesting that it is most important on that crop, and it is this author's experience that downy mildew is not detectable on faba bean until the other three diseases are controlled. Because of these diseases, and their ability to survive in the soil, it is widely recommended that grain legumes are used no more often than every fourth year in the cropping sequence.

Aphanomyces euteiches is an oomycete that has become the major limitation to growing pea in many parts of the world, as it causes a root rot disease and persists in the soil for up to 9 years, so rotations have to be at least that long. Lentil is considered generally susceptible, but resistance exists in some accessions of faba bean and vetches (Moussart *et al.*, 2013).

Broomrapes (*Orobanchaceae*) are flowering plants that parasitize the roots of many crops and are particularly limiting in Mediterranean climates. *Orobanche crenata* Forsk. is the most common one attacking pea, faba bean, lentil and vetches, but most germplasm of chickpea is resistant to it (Rubiales *et al.*, 2004).

The cool-season grain legumes are generally seen as poorly competitive with weeds, owing to relatively slow establishment after sowing and, in several species, low levels of crop cover and thus shading of the ground from the small leaflets and tendrils. Unfortunately, few herbicides are suitable for use on legumes, and even fewer are approved for use on legumes in European countries, so weed control remains difficult. The use of anti-weed net on the soil is an option for weed control in high-value food crops.

Except for the largest-seeded cultivars of faba bean, common bean and chickpea, conventional sowing and harvesting machinery can be used for all of the grain legumes. Target crop densities depend on many factors and local agronomists should be consulted, but the following figures (per square metre) can be used as starting points: 20 for winter faba bean, 30–50 for chickpea, 50–70 for spring faba bean, 70–100 for pea and 140–160 for lentil. Sowing depth is usually three to four times the seed diameter.

The species are presented below in order of the quantity harvested in Europe as mapped by Eurostat, comprising the European Union (EU) and all other European countries west of the former Soviet Union. Eurostat data are not available for lentil, chickpea or common bean, so FAOSTAT data are used for these, according to the Eurostat countries.

Pea

Pea is the most widely grown grain legume in Europe and the fourth most grown in the world (FAOSTAT, 2016). According to Eurostat, total European production in 2013 was 1.26 million t, of which 39% was harvested in France (Fig. 5.3). Pea is also one of the most widely grown vegetables, as a mutation in the gene coding for starch-branching enzyme I leads to a reduction in synthesis of the amylopectin fraction of starch that is not compensated by increased amylose synthesis (Bhattacharyya *et al.*, 1990), so sucrose accumulates in the seed, making it pleasant to eat and causing it to wrinkle when it dries. The pea pod can also be eaten fresh, when it lacks the inner layer of parchment. A new type of horticultural pea, currently grown in Spain, is the 'tear pea', whose grain is consumed very tender and almost raw, with a size of about 3 mm and a sweet taste. By its sensory qualities it is called 'vegetable caviar'. Peas grown for dry use as food or feed are generally smooth and round, and dimpled or blocky cultivars are desired for specific food markets.

Seed size varies from 100 mg to 350 mg, but the majority of cultivars have seeds of 200–250 mg. 'Marrowfat' cultivars are at the large end of the size

