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# Direct and indirect influences of morphological variations on diseases, yield and quality.

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## Abstract

Interest in morphological variation in food legume species is increasing as plant breeders search for new variants to satisfy the adaptation requirements from new or changing environments or the needs of new end-users. Examination of evolutionary pathways often provides leads in understanding morphological or physiological variation, which may offer opportunities for exploitation in plant breeding. Variation has direct and indirect effects on yield stability and quality through several parameters acting within the plant and the crop.

Traits affecting the development of the crop canopy or the seed, including for example photosynthate repartitions, can have an impact on yield, quality and diseases. Yet the information available is often incomplete for practical use or is very environment specific. Examples are given of the potential utilisation of genetic diversity conserved in different geographic areas as are available in lentils (pilosae types) and chickpeas (kabuli-desi introgression). The concept of quality in pulses is often dominated by morphological traits and the appearance of the seed. There are also instances where the morphological traits affect nutritional and processing quality, (e.g., the novel alleles at the loci controlling both seed shape and starch composition in pea or the gene for zero tannin in lentil).

Where prospects are still remote for developing cultivars with high levels of resistance to important diseases, more emphasis needs to be put on other components of integrated disease management. Some plant characteristics, such as growth habit and canopy structure (modulated by sowing date, plant density, etc.), can contribute to control of diseases. However, experiments have shown that an increase in disease incidence due to increased plant density can be compensated for by a yield increase as is the case with chocolate spot and rust in faba bean. Of interest also are morphological traits, which can slow penetration by the pathogen, enabling the plant to deploy post-infection physiological mechanisms of resistance.

Increased attention to these complex interactions through international multi-disciplinary cooperation has contributed, and could further contribute, to progress in breeding and disease management. This will result in an improvement of the yield potential, yield stability and quality of these crops.

# **INTRODUCTION**

The morphology of plants of a species is the result of the interaction between its genome and the environment during evolution, including the action of man who has effected changes in legumes during domestication. Modification has affected growth habit, suppressed seed

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dispersal mechanisms and seed dormancy, changed breeding systems (from exogamy to autogamy) and ploidy levels, etc. (Smartt, 1990). Many components of morphological variation are spatially and temporally variable. These concepts are discussed in two reviews dealing with the canopy (Norman and Campbell, 1989) and root systems (Smucker, 1993). Plant architecture and root form and functions in food legumes are reviewed by Heath et al., (1994) and Gregory et al. (1994), respectively. Other aspects studied include the morphology and physiology of stomata, which regulate gas exchange between the plant and atmosphere (Weyers and Lawson, 1997). The level of complexity increases as we proceed from individual organs to plants and to communities in the field, each level being determined by genotype × environment interactions. This complexity is the reason for sometimes-conflicting reports.

Most plant breeders have a model on which they base improvements of cultivars in their target environments. Sometimes these models have been formulated as ideotypes such as proposed by Berry and by Hedley and Ambrose (Davies et al., 1985) for peas. Testing models is costly and can be misleading as ideotypes tend to be developed for adaptation to specific environments. Yet, genetic variation in morphological traits has attracted interest in improving yields of pulses. Such variation is expressed in the vegetative and reproductive stages and in all plant structures. The interest is not only in morphological traits, which contribute to yield. A large number of mutants have been used to improve other features such as plant height or standing ability required for mechanical harvesting.

Other variants are useful in enhancing the quality of the grain. They can increase disease resistance or reduce disease incidence by acting on factors affecting disease development. New approaches likely to have an impact are techniques such as "positional cloning" which clarifies the role of genes beginning with the identification of genetic loci responsible for phenotype expression (cf. Caetano-Anollés, 1997).

There is a great potential for exploitation, by breeding, of morphological variation in grain legumes and their wild relatives. This paper reviews aspects related to morphology in the broadest sense of the field crop and individual plants. Reviews exist for many aspects not discussed here, (Summerfield and Roberts 1985; Saxena and Singh 1987, Muehlbauer and Kaiser 1994, Ranalli and Graham 1997).

# PEAS

# Effect of phenotype and crop density on the severity of Ascochyta blight in peas.

The severity of Ascochyta blight in field peas (*Pisum sativum* L.) varies between crops and years (Bretag 1991). Plant density and phenotype can influence the microclimate within a crop (Ali et al., 1978; Hedley and Ambrose, 1981) and also effect the severity of the disease.

It is often supposed that Ascochyta blight will be more severe in crops sown at a high seeding rate as this leads to denser canopies and the microclimate in the canopy will be more favourable for the disease. Many varieties, currently grown in Australia (eg. Dun, Dundale, Derrimut) are tall indeterminate, trailing types that form a dense canopy (Gent, 1988). It is important to know whether shorter varieties with a semi-leafless habit are less affected by Ascochyta blight. As varieties vary in their responses to temperature and photoperiod, they mature at different times (Berry and Aitken, 1979). The Australian varieties have a wide range of maturities and it is unclear whether this affects their disease resistance. Previous studies have indicated that early maturing varieties may be more susceptible than late varieties (Hare and Walker, 1944).

By monitoring disease progress during the growing season on a wide range of varieties, with contrasting phenotypes and maturity classes, it should be possible to determine the extent to which phenotype and maturity influence Ascochyta blight. Studies were undertaken in Australia on conventional pea varieties sown at different rates to determine whether differences in height, leaf habit and maturity affected susceptibility to Ascochyta blight (Bretag, 1991; Bretag and Brouwer, 1995).

A wide range of plant densities was tested, Buckley: 11 to 171, Dinkum: 8 to 105, Dun: 9 to 116, Maitland: 9 to 114 and Whero: 6 to 109 plants m<sup>2</sup>, respectively. While there were significant differences between varieties in the severity of disease and yield losses, the effect of plant density was similar for all varieties. Severity was lowest at a seeding rate of 25 kg ha<sup>-1</sup> and increased at higher rates however above 100 kg ha<sup>-1</sup> there was no further increase in severity. Plant density had a greater effect on yield than on disease severity. As density increased, there was an increase in yield which outweighed the decrease caused by disease. The lower the plant density the greater were the yield losses.

