Chapter 2
Pea

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1   Introduction

Pea (*Pisum sativum* L.) is one of the first domesticated crops and is currently grown in most temperate regions of the world. Pea belongs to the Leguminosae family and as such is capable of fixing atmospheric nitrogen, thereby greatly reducing the requirement for petrochemical-based inputs. World production of dry pea ranged from $9.4–11.3 \times 10^6$ t to $6.0–6.6 \times 10^6$ ha between 2000 and 2012 (FAOSTAT 2013). These totals have been relatively steady over the past 50 years; however, the key producing areas have shifted over that time. Eastern Europe was

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the major producer from the 1960s to 1980s, then Western Europe from the 1980s to 1990s, and since then North America, primarily Canada. China and India have had relatively stable production of $2–3 \times 10^6$ t/year over the past 50 years. In terms of world production of dry legume crops, dry pea trails only common bean which had annual production of $17.6–23.3 \times 10^6$ t between 2000 and 2012, and the oilseed legumes soya bean ($161.3–265 \times 10^6$ t) and groundnut ($33.1–42.1 \times 10^6$ t) during the same period (FAOSTAT 2013). World production of vegetable pea ranged from $12.0–17.4 \times 10^6$ t to $1.6–2.2 \times 10^6$ ha between 2000 and 2012 (FAOSTAT 2013). Vegetable pea production has been rising steadily over the past 50 years with China and India being the major producers.

In order to expand world production of pea, breeders, agronomists, end users and producers face several challenges. Grain yield gains must continue for pea to remain an attractive option in crop rotations. This will require a concerted effort from pea breeders internationally. In Western Europe, pea production has declined in the past two decades as producers have focused on high-yielding winter wheat and winter canola crops. This has led to a decline in pea-breeding activity. Pea

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production has increased in North America and Australia over the past two decades and similarly, pea-breeding efforts have increased.

In order to achieve yield gains in pea, many biotic and abiotic stresses must be addressed through breeding. These stresses are specific to each region; however, in general, fungal diseases are the key biotic stress in most pea-growing regions, followed by various insects and viruses. Heat stress at flowering is the key abiotic stress in many pea-growing regions, followed by early-season flooding. Addressing these stresses are key breeding objectives for pea breeders in their attempts to increase and stabilize grain yields.

Greater international exchange of germplasm and increased use of diverse *Pisum* accessions may aid in achieving new yield gains. Use of genomic tools should enhance breeders' ability to substantially enrich their breeding populations with desired alleles, prior to the expensive exercise of yield testing in field trials.

Greater market diversification for pea will create more demand and expand production. Dry pea has typically been used as dhal in Asian markets. A major new use for dry pea is the Chinese vermicelli market which utilizes pea starch which is effective because of its high amylose content. This market has expanded from zero to more than 700,000 t/year over the past two decades (FAOSTAT 2013). Further use of pea and pea fractions (protein, starch and fibre) in diverse food products could promote expansion of the crop. Pea has good potential in new food applications due to its moderate protein concentration, slowly digestible starch and high levels of soluble and insoluble fibre, all of which are attractive for addressing type 2 diabetes and obesity. In addition, pea has low allergenicity and to date is a non-genetically modified organism (GMO), both factors making it attractive compared to soya bean in some markets.

2 Origin and Systematics

2.1 Phylogeny and Taxonomy

Pea belongs to the Leguminosae plant family, the third largest flowering plant family with 800 genera and more than 18,000 species (Lewis et al. 2005). The Papilionoideae is the largest subfamily, with 476 genera and about 14,000 species, which shared a common ancestor around 50 MA (Doyle et al. 1997; Lavin et al. 2005). The largest group of papilionoids, Hologalegina, with nearly 4000 species in 75 genera, includes the large galegoid tribes (including Galegeae, Fabeae, Trifolieae), united by the loss of one copy of the chloroplast inverted repeat. Tribe Fabeae Rchb. (not Vicieae (Bronn) DC., nom. illeg.) currently consists of five genera: *Lathyrus* (grass pea/sweet pea, about 160 species); *Lens* (lentils, 4 species); *Pisum* (peas, 3 species); *Vicia* (vetches, about 160–250 species) and the monotypic genus *Vavilovia formosa* (Mikič et al. 2013; Smýkal et al. 2011; Schaefer et al. 2012). Tribe Fabeae is considered one of the youngest groups in the legumes (Kupicha 1981; Steele and Wojciechowski 2003), and Bayesian molecular clock and ancestral range analysis

suggest a crown age of 23–16 MA, in the mid-Miocene (Lavin et al. 2005; Schaefer et al. 2012). The centre of diversity and postulated area of origin of the Fabeae is in the eastern Mediterranean (Kupicha 1981; Schaefer et al. 2012) with a minimum of three dispersal events to the middle Atlantic islands and seven to the Americas. The tribe is considered monophyletic, nested within the Trifolieae. The crown age of the *Pisum* clade is estimated to 2.3–0.8 MA, while the divergence between *Pisum* and *Vavilovia* dates back to 9.8–4.8 MA (Schaefer et al. 2012).