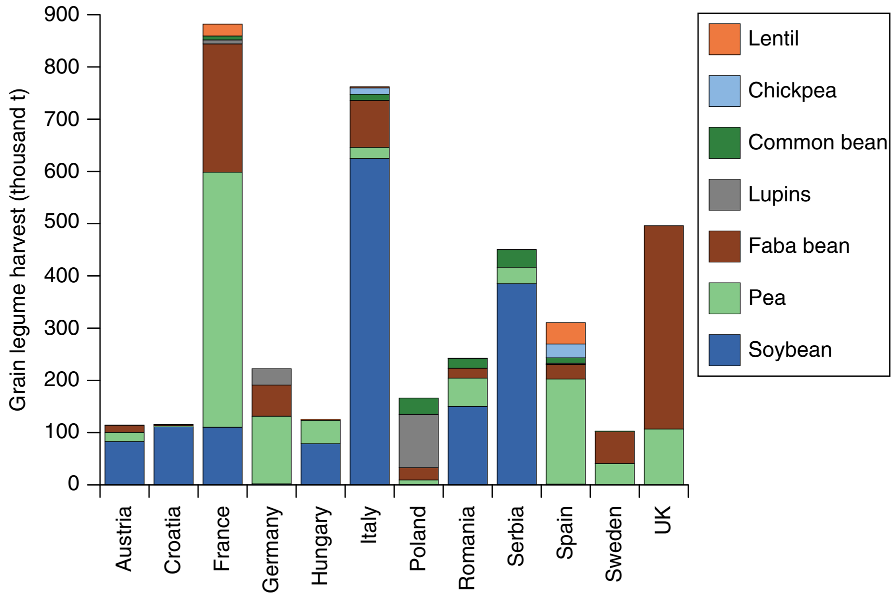

Fig. 5.3. Production of grain legumes in the 12 European countries where the total harvest exceeded 100,000 t in 2013. Data from Eurostat (2016) (faba bean, pea, soybean, lupins) and FAOSTAT (2016) (lentil, chickpea, common bean).

distribution and the seeds are angular rather than round. Cotyledons are either yellow or green, depending on the degradation of chlorophyll during maturation. Most cultivars have white flowers and tannin-free seed coats that are either colourless or pale green, but autumn-sown cultivars and whole-crop forage cultivars have coloured flowers and seed coats. Starting at node 12–16, racemes bearing one to three flowers are borne in the leaf axils. Self-pollination reliably occurs before anthesis and the scentless flowers do not attract pollinating insects. Most cultivars produce between six and ten seeds per pod.

Pea evolved as a tendril-supported climber and its stems are weak. Modern semi-leafless cultivars, where the leaflets are converted to tendrils (gene *af*) and the stipules are greatly enlarged to provide photosynthetic area (gene *St*), support themselves in pure stands by clinging to each other, with greatly reduced lodging in spite of the weakness of the stems. Spring-sown cultivars generally produce one stem and rarely branch, whereas autumn-sown cultivars usually produce three to five stems from the base. Increased basal branching would allow seeding rates to be reduced, but could lead to undesirably later flowering and maturity, unless handled carefully in the breeding programme.

The most important antinutritional factor restricting use in animal feed is trypsin inhibitor (TI). Different TI forms protect the crops from various bruchids so are valuable in crop production, but unless the feed is heat-moisture treated to denature them, they reduce feed conversion efficiency and cause stress to the consuming animal's pancreas. Hence low-TI germplasm has been developed for feed purposes, but it requires better segregation in the crop-handling chain than is currently possible, so it has made little market impact.

Faba bean

Faba bean is a preferred food in West Asia, North Africa and China, while it is more widely popular as a green vegetable and in many countries is used as feed. In spite of its widespread use, the global faba bean area decreased from 5 million ha in 1965 to 2.7 million ha in 2011 (FAOSTAT, 2016). Faba bean production in Europe (Eurostat, 2016) was 1.40 million t in 2013, and the largest producer was the UK producing 0.39 million t (Fig. 5.3). As a result of the strong collaborative research and breeding programmes during the last 40 years, considerable progress has been made in reduction of antinutritional factors, improvement in biotic and abiotic stress resistance, and altered growth habit. Faba bean, among legumes, is a particularly important candidate for increasing BNF in temperate agricultural systems due to its high productivity of dry matter and high proportion of nitrogen derived from the atmosphere (Baddeley *et al.*, 2013). Faba bean is well adapted to heavy clay soils with a pH of 6–8, and its growth suffers when the pH is below 5. Its taproot is larger and more robust than that of the other cool-season legumes.