There were large differences between varieties in plant height, days to first flower, node of first flower on the main branch and the total number of nodes formed. Early in the season, the rate of formation of new leaves was similar on all varieties and differences in plant height were associated with variation in internode length. As varieties changed from the vegetative to the reproductive stage, there was a reduction in the rate of leaf formation. Consequently, the early maturing varieties produced fewer leaves than late varieties. For each variety tested, plant growth, development and disease progress were similar in plots sown at either 40 or 120 kg/ha of seed. Comparison of disease progress showed that while there were differences in the levels of disease at a given time, for each variety, disease progress followed a similar pattern to plant growth. Logistic functions successfully fitted the data. The correlation coefficients showed that the models fitted the observed data with a high level of accuracy.

There were large differences between varieties in the shapes of their disease progress curves, but there was no effect of differences in seeding rate. At maturity, there were no differences between varieties in the amount of disease on the first five internodes of the main branch, but large differences occurred on the internodes 6 to 10. There were few symptoms above the tenth node on any variety. The leaves and stems of early maturing varieties (eg. Buckley) were generally more severely affected than those of late varieties (eg. Mackay). Severity did not appear to be associated with varietal differences in plant height. Likewise, there was little evidence that severity was lower on the leafless (Filby) and semi-leafless (Dinkum, Maitland and Mega) varieties. In addition, the range in severity was similar for all phenotypes despite large differences in canopy structure. The differences between varieties with the same leaf type were as great or greater than the differences between varieties having different leaf types. The late maturing varieties often appeared to have lower disease levels at maturity than the early varieties. This may occur because many of the leaves formed at the end of the growing season on the late varieties escape infection. Conditions are more favourable for infection early in the growing season. As a result, the lower leaves usually become infected, when there are high levels of air-borne inoculum and conditions are ideal for infection. In contrast, little disease develops on the upper leaves produced late in the season when there are low levels of inoculum and conditions are less favourable for infection. Irrespective of plant density and canopy structure, all plants usually become infected by Ascochyta blight early in the growing season. At that time, there are small differences between varieties in their canopy structure and plant height. During the early stages of growth, there is sufficient moisture for infection to occur and plant density appears to have little effect on the amount of disease on each plant. It follows that the varieties best suited to their regions, irrespective of their plant type should be used by growers and sown at their optimum seeding rates for maximum grain yield.

# Cold and drought tolerance

Genes for cold tolerance in peas are linked to *ilo* characters, pigmented hilum and pigmented seed coat (Monti, Frusciante and Romano 1993). Reports on the drought tolerance of the *afila* genotypes differ (Monti, Frusciante and Romano 1993, Gonzalez-Lauck, 1990), but leafless cultivars have advantages over conventional cultivars on heavier soils and under wet conditions (Jackson, 1985).

# Vegetative plant parts

Several studies have indicated that major genes controlling morphological traits (leaflet status, stipule size, internode length, seed shape and bracts) can be associated with variation in yield per plant (Berry, 1981; Gonzalez-Lauck, 1990; Cousin, 1997). It is often difficult to resolve whether these genes have a direct causal effect (pleiotropy) or are linked with other unidentified genes causing differences in yield. The utility of these major genes can be assessed in a range of genetic backgrounds by crossing the parental lines or by using isogenic lines. Some backgrounds may favour differentially specific gene or gene combinations.

Thirty-three genes are known to modify the size or form of pea leaves (Davies et al., 1985). Of these *af*, the *afila* gene, controlling the semi-leafless trait has been used most readily by breeders and has transformed the crop in many countries. The gene *af* confers advantages over traditional types through better standing ability from interplant support and more uniform seed ripening. However, the effect of *af* on yield has varied in different environments. Its effect is not always positive and normal leaf types have often given greater yields (Berry, 1981, Goldman and Gritton, 1992). It is possible that the structural improvement associated with the *af* allele could outweigh the potential yield disadvantage in certain environments. The lower yield of *af* plants may suggest a reduction in source capacity is limiting yield.

A characteristic of the *af* gene is its reproducibility across environments and genetic backgrounds. However, its relationship with yield can be altered by genetic background (Lanfond et al., 1981) and in some cases *af* types yield more only in certain environments (Pate and Armstrong, 1996), especially when the mutant-leaf gene is incorporated into more favourable genetic backgrounds (Gonzalez-Lauck, 1990). However, in most studies, plant densities for the mutant and normal varieties were constant, which makes the comparisons biased as the mutants have a reduced leaf area per plant. Mutant types should be sown at their optimal population density to assess their potential yield (Hedley and Ambrose, 1985).

Another gene which regulates leaf area is St. The recessive st allele causes the stipule area to be reduced by nearly half. The interest in using this gene in combination with af (af af st st as leafless peas) has waned. The decrease in average seed size in st compared to St plants (Berry, 1981) suggests there is a source capacity limitation to yield. However, Blixt (Berry, 1981), found significantly fewer seeds per pod and a lower setting rate in st lines. In contrast, he observed no difference in seed size and little difference in number of pods per node.

Wehner and Gritton (1981) evaluated near-isogenic lines of all possible homozygous combinations of the genes af, st and tl (leaflets in the place of tendrils) in eight different backgrounds of commercial processing (green) varieties at a constant plant density. All mutant genotypes tended to yield the same as the normal leaf varieties except for af tl and af tl st which yielded much less. Snoad (1974) evaluated 15 different experimental lines with the af and st gene combinations and found the dry seed yield was similar to the normal leaf genotype for af or st individually. If both genes were together, in the af st combination, yield decreased significantly. With near-isogenic genotypes, Snoad (1981) determined that semi-leafless af peas yielded less even though they had a higher harvest index. Cardi and

Monti (1985) grew dry peas on trellises and reported that *st* had a negative effect on yield and its components. This was especially true in combination with the *af* gene.