The genus *Pisum* L., originally described to be distinct from *Lathyrus* L. (Linnaeus 1753), has recently been shown to be included in the *Lathyrus/Vicia* complex (Schaefer et al. 2012). Interestingly, Lamarck (1778), who was certainly aware of Linné's description, designated pea as *Lathyrus oleraceus*. Depending on how the *Lathyrus/Vicia* complex is treated, the genus *Pisum* may be incorporated into a larger *Lathyrus* genus to achieve monophyly. Thus, the taxonomic nomenclature used here will undoubtedly be revised. The classification of taxa within *Pisum* L. based on morphology and karyology has changed over time from being considered a genus with five species (Govorov 1937) to the currently widely accepted version with two species, *P. fulvum* and *P. sativum,* recognized (Kupicha 1981; Davis 1970). Numerous names have been proposed for wild representatives of *P. sativum.* In the review of Yarnell (1962), *P. humile (P. syriacum, P. sativum* subsp. *sativum* var. *pumilio), P. elatius*, *P. abyssinicum* and *P. sativum* were considered conspecific, even though they often differ by inversions and translocations. In this chapter, we will refer to the following taxonomic definitions of *Pisum: P. sativum* L. with subsp. *sativum* (includes var. *sativum* and var. *arvense*), subsp. *elatius* (Bieb.) Aschers. and Graebn (includes var. *elatius,* var. *brevipedunculatum* and var. *pumilio*), and subsp. *abyssinicum* (A. Braun) Govorov and *P. fulvum* Sibth. and Sm.

P. abyssinicum, has been resurrected as a third species by some recent authors (Maxted and Ambrose 2001; Vershinin et al. 2003; Jing et al. 2007), but for reasons detailed below, this taxon will be maintained as a subspecies of *P. sativum* in this chapter. Other 'species' such as *P. jomardi, P. transcaucasicum* and *P. arvense* have also been included within *P. sativum* by most recent treatments (Jing et al. 2007; Zaytseva et al. 2012). The most appropriate status for *P. sativum* subsp. *abyssinicum* is still under debate (Maxted and Ambrose 2001; Zaytseva et al. 2012). This taxon is native to Ethiopia and Yemen and has very low genetic diversity as demonstrated by morphological, allozyme (Weeden and Wolko 2001) and DNA analyses (Pearce et al. 2000; Vershinin et al. 2003; Jing et al. 2005, 2010). It possesses a distinct phenotype (early flowering and strongly serrate leaflets) as well as unique alleles at particular loci. Similar to most *P. s*. subsp *elatius* accessions, this taxon differs from the standard *P. sativum* subsp. *sativum* karyotype by at least a reciprocal transloca-tion (Ben-Ze'ev and Zohary 1973). Hence, it qualifies for species status on the basis of phenotype and biological isolation. However, recent DNA sequence comparisons have shown this taxon to fall within the *humile/elatius/sativum* cluster or between it and *P. fulvum,* depending on the sequence being analysed (Jing et al. 2007, 2010; Ellis 2011; Smýkal et al. 2011; Vershinin et al. 2003; Zaytseva et al. 2012). The taxon has been used as a bridge between *P. fulvum* and *P. sativum* because it crosses reasonably well with both. Many crosses have been attempted with abyssinicum

lines, and the most fertile crosses were to *P. sativum* subsp. *sativum* germplasm rather than to subsp. *elatius* accessions, although the presence of the reciprocal translocation definitely leads to reduced fertility in the F1 and F2 generations (Weeden, personal communication). Thus, if the abyssinicum variation is to be given specific status, it appears appropriate for consistency sake to also raise at least a portion of the elatius accessions to species status. From a practical viewpoint, the current authors do not see much advantage to splitting the abyssinicum/elatius/ sativum germplasm into three or four species at the present time. Another taxon that has recently been suggested to be included in *Pisum* (Maxted and Ambrose 2001), *V. formosa,* we retain as a distinct genus (Smýkal et al. 2013; Mikič et al. 2013).