Seed size is exceptionally variable in this species, leading to a complex nomenclature. Accessions with seeds < 250 mg are placed in var. *paucijuga*, and larger-seeded materials are in var. *faba*, with three subdivisions: (i) *minor* (< 500 mg); (ii) *equina* (500–800 mg); and (iii) *major* (> 800 mg). The *major* types, known in English as broad beans, can have seeds up to 3 g in size. The distinctions of *minor*, *equina* and *major* are for commercial convenience and have no botanical value, as seed size and other traits are continuously distributed. Small seeds are round, almost as round as peas, and large seeds are flat. Seed protein concentration is higher in faba bean than in the other cool-season starchy legumes, with a world average around 29% and values in favoured situations approaching 35% (Crépon *et al.*, 2010). Many faba bean breeders aim to increase seed protein concentration further.

The first factors limiting use of faba bean are the pyrimidine glycosides, vicine and convicine that comprise about 1% of the dry weight of wild-type seeds (Khamassi *et al.*, 2013). The aglycones, divicine and isouramil are powerful oxidants that cause acute haemolytic anaemia (termed 'favism') in susceptible humans with a deficiency in glucose-6-phosphate dehydrogenase, and also in chickens (Crépon *et al.*, 2010). The *vc-* gene reduces the vicine-convicine content below one-tenth of normal values, to levels that are considered safe, and has been used in the breeding of several French cultivars.

As in pea, autumn-sown cultivars produce many stems but spring-sown ones generally produce only one. Spring cultivars most often produce their first flowers in the axil of the seventh true leaf, but a landrace that flowers at the third true leaf has recently been identified. Autumn-sown cultivars require some vernalization (weeks of chilling at 0–4°C) in order to flower (Link *et al.*, 2010), so the node count is less certain. The number of flowers per raceme is highly variable and can be as high as 15, but is more usually around four to six (Fig. 5.2). Most cultivars produce three to four seeds per pod, and some produce up to ten.

Faba bean, unlike the other cool-season legumes, has a mixed breeding system, with both self- and cross-pollination. Within a mixed population such as a landrace or a composite cultivar, hybrid individuals are generally able to pollinate themselves ('autofertile'), while inbred individuals are reliant on bee activity to bring pollen into contact with the stigma (reviewed by Stoddard and Bond, 1987). The corolla tube is too long for honeybees or short-tongued bumblebees to reach the nectar, but they can gather pollen, while long-tongued bumblebees and other wild bees make use of the nectar as well as the pollen. Depending on the cultivar, its level of inbreeding, its autofertility, and the available population of pollinators, outcrossing rates range from essentially zero to 83%. This feature affects seed multiplication in a breeding programme, as the valuable early-generation seed crop must be isolated from other sources of pollen by distance or in a cage. It also confers a positive environmental impact, as flowering faba bean crops support populations of wild bees. A related aspect of the reproductive biology is the production of excess flowers that serve to attract pollinators, thus providing an evolutionary advantage by sending the pollen further than the seeds can spread. Novices growing faba bean for the first time are often distressed by the loss of flowers, but this is seldom due to lack of pollination.

Lentil

By the Bronze Age, lentil had spread throughout the Mediterranean region and into both Asia and Europe. Lentil was used by the ancient Greeks for soup and a kind of bread. Pliny the Elder recorded how the plant grows and noted its therapeutic qualities as well. Lentil is currently an important crop throughout the Mediterranean region, Western Asia and North America (Erskine, 1997), with Canada being the largest producer (FAOSTAT, 2016). Lentil production in Europe in 2013 was 70,000 t, 59% of which were harvested in Spain. It is a food crop, as yields are too low and production costs too high for it to be used as feed. It is considered sensitive to waterlogging, and grows best on well-drained mineral soils in regions with dry autumns.

Seed size varies widely, from 30 mg to 70 mg, and large-seeded cultivars tend to be later maturing than small-seeded ones. Small-seeded cultivars (< 45 mg) are sometimes called *microsperma* or Persian, and large-seeded ones *macrosperma* or Chilean, but the distinction is artificial and seed size is continuously variable rather than bimodal. The plant is relatively short (often only 40 cm tall), and more highly branched than pea or faba bean. The leaves produced from reproductive maturity onwards end in small tendrils that tie the plant stand together. Short racemes bearing one to three flowers are borne in the leaf axils, usually starting at node 11–14. The small flowers are reliably self-pollinating and produce pods with one to two seeds each. In order to bring the indeterminate growth to an end and allow maturity and harvesting, some farmers in Canada apply a desiccant.