Little agronomic advantage over conventional leaf types for green pea production could be demonstrated from plants carrying the *tac* gene (tendriled acacia) in combination with *af* in comparisons of near-isogenic sets in three genetic backgrounds at two plant densities (Goldman and Gritton, 1992; Goldman et al., 1992). The expression of the gene varied significantly with genetic background. Where source capacity is limiting, the complementary dominant Br and Bra genes which produce leafy bracts on the inflorescences, could usefully contribute to yield. The expression of the trait is variable and depends on the environment as well as the background genotype. Berry (1981) found that plants with bracts were on average much higher yielding than those without bracts. The difference was probably due to an association with apex longevity. On average there were about five more reproductive nodes on the main stem of the plants with bracts than on those without them. Plants with bracts also had more reproductive nodes on branches.

# **Growth development**

Generally, the leaf mutant genes can be demonstrated to have differential effects on dry matter accumulation, root growth (Berry, 1981), light interception (Hedley and Ambrose, 1985), photosynthesis (Gonzalez-Lauck, 1990), and semi-leafless plants show an intermediate growth rate compared to the normal and leafless peas (Hedley and Ambrose, 1985). Associations with final yield are more difficult to prove, probably because "only a small part of production capacity is used" in peas (Pate, 1975), although most studies show a good relationship between light interception and grain yield (Gonzalez-Lauck, 1990). There is no difference in stem, petiole, rachis and tendril anatomy for conventional or *afila* peas (Gonzalez-Lauck, 1990). Tendrils have 50% less stomata than the mean of the upper and lower leaf surfaces of both normal and semi-leafless varieties. The chloroplasts in tendrils of semi-leafless and normal genotypes are of the same size and distribution. However, genes *sa1*, *sa2*, *sa3*, can be used to vary the density of the stomata.

#### Growth habit and stems

In *Pisum sativum* 27 mutant genes are known (Davies et al.1985) to affect stems. Breeders have mostly used the dwarfing gene *le*. Berry and Blixt agreed that tall plants (*Le*) had a yield advantage over dwarf (*le*) plants due to more pods per node, which is reflected in a higher pod number and hence seed number (Berry, 1981). Plants possessing the dominant *Le*, were of greater vigour (Berry, 1981) and this was reflected in the higher yields, principally through greater seed numbers.

Stem fasciation, in particular that controlled by the genes fa and fas, has also been proposed (Berry, 1981) as a trait to improve growth habit and the mutual support of plants. On fasciated plants the leaves occur all around the stem instead of in one plane, thus increasing tendril contact between plants at the reproductive nodes. The spatial distribution of seed yield should also be improved as a false umbel of pods is produced at the top of the plant rather than at axillary inflorescences along the stem. The key is the flowering gene Hrwhich as a recessive allele hr brings about rapid apical senescence after commencement of flowering. In contrast, Hr delays apical senescence. Thus, fasciation and the gene hr are both necessary to produce the cluster of pods, if this is a desirable trait for adaptation to specific environments or cropping systems where uniformity of maturation is essential.

Increased stem lignification and strength associated with the *rms* gene may also have significance (Erskine et al., 1988).

Armstrong and Pate (1994) attributed the poor growth of semi-leafless and tare-leaved types, compared to conventional types grown in Western Australia, to their lower vigour which resulted in poorer ground cover, reduced photosynthetic area and lower photosynthate

production. Floyd and Murfet (1986) found an interaction between dwarf and flowering genes in their effect on branching habit in that lines which had shorter internodes and were photoperiod sensitive also tended to have more basal laterals than taller or photoperiod neutral lines. Non-competitive plants with an unbranched habit have been suggested for the UK (Hedley and Ambrose, 1985). However, there is trend now among European breeders to select for types with basal branching because of the high seed cost of sowing required to achieve the high plant density necessary when sowing single-stemmed plants (P. Lonnet, personal communication).

Walton (1990) in Western Australia found that tall cultivars had a higher number of aerial branches whereas dwarf cultivars produced a higher number of basal branches. The proportion of basal to aerial branches varied for cultivars but together they contributed over 50% of the seed yield in low rainfall environments. Non-branching plants (especially tall in peas) allow greater control over the relationship between vegetative and reproductive growth by adjustment via plant density. However, contributions to grain yield from aerial branches tend to increase where environments are more favourable (Armstrong and Pate, 1994; Walton, 1990).

# **Root morphology**

Seven root and shoot characters of peas were studied to assess genetic variability and to measure broad sense heritability. Estimates of heritability exceeding 50% were noted for the number of laterals, length of shoot and weight of shoot and root in *P. sativum* and *P. fulvum* (Ali-Khan and Snoad, 1977). The seed weight was correlated with the length of the longest lateral and weight of the root.

#### **Reproductive structures**

Some of the factors, which control the number of flowers initiated in each raceme, have been identified (Davies et al., 1985; Hardwick 1988). The number can vary from one to seventeen and is controlled by two duplicate recessive genes. Most cultivars have one or two flowers per node. Multi-podded lines usually set fewer seeds per fruit and similar numbers of seeds per node can be found on single-podded types with a high ovule fertility (Davies et al., 1985). Consequently, there is less interest in the 'multi-podded' habit in peas than in chickpeas or faba beans.

Walton (1990) suggested that for the drier areas of Western Australia pea breeders should select for increased seed number per pod in early flowering, medium to tall plants, to improve the total seed weight from the first three reproductive nodes on the main stem. A highly determinate flowering pattern has also been advocated in Europe (Walton, 1990), but some degree of indeterminacy would be beneficial in seasons where finishing rains permitted the filling of later-formed seeds (Pate and Armstrong, 1996).

Five major genes have been shown to control in pod shape. One gene, bt, which determines pod apex shape, has an effect, either by linkage or pleiotropy, on ovule number (Berry, 1981), for in all segregating populations, in several studies, blunt pods (Bt) were associated with low ovule number and pointed pods (bt) with high number. Ovules do not abort at random with respect to position within the pod. There is evidence of within-fruit positional variation in *Pisum* as well as *Lupinus* (Hardwick, 1988).