The centre of pea genetic diversity is the broad area of the Fertile Crescent through Turkey, Syria, Iraq, Israel and Lebanon. It extends further east to Central Asia (Iran, Afghanistan, Pakistan and Turkmenistan; Smýkal et al. 2011). Ethiopia has been postulated as a secondary centre of diversity (van der Maesen 1998). Vavilov (1950) considered Ethiopia together with the Mediterranean and Central Asia as primary centres, and Near East as secondary. *Pisum sativum* subsp. *elatius* and subsp. *sativum* are found naturally in Europe, northwestern Asia and extend south to temperate Africa, while *P. fulvum* is restricted to the Middle East.

2.2 Origin and Domestication

Pea is one of the world's oldest domesticated crops. Archaeological evidence dates the existence of pea back to 10,000 BC in the Near East (Baldev 1988; Zohary and Hopf 2000) and Central Asia (Riehl et al. 2013). Pea, among other grain legumes, accompanied cereals and formed important dietary components of early civilizations in the Middle East and Mediterranean. In Europe, it has been cultivated since the Stone and Bronze Ages and in India from 200 BC (De Candolle 2007). The Near East and Mediterranean regions are also the area of origin and initial domestication. Cultivation of pea spread from the Fertile Crescent to today's Russia, and westwards through the Danube valley into Europe and/or to ancient Greece and Rome which further facilitated its spread to Northern and Western Europe. In parallel, pea was moved eastward to Persia, India and China (Makasheva 1979; Chimwamurombe and Khulbe 2011).

Phylogenetically, there are two wild populations variously described as subspecies of *P. sativum* or as species, *P. sativum* subsp. *elatius* Bieb. and *P. sativum* subsp. *sativum* (= *P. humile* Boiss and Noe (syn. *P. syriacum* (Berger) Lehm.; Ben-Ze'ev and Zohary 1973; Smýkal et al. 2011). These two wild groups are morphologically, ecologically and also genetically distinct (Ben-Ze'ev and Zohary 1973; Abbo et al. 2013). The domestication of cultivated pea from northern populations of '*humile*' was proposed by Ben-Ze'ev and Zohary (1973), but the source could equally be the 'northern elatius' (Kosterin et al. 2010; Smýkal et al. 2011). Recently, *P. humile* was included into so-called lost crops, for example, additional taxa that were at certain points in time and in certain locations' genuine crops, but were later abandoned

(Abbo et al. 2013). It is notable that despite its wild-type seed dispersal mode and wild-type seed dormancy, these southern *P. humile* are currently found only in secondary habitats and never invade adjacent less disturbed habitats, in contrast to *P. fulvum* and *P. elatius*. Cytogenetic differences and analyses of genetic diversity support the view that the majority of cultivated peas originated from a distinct gene pool within var. *humile* (Zohary and Hopf 2000), although recent molecular studies also highlight the likely genomic contribution from other wild forms and emphasize the importance of introgression and recombination within the complex (Jing et al. 2010).

The domestication of pea has been experimentally tested, both in order to determine the genetic basis which led to the cultivated crop from the wild plant (Weeden 2007), as well as wild pea harvesting (Abbo et al. 2010). The so-called domestication syndrome in the case of pulses applies to increases in seed size, reduction or elimination of pod shattering, and loss of germination inhibition, shoot basal branching and seed toxins and antimetabolites (Smartt 1990; Zohary and Hopf 2000; Weeden 2007). Altogether, at least 11 loci involved in domestication traits have been identified (Weeden 2007). In pea, explosive pod indehiscence and seed dormancy (hard seededness) were probably the greatest barriers to domestication (Smartt 1990). Pod dehiscence is primarily influenced by the *Dpo* gene (Lamprecht 1957a), although other genes also affect this trait (Weeden et al. 2002). The genetic basis of hard seededness has yet to be fully elucidated, although it is clear that the *a* mutation (lack of anthocyanin production) reduces testa thickness, thereby affecting dormancy. Other traits selected during domestication and development of modern cultivated forms, include several morphological characters that are determined by one or a few genes. These genes include *le* (semidwarf growth habit), *r* (wrinkled seed in garden types), *af* (conversion of leaflets to tendrils), and *p* and *v* (absence of sclerenchymatic tissue in pods). Both *a* and *r* improved seed palatability, *le* and *af* increased the efficiency of mechanical harvesting, and *p* and *v* lead to the development of edible-podded types.