The pods hang close to the soil, so farmers are advised to have as even a soil surface as possible, and to set the cutter bar of the combine harvester low. The seeds are easily handled by conventional farm machinery that is set up to handle small-grain cereals such as wheat and barley.

Cultivars with red cotyledons are generally sold as decorticated, split cotyledons, so ease of dehulling is an important trait, whereas those with yellow cotyledons are generally sold whole and there is no need to select for dehulling ability.

In continental climates, lentil is spring sown and in Mediterranean climates, autumn sown. A reputedly winter-hardy cultivar, 'Morton', was developed at Washington State University in the USA and has survived some winters in the nemoral to boreal climates of Saskatchewan, Canada and southern Finland, but not reliably so.

Chickpea

Chickpea spread westwards from the Middle East to the countries around the Mediterranean and eastwards to India. In classical Greece it was called Erevinthos and was eaten as a main dish or as a green vegetable. The Romans ate it in soup or roasted as a snack, much like we have them today. Chickpea is grown on over 10 million ha, primarily in arid and semi-arid areas worldwide (FAOSTAT, 2016). It is second to common bean in terms of spread and third in terms of production among the grain legumes. The major producer is India, with 65% of the world harvest, followed by Pakistan and Turkey. In Europe, the largest producer is Spain, producing 52% of the continent's 50,000 t.

The chickpea plant is similar to lentil, being relatively short (40–70 cm) and highly branched, with many leaflets per leaf. The leaves bear numerous glandular hairs and release oxalic and malic acids, so chickpea breeders are often recognized by their holey trousers. After 12–14 vegetative nodes, the plant starts producing one (occasionally two) flowers per node, each of which produces one to two seeds. Like the other cultigens of the *Fabeae*, chickpea has a wide range of seed sizes, from 120 mg to 600 mg, and two size classes are generally recognized, desi and kabuli. Desi chickpeas are relatively round-seeded, < 300 mg in size, with a coloured (tannin-containing) seed coat and coloured (pink) flowers, and are generally used for split cotyledons. Kabuli chickpeas have a characteristic 'ram's-head' shape and are > 260 mg in size, with a thin and colourless seed coat and colourless (white) flowers, and are generally cooked whole. The kabuli seed coat is relatively thin and easily damaged during harvest, and the seeds are less tolerant of cold soils at germination time in comparison with desi seeds.

Like lentil, chickpea is spring sown in continental climates and in autumn in Mediterranean areas. The severity of its ascochyta blight restricted autumn sowing for many centuries, and it is only in recent decades with the advent of resistance breeding that autumn sowing has spread, inspired by successes in southern India (O'Toole *et al.*, 2001).

Lupins

Narrow-leafed lupin (*Lupinus angustifolius* L.), white lupin (*Lupinus albus* L.) and yellow lupin (*Lupinus luteus* L.) all originated in the Mediterranean Basin. Owing to their high alkaloid content, lupin seeds had to be washed in running water for up to 2 days before consumption, until low-alkaloid germplasm was developed in the 20th century, largely through mutation breeding. The domestication of these still half-wild crops was driven particularly in Western Australia from the 1950s. The Andean 'tarwi' or pearl lupin (*Lupinus mutabilis* Sweet) is evolutionarily remote from the Mediterranean species and was domesticated in middle altitudes along the central Andes of South America. Total European production of domesticated lupins was 151,000 t in 2013, two-thirds of which was grown in Poland (Eurostat, 2016). The lupins form symbiosis with a rhizobium that has not been taxonomically characterized and is usually called *Bradyrhizobium* '*lupini*'. Lupins are covered in greater detail in this volume by Gresta *et al.* (see Chapter 6, this volume).