The photosynthesis by pods is important in seed filling and the optimum positioning of pods in the canopy of leafless peas may thus be equally important (Erskine et al., 1988). There is considerable variation in size, shape, wall thickness and growth rates of pods but associations with yield are not known. One might expect a less efficient conversion of assimilates by genotypes with thick-walls, in view of the greater investment in non-metabolizable dry matter of walls and possibly poorer photosynthetic conservation of respired carbon (Pate and Armstrong, 1996).

Relatively high proportions of seed mass occur as the seed coat (14-29%) in smallseeded primitive forms (*Pisum humile* and *Pisum elatius*) as compared to the 8-9% typical of large-seeded modern cultivars of *P. sativum*. This should be considered when using 'wild germplasm' for genetic improvement as it is likely to impair the conversion of assimilates into cotyledonary reserves. Pod dehiscence is a problem under dry hot conditions at harvest. Three genes reduce seed losses from pod shattering. The first two (*p* and *v*) suppress the production of sclerenchymatous cells and lignification in the pod wall (giving edible pods), resulting in a wall which closely envelops the seeds at maturity. The other gene (*def*) increases funicle strength and the attachment of the seed to the pod, even after dehiscence (Erskine et al., 1988). The funicle part, which may remain attached to the seed, even after threshing, may affect the marketability of the grain.

## Effect of seeds on growth or yield

About 50 genes are known to influence seed shape, seed size, and colour of the testa, but most of these control the patterns and colour of the testa. Large seed usually produce a more vigorous seedling which favours the rapid establishment of a canopy. Seed size is highly heritable and simple to breed for. Interactions between size and number of seeds can be significant but have only minor effect on yield per plant (Berry, 1981). Both components are largely independent and crosses between lines of widely different seed size are likely to produce families with much higher yields than either parent.

#### Lodging

The performance of the pea as a crop plant is affected by the weakness of lower stems, a procumbent habit and a tendency for potentially productive source leaves to become buried by later-developing shoot parts (Pate and Armstrong, 1996). Lodging not only reduces light conversion to dry matter (Heath and Hebblethwaite, 1987) but affects yield and quality (Gonzalez-Lauck, 1990; Pate and Armstrong, 1996). Both conventional leaf (Af) and semileafless types (af) can lodge completely by maturity. The main difference is that the semileafless trait delays lodging. Although leaf type influences lodging, there are factors such as basal stem stiffness, intensity of inter-winding and differences in top growth with environment that have a major impact on standing ability.

#### Yield components and harvest index

Negative correlations are often found between the components of yield and compensation occurs. Correlations vary with plant density. Developmental homeostasis occurs through the abortion of buds, flowers, immature pods, ovules and seeds within pods (Hardwick, 1988). Selecting too intensely for one yield component can disrupt the balance between components. Hedley and Ambrose (1985) pointed to the association of large seed size with high variance for plant size and for partitioning of dry matter into grain within the pea crop as this leads to lower harvest indices among the plant population. They suggested selection for large embryonic axis and relatively small seed size, which would give increased growth rate early in the season without the problem of seed abortion, normally associated with large seeds or high planting density. In general, leafless and semi-leafless peas have higher harvest index values than conventional peas (Erskine et al., 1988; Gonzalez-Lauck, 1990). Pate and Armstrong (1996) suggested that yield improvement could be achieved from increased synchrony of seed maturation through multi-podded nodes and near-simultaneous flowering of neighbouring nodes. An increase in pods per node, using the genes fn and fna, can increase sink size without changing the duration of flowering period. Berry (1981) however, did not detect a corresponding increase in source capacity and multi-podded genotypes had generally poor seed setting rates.

# Quality

In morphological terms, texture, size and colour define quality. Requirements for these attributes differ with traditions and end-uses of the grain. Dark pigmented testas contain tannins which can lessen digestibility and the availability of proteins when the grain is used as stockfeed.

Quality can be influenced by the lack of standing ability at harvest with significant percentages of the grain being classed as 'waste and stain' (Davies et al., 1985). A reduced 'blonding' problem was observed in shelled peas from semi-leafless plants (Wehner and Gritton, 1981). The difference between smooth-seeded and wrinkled-seeded cultivars has determined their usage as dry field (combining) peas or as green processing (vining) peas respectively. The genetic mechanism for smooth versus wrinkled seed has been shown to have a pleiotropic effect on grain yield, 100-grain weight and protein content (Shia and Slinkard, 1977). Wrinkled seeds, as governed by the complementary r and rb (rugosus) loci, have a reduced starch content. Some of the alleles at the r and rb loci change the amylose proportion of the starch and another changes the shape of the starch granules. Additional mutations have been generated, which are not complementary to r and rb such as rug-3, rug-4 and rug-5 but also are associated with wrinkled seed. The rug-3 alleles have been shown to give rise to mature seeds with virtually no starch or, when starch is present, it contains no amylose but only amylopectin (Harrison and Wang, 1995). Starches of such different compositions and structures are of interest in processing for food and industrial purposes.

# **CHICKPEA**

# Agronomic and physiological factors influencing Botrytis gray mold of chickpea

Botrytis gray mold (BGM) disease of chickpea (Cicer arietinum L.) caused by Botrytis cinerea Pers. ex Fr. is common in areas where humidity and temperatures are high. Prospects of developing cultivars with high levels of resistance seem unlikely in the immediate future. Emphasis has to be put on chemical, biological, and agronomic components of integrated disease management, which are effective in augmenting the low levels of resistance. Management factors (eg. sowing date, row spacing, and plant density) and plant characters (eg. growth habit and open canopy structure) have been studied as a means of reducing BGM incidence. Relative humidity (RH), duration of leaf wetness (Butler 1993) and temperature of the air in canopies seem to be important. Direct effects of temperature have been found on the epidemiology of the disease (Rewal and Grewal 1989), with possible indirect effects on duration of leaf wetness. A flow of air could modify humidity and temperature in canopies, and change leaf wetness and disease incidence. There is no detailed published work on such effects. Light (photoperiod) seems to affect the reproduction of the pathogen (Rewal and Grewal 1989), and foggy (Mahmood et al., 1989) and cloudy conditions seem to favour disease development. In the subtropics of South Asia where BGM is important, residual soil moisture from the rainy-season, and winter rains, combined with mild winter temperatures result in profuse growth if the crop is sown soon after the rainy-season (in October or early November). High seed rates and close row spacings contribute to the development of dense canopies. These conditions are conducive to the development of BGM.