Monogenic inheritance is also known for several physiological traits that have been altered during domestication. Wild *Pisum* in its native range displays a typical winter habit in which plants germinate in autumn, overwinter in the vegetative state and flower in response to increasing day length in spring (Weller et al. 2009; Abbo et al. 2013). The obligate or near-obligate requirement for long days suits pea to a winter cropping cycle and has been retained in some forage cultivars. However, most of the cultivated pea accessions from higher latitudes have a quantitative long-day response and are grown as a spring crop (Weller et al. 2009). Some pea varieties are very early flowering and not photoperiod sensitive. The genes controlling flowering in pea include *Lf, Sn, Hr* and *E* (Murfet 1973; Weller et al. 2009). The obligate long-day (wild type) genotype is *Lf, Sn, Hr,* with *E* or *e*. The quantitative long-day phenotype of many cultivars has the genotype *Lf, Sn, hr*. Day-neutral cultivars are *Lf, sn* (*Hr* is not strongly active in *sn/sn* plants), and the very early flowering types are *lf, sn*. Hence, *lf, sn* and *hr* could all be considered 'domestication' alleles. Domestication has also resulted in increased seed and pod size in pea, although not as markedly as in other crops, with a correlated increase in leaf size and stem

strength (Swiecicki and Timmerman-Vaughan 2005; Weeden 2007). The genetic basis of seed size appears to be quantitative (Timmerman-Vaughan et al. 1996), and there are several genes known to influence pod and leaf size (Lamprecht 1953, 1954, 1957b, 1960, 1963). At present, no single or small set of these genes can be identified as crucial for domestication.

Based on these morphological and genetic studies, *P. humile/syriacum, P. elatius* and *P. fulvum* were identified as 'wild' germplasm in that they display traits such as dehiscent pods and seed dormancy (thick testa), that are necessary for survival in the wild and undesirable in a domesticated annual crop. In contrast, *P. sativum* including var. *arvense, transcaucasicum* and *asiaticum* generally display indehiscent pods and little seed dormancy, and could be considered domesticated. *P. abyssinicum* is early flowering, with indehiscent pods, moderately large seeds and lacks seed dormancy. Based on this phenotype, it has been identified as partially domesticated.

One interesting feature regarding the domestication of pea is that not all changes have been unambiguous improvements. Rather many are trade-offs sacrificing certain adaptations for other advantages. For instance, incorporation of the *a* allele into cultivars improved the taste of the seed but also made the plant more susceptible to pathogens such as *Pythium* and *Fusarium*. Elimination of the *Np* gene increases seed size but also increases susceptibility to bruchid attack (Berdnikov et al. 1992). Incorporation of the 'wrinkled seed' *(r)* and 'afila' *(af)* alleles leads to a reduction in yield in some environments. The sugar snap pea, with its combination of four or five mutations (*a, r; p* or *v, n* and *sin*) is notoriously susceptible to soil pathogens. Once genes controlling main domestication traits are identified, along with the full pea genome sequence, we might expect and look forward to comparative evolutionary studies across independently domesticated legumes.

2.3 Pea Genus Genetic Diversity

Based on morphology, *Pisum* sp. is one of the most diverse crop species known, comparable to *Zea mays, Cucurbita pepo* and *Brassica oleracea* (Hancock 2012). There are several user-defined classifications of cultivated pea diversity. Four simply inherited characters determine the main use types of peas within subsp. *sativum:* the presence or absence of pod parchment, flower anthocyanin, leaflets occurrence and whether the starch grains in the dry seed are simple or compound (Green 2008). This classification is similar to that proposed by Lehmann (1954) except for the *afila* type which was unknown at that time. Early data from electrophoretic patterns of major seed proteins: albumin and globulin (Waines 1975), allozymes (Hoey et al. 1996) and chloroplast DNA polymorphism (Palmer et al. 1985) separated *P. fulvum* as a distinct species and *P. sativum* as an aggregate of ' *humile*', *P. sativum* subsp. *elatius* and *P. sativum*, in agreement with the current view of the genus. Chemosystematic studies using flavonoids (Harborne 1971) showed that *P. fulvum* contains quercetine 3-glucoside, primitive cultivars from Nepal and *P. abyssinicum* contain kaempferol and quercetine 3-sophoroside, while modern pea cultivars contain