Typical target seedling rates are 50–70/m^2 for white lupin, and 120–140/m^2 for narrow-leafed and yellow lupin. Lupin germination is epigeal, bringing the cotyledons and cotyledonary buds above ground, so the seedlings may be killed by physical damage during crop management that would only set back hypogeal germinating species. The leaves are palmately compound with long and narrow leaflets held almost at right angles to the petiole. After several nodes of vegetative growth, the main stem produces some axillary flowers and develops into a spike with whorls of flowers. The axils of the last two to four leaves then produce branches that repeat the growth pattern of the main stem, subsequently producing another order of branches. In some growing conditions, up to five orders of branches may be produced. For cropping purposes, however, reduced branching is desirable in order to bring the crop to maturity and harvest readiness.

Non-branching cultivars have been produced in narrow-leafed lupin, reducing the growing season to a length that allows the crop to be grown up to 63°N in Finland, but biomass production and seed yields are low. Reduced- or non-branching cultivars have been developed in both yellow and white lupin cultivars, with similar detriment to yield potential. Non-branching cultivars cover the ground poorly, so they have little ability to suppress weed growth, and they require high sowing densities. Thus a balance is required, and it may be that a reduced-branching cultivar, rather than non-branching, will provide the best combination of sowing density, ground coverage and maturity date for all but the most extreme climates.

Like faba bean, lupins produce far more flowers than can mature as pods. Narrow-leafed and yellow lupins self-pollinate in the bud, but are still attractive to pollen-collecting bees. White lupin self-pollinates shortly before anthesis, and its outcrossing rate is higher than those of the other two. It is generally acknowledged that these three species have no detectable nectar. Each flower contains four to five ovules. Seed size is less variable than in some of the other grain legumes, with most white lupins being around 300–320 mg, Andean 200 mg, narrow-leafed 140–170 mg and yellow 130–140 mg.

The agricultural lupins are adapted to acid, sandy soils and are exceptionally sensitive to waterlogging and free calcium, although there has been some success in breeding calcium-tolerant germplasm. Winter-hardy cultivars of white lupin have been developed for the oceanic regions of France by the Jouffray-Drillaud company.

Lupin seed composition is radically different from those of the other legumes. There is significant oil content, averaging about 6% in narrow-leafed and yellow (Sujak *et al*., 2006; Lizarazo *et al*., 2015), 10% in white (Annicchiarico *et al*., 2014) and 15% in Andean (Carvalho *et al*., 2005). The main form of energy storage is beta-galactan, a complex polysaccharide deposited in the heavily thickened cell walls of the cotyledons. Seed protein content is about 32% in narrow-leafed lupin, 35% in white lupin, 40% in Andean lupin (Clements *et al*., 2008) and 45% in yellow lupin (Sujak *et al*., 2006). The seed coat is relatively thick, and the protein content of dehulled cotyledons is several per cent higher than these values. The amino acid composition of yellow lupin has been claimed to be superior to that of soybean (Hudson, 1979).

The main restricting factor in lupin usage is quinolizidine alkaloids that are up to 2% of the dry matter of landraces. These are highly diverse chemicals and their profile differs in each species. The alkaloids are synthesized throughout the plant and transported to the seed, so the development of a lupin with sweet seeds but bitter leaves that protect it from herbivores would depend on the identification and silencing of a still unknown alkaloid transporter (see Chapter 6, this volume). In several countries, including the UK and France, the maximum alkaloid content in lupin seeds for food and feed use is 200 mg/kg, and most current cultivars are below this level.

The main limiting disease is anthracnose, caused by *Colletotrichum lupini*. Phomopsin, a mycotoxin produced by *Diaporthe toxica*, causes poisoning of ruminants grazing lupin residues. There is a large literature on diseases of lupins caused by *Fusarium* species. The same aphids and leaf weevils attack lupins as *Fabeae* legumes, along with two European specialist *Sitona* species, *S. gressorius* and *S. griseus.* Alkaloid content appeared not to affect attractiveness to leaf weevils (Strocker *et al.*, 2013), but alkaloid composition affected aphid infestation, indicating that there is potential for combining low overall alkaloid content and aphid resistance (Adhikari *et al.*, 2012).