Late sowing of chickpea, in which BGM incidence is low, seems to create a mismatch between the phase of the crop most vulnerable to the disease and climatic conditions favourable to disease development. For example, at Gurdaspur in Punjab State, a location where epidemics occurred during 1980-81 and 1981-82, sowing in October exposes the crop to increasing RH and falling temperatures during the period the crop is progressing towards flowering. Sowing in late November or early December results in this phase coinciding with periods of falling RH and increasing temperatures.

A similar effect of climatic conditions on Ascochyta blight (AB) is seen in Mediterranean environments in the West Asia and North Africa (WANA) region. Low AB incidence on spring (March/April) sown, compared with winter (November/December) sown crops seem to be due to the unfavourable climatic conditions for AB during spring. Although yields of spring sown chickpea are almost half those of winter sown crops (Saxena 1984), spring sowing developed as a traditional practise because cultivars resistant to the disease and cold were not available in the past. These traits are essential if chickpea is to be grown as a winter crop in WANA.

In Australia it has been observed that early sowing causes excessive vegetative growth and greater BGM incidence, and late sowing causes reduced dry matter production, both conditions reducing yield, (Brinsmead 1992; Haware and McDonald, 1993). Effects of sowing date on phenology, shoot mass, yield and harvest index are also commonly observed in India. At Hisar, a lower shoot mass and higher harvest index from late sowing shows that vegetative growth is inhibited in the late-sown crop. Crop growth is related to temperature, terminal heat and a fall in RH. It is presumed that excessive vegetative growth and dense canopies, following early sowing, causes microclimate conditions favourable to disease incidence. The reverse is expected to be true from late sowing. However, data are not sufficient to support these supposed effects.

A wider row spacing at a constant plant density reduces disease incidence (Reddy et al., 1993), perhaps because of improved ventilation in the canopy. The advantage of sowing paired rows, compared with uniform row spacing (ICRISAT 1995), should combine the positive effects of wide spacing, and increasing plant densities, but this needs to be confirmed. There are few studies on the effects of sowing geometry, row spacing, and row orientation, with respect to wind direction and effects on airflow through crop canopies, leaf wetness, and disease incidence. Information on these aspects would be useful to improve management of the disease.

Genotypes with an erect compact growth habit have less BGM than genotypes with a bushy spreading habit (Reddy et al., 1993). Again the effect is attributed to the differences in microclimate conditions however, no data are available to confirm this conclusion.

A large variation in the number of leaves or nodes per plant exists within chickpea germplasm. The variation in leaf number is generally associated with differences in seed size, large-seeded types having fewer leaves. For example, K 850 (28 g/100 seeds) has fewer nodes and therefore, leaves per plant (129 nodes plant<sup>-1</sup>) than Annigeri (145 nodes plant<sup>-1</sup>; 18 g/100 seeds), when grown at ICRISAT Asia Center.

K 850, a genotype with a semi-compact growth habit, has less disease than the bushy types (M.P. Haware, personal communication). However, large-seeded types have large pinnule size. Accessions with fewer pinnules (ICC 5680) or narrow pinnules (ICC 14330) are available. Both traits could be useful to reduce the pinnule size of large-seeded commercial varieties, provided the two traits are not closely linked.

Some farming practices, which reduce vegetative growth, also may influence disease incidence. Detopping (nipping) of young shoots and the top portion of branches with three to four leaves, is a practice where growth is profuse, as in some parts of India (Saxena and Yadav, 1975) and Bangladesh. The shoots are used as a vegetable ("Shag"), in the Barind tract of Bangladesh. Light grazing by goats or sheep is practised in some regions of India and Pakistan. The effect of these practices on disease is not well known.

# Effects of host morphology and physiology on Ascochyta blight

In many plants, pre-infectional physical barriers such as cuticle, epidermis or other structures may prevent or slow down penetration by the pathogen, (Akai and Fukutomi,

1980; Campbell et al., 1980). In order to find the relation between morphology and resistance to Ascochyta rabiei, four kabuli cultivars with different morphological and agronomical characteristics and various reactions to A. rabiei (Pass.) Labr. [teleomorph: Didymella rabiei (Kovachevski) v. Arx] were studied (Venora and Porta-Puglia, 1993). The cultivars showed differences in epidermal and sub-epidermal structures of the stem in terms of cell wall thickness and cell volume. The cell walls of the epidermis were thicker in the resistant cultivars. In cross sections studied by image analysis, 'Sultano' had the thickest epidermal cell walls and the largest mean area of the parenchymal cell of the outer laver. This cultivar was one of the most resistant to Ascochyta blight among accessions tested in Italy (Saccardo et al., 1987; Calcagno et al., 1992). Since the epidermal layer is also the site of storage of the isoflavones biochanin A and formononetin, precursors of phytoalexins in C. arietinum (Barz et al., 1993), we could assume that the protection provided by a thick wall can be completed by chemical mechanisms of resistance. Furthermore, the resistance in cy Califfo seems to be associated with both wall thickness of the epidermal cells and size of the first parenchyma cell layer. The susceptible cvs Principe and Calia do not differ significantly in cell wall thickness of the epidermal layer, while the cell area of the first parenchyma layer is significantly different between the two cultivars.