kaempferol and quercetine 3-(cumaroyl-sophorotrioside). Petals of wild peas contain delphinidin, petunidin and malvidin 3-rhamnoside-5-glucosides, while coloured petals of cultivated garden pea contain, in addition, pelargonidin, cyanidin and peonidin 3-rhamnoside-5-glucosides (Harborne 1971). Unfortunately, the yellow colour *P. fulvum* petals were not studied. Moreover, the *Pisum* genus contains the flavonoid phytoalexin pisatin, which is shared with the genus *Lathyrus* but not found in *Vicia* species (Bisby et al. 1994), which have wyerone instead. Serological reactions of *Pisum* taxa by Kloz and Turkova (1963) indicated a close relationship of all studied taxa, except of *P. fulvum* and *P. abyssinicum*. They were possibly the first to indicate that *P. abyssinicum* might have originated from hybridization between *P. sativum* subsp. *elatius* and *P. fulvum*. Hoey et al. (1996) using morphological, allozyme and random amplified polymorphic DNA (RAPD) characteristics on a set of Ben-Ze'ev and Zohary (1973) accessions showed a separation of *P. fulvum* and 'southern *humile*', while cultivated peas were among *P. sativum* subsp. *elatius* accessions. The position of 'northern *humile*' varied between a sister group to cultivated peas and *P. sativum* subsp. *elatius*. More recently, studies of internal transcribed spacer (ITS) sequence variation (Saar and Polans 2000) and histone H1 subtype five gene (Zaytseva et al. 2012) have supported this. Recent phylogenetic studies based on retrotransposon insertion markers support the model of *P. sativum* subsp. *elatius* as a paraphyletic group, within which all *P. sativum* are nested (Nasiri et al. 2010; Vershinin et al. 2003; Jing et al. 2005, 2010). Although pollination strategy is highly relevant for genetic diversity, it has not been properly studied in wild pea. Pea is considered a self-pollinating species; however, cross-pollination is likely to occur in wild pea populations. The reported cross-pollination rate in cultivation ranges from zero (White 1917) to 60 % (Harland 1948), depending on genotype and environment. The percentage reported for commercial cultivars is less than 1 % (Dostálová et al. 2005). In addition to biological consequences, self-pollination reinforced genetic barriers between wild and cultivated populations, facilitating fixation of the desired genotype (Zohary and Hopf 2000).

Molecular analysis of pea diversity preserved in germplasm collections was done using amplified fragment length polymorphism (AFLP; Ellis et al. 1998), its derived retrotransposon insertion-based marker method, sequence-specific amplification polymorphisms (SSAP; Pearce et al. 2000; Majeed et al. 2012; Vershinin et al. 2003) and gene sequences (Jing et al. 2007; Zaytseva et al. 2012). In all analyses, *P. fulvum* and *P. abyssinicum* formed neighbouring but separate branches, a subset of *P. sativum* subsp. *elatius* was positioned between *P. fulvum* and *P. abyssinicum,* and further branches were found within cultivated pea. The most recent studies of *P. abyssinicum* place it between *P. fulvum* and a subset of *P. sativum* subsp. *elatius* (Ellis 2011; Smýkal et al. 2011; Vershinin et al. 2003; Jing et al. 2010) and showed its very low genetic diversity, which could be explained by passage through a genetic bottleneck. Importantly, high conservation between retrotransposon sequence-specific amplification polymorphism (SSAP; Vershinin et al. 2003), retrotransposon insertions (Jing et al. 2005) and gene-based derived (Jing et al. 2007) trees was observed, in spite of the fact that they derive from different genomic compartments.

Another study on relationships among wild *Pisum*, using a combination of mito-chondrial, chloroplast and nuclear genome markers (Kosterin and Bogdanova 2008; Kosterin et al. 2010), separated *P. fulvum* and *P. abyssinicum* accessions. Interestingly, Afghan types (originating from Afghanistan, Iran, Pakistan) are not nodulated by ordinary European and North American strains, but require specific *Rhizobium* strains for symbiosis (Young and Matthews 1982). Afghan types were clustered separately in diversity analysis based on retrotransposon insertions (Jing et al. 2010). Genetic discontinuity in root-nodulating bacteria of cultivated pea was shown in the trans-Himalayas between India and China (Rahi et al. 2012). The example of coevolution was found in a south Turkey pea line, which was found to form an effective symbiosis only with local *Rhizobium* strains but not with strains from other parts of Turkey (Lie et al. 1987). These authors suggested that the ge-netic uniformity of European *R. leguminosarum* strains is the result of selection and domestication of *Rhizobium* strains originally derived from the gene centres of pea.