The Warm-season Legumes

The warm-season legumes in the *Phaseoleae* have numerous distinctions from the crops described so far. The natural habit of the wild species is generally vining, not clasping with tendrils. There is little frost hardiness in most species, and the optimum growing temperature is above 24°C. Seedling emergence is epigeal, so the cotyledonary buds are susceptible to damage. The leaves are trifoliolate, and the leaflets are heart-shaped. As is typical of tropical and subtropical species, flowering in warm-season legumes requires days that are shortening and below a critical length in order to flower. At medium to high latitudes, these shorter days are not reached until too late in the growing season, so selection by farmers and breeders has gradually changed the critical photoperiod. Insensitivity to photoperiod has been identified in common bean and a major gene conferring this trait, *Ppd*, has been identified (Gu *et al.*, 1998), but more than one gene is required in soybean (Xu *et al.*, 2013). Racemes are borne in the leaf axils after a certain number of vegetative nodes, as in the *Fabeae*. The flowers of common bean and soybean pollinate themselves before opening. The development of determinate cultivars has been important in the domestication of these crops, making them uniform in maturity and suitable for mechanical harvesting. Determinate cultivars produce several branches, whereas indeterminate ones branch more rarely. The usual seeding rate is 30–50/m^2 for both species, depending on soil type, maturity group and branching pattern.

Common bean

Common bean comes from the Americas, with apparently independent domestication events around 4000 BC in Mexico, Colombia and Bolivia (Barker, 2006). It was brought to Europe shortly after the first European contact at the end of the 15th century, and gradually, through the trade of the Spanish and the Portuguese, it spread to Africa and Asia. The spread of common bean in Europe was complex, with several introductions from the New World combined with direct exchanges between European and other Mediterranean countries (Angioi *et al.*, 2010). Most European landraces of common bean are from the Andean gene pool, with minor differences across European regions in the proportions of the Andean and Mesoamerican gene pools. Recombinant forms between both genetic pools have been described from Europe, which is considered a secondary area of domestication of the species (Santalla *et al.*, 2002). Europe produced 245,000 t of dry bean in 2013, and Serbia was the largest producer (Fig. 5.3). FAOSTAT (2016) showed world production as 23 million t in 2013, making it by far the most-produced grain legume after soybean, but this value included some other *Phaseolus* and *Vigna* species.

Seed size in common bean ranges from at least 170 mg to 1000 mg. Seed-coat colour is highly variable, and there are cultural preferences for colour and seed size in many regions of the Americas. It is considered a food crop and is seldom used for feed, owing to its high cost and the presence of phytohaemagglutinins that require denaturing by cooking before monogastrics can consume them. Each pod contains up to eight seeds, and the long pods often reach the soil surface and are liable to rot, so plant height and an upright growth habit have been important breeding objectives. The fresh pods without fibre can be consumed as snap beans. The seed coat is very thin and is easily damaged during sowing and harvest, leading to poor viability.

Common bean is highly sensitive to frost at all growing stages, and requires warm soils for germination. It is also sensitive to water deficit, waterlogging and salinity. It is notoriously poor at nodulating and nitrogen fixation, and the causes and solutions have yet to be established. The most important diseases are due to the generalist fungus, *Sclerotinia sclerotiorum*, and the specialist bacteria that cause: (i) common blight, *Xanthomonas campestris* pv. *phaseoli*; (ii) halo blight, *Pseudomonas syringae* pv. *phaseolicola*; and (iii) bacterial brown spot, *Pseudomonas syringae* pv. *syringae*. Resistance breeding has made progress against the bacterial diseases, but not significantly against sclerotinia.