In another investigation (Angelini et al., 1993), the first and fourth internodes of the stem of fifteen-day-old plants of cv Calia and Sultano were analysed histologicaly. 'Sultano' had a higher number of xylem cells and xylem parenchyma cells produced by the vascular cambium in the interfascicular regions, when compared with 'Calia'. Although these results need to be confirmed with more varieties, they may be indicative of the defence mechanisms acting against penetration by A. rabiei. Whether A. rabiei penetrates by mechanical force or with the aid of cell-wall degrading enzymes, a thick epidermis is desirable in that it retards penetration and gives time for the plant to deploy defence mechanisms triggered by the penetration. Among these mechanisms, peroxidase (POD) and diamine oxidase (DAO) can play an important role (Angelini et al., 1990). Structural differences between 'Sultano' and 'Calia', as well as wall autofluorescence and lignosuberized depositions during fungal infection were investigated. Non-inoculated fourth internodes of the resistant 'Sultano' showed a greater POD and DAO activity than the susceptible 'Calia'. After inoculation, both enzyme activities were significantly higher in 'Sultano'. A crucial difference between the cultivars is that invasion of pith parenchyma cells in the fourth internodes was never observed in 'Sultano' while massive lysis of these cells occurred in 'Calia'. The infection areas in both cultivars were surrounded by a barrier made by lignosuberization of cell walls of cortical parenchyma. It is noteworthy that lignosuberized barriers appeared to a greater extent in the resistant ' Sultano'. Histochemical POD and DAO activities were detected in the barriers. Similar findings were observed in infected first internodes. These results suggest that both the structure of xylem tissue and the higher enzymatic activities of DAO and POD after inoculation may play a role in the complex process of to A. rabiei.

# **Vegetative plant parts**

Various mutant leaf forms for shape and positional arrangement are known. They are controlled by single recessive genes (Muehlbauer and Singh, 1987; Erskine et al., 1988). Benefits from the simple leaf mutant on yield still need to be established.

#### Growth habit and stems

Variation in growth habit and branching is used by breeders to improve erectness and suitability for mechanized harvesting. Growth habit, which can be prostrate to erect, is controlled by dominant Mendelian genes, Hg for erectness over prostrate (hg) and Br for basal branching over "umbrella" type branching (br) (Muehlbauer and Singh, 1987). There is quantitative genetic variation in the degree of branching (Erskine et al., 1988). In Western

Australia, when Siddique and Sedgley (Erskine et al., 1988) eliminated the later formed basal laterals by debranching, no effect was observed on above-ground biological yield but harvest index increased by 13% and yield from 1.35 t ha<sup>-1</sup> to 1.87 t ha<sup>-1</sup>

Tall plants are easier to harvest mechanically. Variation for height is considerable in kabuli germplasm, with a range from 15-50 cm and a mean of 29.7 cm (Erskine et al., 1988). Tall genotypes have an increased internode length and node number and a more compact habit because of their narrower branching angles, but they have a similar yield potential to winter-planted conventional types in West-Asia. There is a tendency for tall kabuli accessions to have small seeds, with a seed type intermediate between desi and kabuli, but this negative correlation can be broken.

According to Sedgley et al., (1990), an erect habit and few branches is the most suitable plant habit for high input systems and good weed control. This type, when sown at high densities, reduces water depletion in winter resulting in a higher biological yield and harvest index.

Kumar et al. (1996) compared the conventional bushy type and the tall, erect type which are both in cultivation, with intermediate types developed at New Delhi. The traits included yield, number of branches, seeds per pod, pod number, seed weight and plant height. The tall types recorded the highest values for the traits which had the lowest values in conventional types and vice-versa. They concluded desirable genes with positive contributions to productivity may occur in both tall and bushy types. The intermediate plant types had high mean values for most yield components indicating that they possess better combinations of desirable traits inherited from both the bushy and the tall types.

## **Root morphology**

Genetic differences in the rooting patterns of seedling have been recorded in chickpea (Erskine et al., 1988) with tolerance to drought being found in small seeded cultivars with long roots and a root length/plant height or root weight/biomass ratio of 2 (Calcagno and Gallo, 1993). Selection for large root size gave a greater degree of drought resistance measured as the decrease in yield with progressively increasing drought (Saxena and Johansen, 1996).

# **Reproductive plant parts**

Although one flower or one pedicel per peduncle is normal, double flowered genotypes are quite common. A single recessive gene (*sfl*) controls the difference. The proportion of double podded nodes on double-pedicel genotypes varies over environments but when well expressed, it confers a yield advantage of 6-11% (Erskine et al., 1988). Pods and seeds from double-podded mutants are generally smaller. A recessive pod disposition gene (*pdfr*), which places the pods above the leaves rather than in the normal pendant position (Muehlbauer and Singh, 1987) is of interest with the view to improving pod photosynthesis. However, when pods of normal cultivars were reorientated and exposed to the sun, in each of three locations, no yield advantage could be demonstrated (Erskine et al., 1988). Pod dehiscence is not a problem (Erskine et al., 1988) but genetic variation exists for resistance (E.J. Knights, personal communication). Pod drop is a problem for mechanical harvesting during the hot summers in areas of south-eastern Australia but little information is available on its inheritance.

#### Yield-associated traits and harvest index

Progress in increasing harvest index by selecting for determinant flowering is expected to be slow as the heritability of determinancy is poor and characterised by a predominance of non-additive gene action (Erskine et al., 1988). Pod number per plant and seed size have the greatest direct effect on seed yield (Muehlbauer and Singh, 1987). Branching per plant and pod number per plant are consistently correlated with grain yield in segregating populations. Increased branching tends to increase flower and pod numbers, with positive effects on yield. Branch and pod numbers are the most important components of yield and most often used for selection. Yet, no correlation of pod number with seed yield was found when 3,269 kabuli germplasm accessions were evaluated at ICARDA (Muehlbauer and Singh, 1987). Strong correlations have also been reported between seed yield and biological yield and to a lesser extent with plant height (Muehlbauer and Singh, 1987). Indirect effects on yield are also expected from non-random associations found between five morphological traits (growth habit, canopy width, days to flowering, plant height and seed weight) and plant responses to cold stress, Ascochyta blight and leaf miner infestation (Jana, 1995). A multivariate analysis of 6,400 kabuli accessions indicated that these associations developed in the process of adaptation to diverse agroclimatic conditions in five continents.