Several studies of pea germplasm using morphological descriptors and agronom-ical traits and lately DNA markers have been published (see 'Genetic resources and utilization', Sect. 4). These gave a consistent view. In spite of being a rather small genus with two or three species, *Pisum* is very diverse and diversity is structured, showing a range of degrees of relatedness that reflect taxonomic identifiers, eco-ge-ography and breeding gene pools (Ellis 2011; Smýkal et al. 2011; Jing et al. 2012).

In summary, pea belongs to the early domesticated legume crops accompanying cereals and formed an important dietary component of early civilizations. The Near East and Mediterranean regions are both the area of origin and initial domestication. In the process of domestication, two key traits have been modified, pod dehiscence and seed dormancy. Additional traits include seed size, flowering-time control and branching pattern. Pea belongs in the Fabeae tribe together with lentil, faba bean, common vetch and grass pea. Recent phylogenetic analysis has shown the *Pisum* L. genus to be positioned within the *Lathyrus/Vicia* complex to obtain monophyly. Despite high morphological variation and an extensive geographical range, two true species are recognized: *P. sativum/elatius* complex and the more distant *P. fulvum,* consisting of the secondary gene pool. These can be intercrossed and fertile progeny obtained, although there is some reduction in fertility due to chromosomal trans-locations and nucleo-cytoplasmic conflict. Phylogenetically related *V. formosa,* a perennial mountain species, consists of the tertiary gene pool.

3   Varietal Groups

Pea has a wide range of market classes and uses (See Fig. 2.1).

Field Pea Also known as dry pea and combining pea. The mature seed phenotype for field pea is round (genetically *RR*). Field pea includes yellow, green and red cotyledon varieties typically used in the dehulled/split form in foods such as dhal. New markets are emerging for pea flour in baked products, extruded snacks and

Fig. 2.1 Diversity of seed colour, shape and size in pea. Among 15 genotypes shown, testas have been removed from one seed of every line to show the cotyledon colour. The phenotypes reflect variation at several genetic loci, including *A, r, i* and *s*
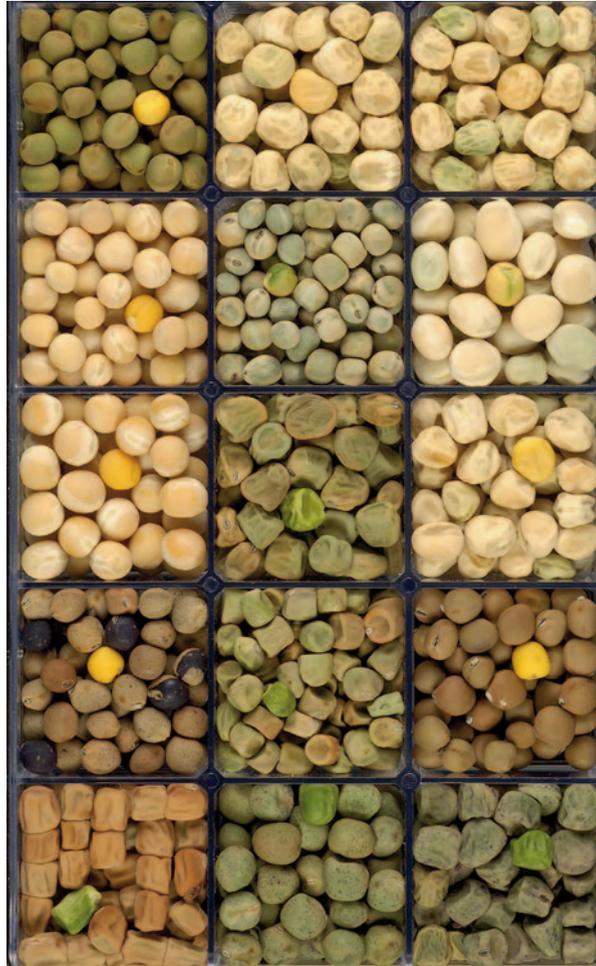
noodles. Starch fractions, typically from yellow cotyledon pea, are used widely in China for production of vermicelli noodles. Protein and fibre fractions are also used in the food industry.

Smaller market classes include:

- Dun (pigmented seed coat) which is also used in the dehulled/split form for foods such as dhal
- Marrowfat (large seeds, blocky shape, green cotyledons, appealing flavour profile) for snacks and mushy pea
- Maple (mottled seed coat) for bird seed mixtures
- Forage (high biomass) cut prior to dry seed maturity for ruminant feed