Soybean

Many authors and databases categorize soy as an oilseed, but taxonomically it is a legume, so it should be considered here. After the cereals maize, wheat and rice, it is the world's most widely grown grain crop, with 308 million t harvested in 2014 according to FAOSTAT (2016). Production in the EU in that year (Eurostat, 2016) was 1.85 million t, of which 50% was harvested in Italy. The European region as defined by Eurostat imported 27 million t of soymeal and 15 million t of soybeans. Production in countries neighbouring the EU is very significant with 3.9 million t and 2.6 million t produced in Ukraine and Russia, respectively (see Chapter 7, this volume).

The species is an ancient tetraploid, with the genome duplication estimated at 8 million years ago (Shoemaker *et al.*, 1996), which affects the practical breeding of the crop, as often two genes need to be altered in order to achieve a desired phenotype. Soybean is discussed at greater length in this book by Fogelberg and Recknagel (Chapter 7, this volume).

The oil content of soybean (around 20%) is lower than that of most other oilseeds, and the protein content (around 40%) is somewhat higher, so the oil-free meal is usually 45–50% protein. The amino acid composition of the meal is considered excellent for most feed and food purposes. Usage in food and feed is limited by two strong trypsin inhibitors, one a Bowman–Birk type and the other a Kunitz type, that require heat treatment for denaturation.

The strong photoperiod dependence of soybean has led to the development of numerous ‘maturity groups’ with narrow (2–3° of latitude) zones of adaptation in North America. Maturity groups 000 to 2 cover most of Europe’s needs from the southern shore of the Baltic to the northern shore of the Mediterranean.

Seeds of modern cultivars of soybean are 150–250 mg in weight. The seed coat is usually yellow, but may be green, brown or black. Unlike most of the other legumes, soy is not considered to be restricted to certain soil types or pH values. The first two true leaves are unifoliolate, and thereafter trifoliolate leaves are produced. The first raceme is borne in the axil of the fifth to seventh trifoliolate leaf, and the racemes carry three to five flowers that pollinate themselves before anthesis. More flowers are produced than can mature, as in most other grain legumes. The pods contain three to four seeds. Indeterminate cultivars produce one to two stems, determinate ones two to six.

Although soybean has a reputation for being frost-tender, young plants of many cultivars can survive temperatures of –3°C. If the exposure to frost is short (an hour rather than overnight), and the seedling or young plant has been hardened by exposure to cool temperatures (< 10° for several days), then a substantial portion of the crop can survive –4°C (Badaruddin and Meyer, 2001).

Several rhizobia nodulate soybean, but two species predominate: (i) *Sinorhizobium fredii* on neutral to alkaline soils; and (ii) *Bradyrhizobium japonicum* on acid or saline soils (Tian *et al*., 2012). Since these species are not widespread in Europe, it is necessary to inoculate soybeans before sowing the crop for the first time in a field.

Since it is grown on all inhabited continents, it is exposed to a wide range of diseases and pests, and the literature on crop protection is vast. In Europe, the main pathogens are *Peronospora manshurica* (downy mildew) and *Pseudomonas syringae* pv. *glycinea* (bacterial blight) on leaves, *Diaporthe phaseolorum* var. *caulivora* (canker) and sclerotinia on stems, and *Macrophomina phaseolina* (charcoal rot) on roots (Vidic and Jasnic, 2011). The range of pests is similarly wide, and includes the leaf weevils and aphids that attack the cool-season legumes (Sekulic and Keresi, 2011).

Conclusion

The grain legumes are diverse in taxonomy, seed composition and environmental requirements. This diversity means there is a potential legume crop for every arable field in Europe, but it has the disadvantage that breeding effort has to be spread across many species, and they cannot be easily substituted for each other in processes such as feed manufacture. With the rapid development and application of genomic technologies, these crops are no longer the ‘orphans’ that they were just 5 years ago (Sharpe *et al*., 2013). Complete genome sequences are available for some and are in development for others, while the expressed portion alone (the exome) may be the target for large genomes such as that of faba bean. These technologies will allow information obtained in one species to be rapidly applied to the improvement of another. The breeding of legume crops is the subject of a new book (De Ron, 2015).

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