## Evolution and effects of seed on yield and quality

The intra-specific classification of Cicer arietinum into macrosperma and microsperma types based on seed and other morphological characters indicates a divergent geographic distribution. The microsperma group is found throughout the geographic distribution of the species but is scarcer in the Mediterranean region where the macrosperma group predominates. The distinction into desi, kabuli and "pea" or "intermediate" types is a parallel system more commonly used by traders (Hawtin and Singh, 1980). It is based on seed shape, size and colour, and takes into account geographic origin and use as food. The kabulis originated from the more primitive desi by selection primarily for seed size and suitability for human consumption. White flowered phenotypes became more acceptable as a result of the correlated response, commonly observed in legumes, where white flowered genotypes show low or zero tannin and a reduction in other anti-nutritional factors. Useful traits can be found in both kabulis and desis and can be transferred by intercrossing (Hawtin and Singh, 1980). The kabuli group has a greater range in seed size, tends to have more primary branches, greater cold tolerance, a more upright and, in some cases, taller growth habit and greater resistance to Fe chlorosis. Desis tend to have a bushier growth habit, more seeds per pod, more pods per plant and greater tolerance to drought and heat. Traits such as double-podding and resistance to wilt and salinity were also identified in desi backgrounds. As the gene pools have been separated for many years, genes for traits related to yield may differ between the groups. Reports of transgressive segregation for growth habit, number of branches, plant height, seed size, pod number or yield from kabuli x desi crosses are therefore not surprising (Bahl, 1980; Hawtin and Singh, 1980). Other associations relate to more rapid seedling growth of kabulis or to a higher percentage of field emergence in desis with a pigmented seed coat compared to non-pigmented kabulis (Auld et al., 1988). In both groups an effect of larger seed size can be demonstrated on germination, emergence and seedling (Roy et al., 1994; Saxena, 1987; Smith et al., 1987). Biderbost et al. (1980), who compared four seed-size categories of one cultivar for germination rate, total germination percentage and seed yield, did not find an effect of seed size on grain yield. However, others (Carter and Bretag, 1997; Eser et al., 1991; Vadivelu and Ramkhrishnan, 1983) have obtained higher yields from using the larger seed within cultivars. Murray and Auld (1987) reduced sowing costs by 30%, without sacrificing grain yield or 100-grain weight, when they used seed 14% smaller than the largest size seed in seed lots of the kabuli cv UC-5.

There is a strong financial incentive for growers of kabuli cultivars to sell their largest grain and keep the smallest for sowing as there can be a large price differential on grain size. In Australia, growers have noticed that grain size and size distribution vary from year to year and want to know how to produce high yields with large grain. Seeds of cv Kaniva kabuli were graded into different size lots (6,7,8 and 9 mm screen sizes, the equivalent of 19.5, 29.2, 38.1 and 43.2 g/100 seeds) and sown at different densities (Carter and Bretag, 1997).

Crop establishment was poorest from the smallest seed. At least twice the number of 6 mm size seeds were required to achieve similar plant populations to those obtained with 8 mm or 9 mm size seeds. Highest yields were obtained from the largest seeds (8 mm and 9 mm). Increased seeding rates resulted in large increases in grain yield (0.92 to 1.83 t ha<sup>-1</sup>) but a small reduction in grain size (8.6 to 8.1 mm or 39.2 to 33.6 g/100 seeds). Reducing seeding rates can result in small increases in grain size but is likely to cause a large reduction in yield. Thus, growers will not save money by using small seeds (<8 mm) for sowing, as the large seeds are more likely to result in higher yields.

# Quality

There is strong consumer preference for specific seed sizes in different countries. A difference between consumers in their preferences occurs particularly for kabuli types but preferences also vary among consumers of desi types. Larger seed are often cooked whole, rather than split into dhal. In kabuli the small-seeded class is <25 g/100 seeds, medium size 25-40 g and large-seeded >40 g (Singh, 1987). In some countries such as Spain, consumers will not accept any size less than 60 g/100 seeds and in Canada anything less than 52 g/100 seeds. Seed size for canning should be around 50 g/100 seeds.

Seed size is positively correlated with longer cooking time and hydration capacity (Williams and Singh, 1987) but not with seed coat thickness (Gil and Cubero, 1993; Williams and Singh, 1987), which indicates that development of larger desi types with a thin coat would be feasible. Coat thickness is linked with flower colour and exhibits monogenic inheritance with the thin kabuli seed coat being recessive (Gil and Cubero, 1993). It affects dhal recovery in processing desi grain.

Seed size uniformity is important as a high proportion of small seeds lowers the value of a sample. Larger seeds process more easily into foods and have a lower husk content (Williams and Singh, 1987). Seed shape also influences processing. Rounder seeds are easier to mill, roast or coat with sugar. Deeply convoluted seeds carry more dirt and seeds with a pronounced beak tend to lose more on decortication. Decortication loss is a significant factor in processing and market value and is determined by seed shape and size, thickness of the hull, hardness of the seed and the decortication process. The larger the seed, the smaller the proportion removed by decortication. However in kabulis, which are usually consumed without decortication, consumer preference is for a seed with deep surface folds.

Both positive (Muehlbauer and Singh, 1987) and negative (De Haro and Moreno, 1992) correlations have been found between seed size and protein content. Oil content in both kabuli and desi types were positively correlated with seed size, while positive correlations were found for seed size with stearic acid content in kabulis and with oleic acid content in desis (De Haro and Moreno, 1992).

Preferences for colour of the seed can vary considerably. In the kabuli type, preference is for beige or light cream-white colour. Among desis the preference varies between countries and even within country. Some preferred colours are yellow, brown, black, green and pink. Numerous genes influence colour and several have pleiotropic effects on flower, stem and leaf colouration. Their interactions cause a wide range of seed phenotypes, which are of interest to breeders satisfying diverse market requirements (Muehlbauer and Singh, 1987). Gene gr, for example, causes green cotyledons, green testa and bluish-green leaves and three dominant genes (Rs, Rsa and Rsb) control rough seed surface.

# FABA BEAN (VICIA FABA L.)

#### Resistance to chocolate spot and mode of inheritance

Chocolate spot (*Botrytis fabae* Sard.) is a major constraint to faba bean production in many areas of the world. In Egypt, chocolate spot and rust [*Uromyces fabae* (Grev.) DeBy ex Fuckel] seriously affect production in the Nile Delta region (Bernier et al., 1984), with losses from both diseases of up to 50% (Ibrahim et al., 1979) or more (Mohamed, 1982). A collaborative program between ICARDA and the National Agricultural Research System in Egypt, identified sources of resistance to these diseases (Khalil, et al., 1984). Large differences were found by Abo-El-Zahab et al.(1994) among genotypes across seasons and generations in their reaction to chocolate spot. Crosses involving the resistant parents ILB 438 and ILB 938 gave the highest levels of resistance. These ICARDA lines, along with BLP 710, BLP 1179 and BLP 1196 have been used in breeding programs in several countries (Duc, 1997). Both general and specific combining ability occur indicating that additive and dominance components affect resistance, with the additive variance being more important. The above lines are recommended as parents in any crosses if the additive x additive genetic variances are to be exploited.

#### Utilisation of genetic resources

Khalil et al (1993c) evaluated 21 F5 lines from six crosses. Trials were conducted during three years in two North Delta locations in fields and pots. Plants in the pots were inoculated with a highly virulent isolate of *B. fabae* and revealed large differences. Eight lines were selected for their chocolate spot resistance and yielding ability. The overall disease score was 36%, 34% and 44% lower than for the check cultivars Giza 2, Giza 3 and Giza 402, respectively.

The average 100-seed weight of the resistant lines was greater (18.4%) than that of the check cultivars. The dark or light green seed coat colour was associated with highly or moderately resistant recombinants, derived from crosses involving ILB 938 or ILB 438. Seed weight and seed-coat colour were used as indicators or gene markers during the breeder seed production to maintain resistance and seed quality.

Six new cultivars have been developed from ICARDA, Egyptian, Mediterranean and European material: Giza 461 (Khalil et al., 1994), Giza 714, Giza 717 (Khalil et al., 1993a), Giza 716, Giza 643 and Gizablanca (Khalil et al., 1996). All have a higher yield potential than the check varieties and were resistant to rust and chocolate spot. The new varieties are also resistant to lodging and produce seeds with improved commercial quality. They were released to the farmers in the North Delta and Nubaria areas.

# **Integrated approaches**

To investigate the possibilities for an integrated approach to disease management, experiments were carried out in Egypt over three years (Khalil et al., 1993b) with the recommended cultivar Giza 3 (medium seed size) and the accession Reina blanca (large seed size) sown at two densities (16 and 33 plants m<sup>-2</sup>) with and without chemical control of disease. 'Reina blanca' was more resistant to chocolate spot and rust than 'Giza 3'. The severity of both diseases was increased at the higher seeding rate. The average yield of 'Reina blanca' was 45% higher than that of 'Giza 3'. The higher plant density gave higher yields. Giza 3' was taller and produced more pods and seeds per plant than 'Reina blanca'. However, the latter gave more yield and heavier seeds (31.1% and 83.30% increase respectively). Higher plant density increased plant height, while lower density increased number of pods, number of seeds per plant and yield per plant. Chemical control with

mancozeb increased yield by an average of 92.8%, together with plant height, number of pods, seed per plant and 100-seed weight.

Studies on cultivars, resistant and susceptible to chocolate spot, indicated that resistance was associated with the accumulation of phytoalexins in plant tissues. The highest concentration was found in the resistant accession ILB 938, followed by the new cv Giza 461, while the lowest was in the susceptible 'Giza 402' (Omar et al., 1992).

#### Plant architecture and yield

Natural variability and induced mutation are available and are used when breeding for reduced lodging and abortion of reproductive organs. Indeterminate cultivars are tall, but short-strawed cultivars are available. In determinate types ("topless") the *ti* gene is present (Sjödin, 1971). A *ti-s* gene, controlling the "semi-determinate" growth habit was also described (Frauen and Brimo, 1983). In semi-determinate winter types developed by Le Guen and Duc (1992), meristems senesce after 10-12 flowering nodes, whereas conventional types may reach 25 nodes. Frauen and Sass (1989) have identified a "stiff-straw" character, which is of simple, monogenic inheritance.

Effects of plant architecture on crop performance and productivity is discussed by Heath et al. (1994), Bond (1987) and Duc (1997). Determinate types produce less yield than indeterminate types, because of their less efficient plant architecture and physiological disadvantages in assimilate transfer from stem to pod (Pilbeam et al., 1989).

In spring sown faba beans the optimum plant densities for determinate types are higher than for the indeterminate types (Pilbeam et al., 1990). No difference was observed between short strawed and indeterminates (Cleal, 1991). By contrast, plant morphology does not affect the optimum density in winter sown cultivars (Pilbeam et al., 1991).

The trait of independent pod vascular supply has been used to reduce reproductive losses. The high pod number per node and the high number of seeds per pod are generally considered to be positive traits, aimed at concentrating yield on a few nodes (Duc, 1997).

# Relationship between flower colour and yield

S.A. Khalil (unpublished data, 1995) crossed a tannin-free accession, Triple White, which has a white wing petal (WF), with five other genotypes all with black spotted wing petals (BS). The F1 plants showed complete dominance of BS over WF. However, the F2 segregated into BS, WF and yellow spotted wing petal colours (YS). The BS plants gave the highest estimated yields, the YS plants the lowest and WF plants had intermediate yields. These findings indicate the relation between quantitative and qualitative characters. Undesirable characters, such as smoken seeds (Ibrahim, 1963), are genetically linked with white flowers. Other examples are yellow flowers being linked with pod dehiscence, pod shedding and shattering and to susceptibility to chocolate spot and rust, all of which have an effect on yield (Mohamed, 1982).

# LENTIL

#### **Vegetative plant parts**

Several atypical leaf types are known in lentils (*Lens culinaris* Medik.) but they do not appear to have the potential to improve yield (Erskine et al., 1988). However, the gene *tnl* which governs the presence of tendrils at the end of the leaves may be useful for canopy formation and the standing ability of the crop, making it more suitable for mechanized harvesting (Muehlbauer et al., 1995).

#### Growth habit and stems

Lentil plants have a freely branching growth habit and poorly defined stems. A single gene Gh controls growth habit, with ghgh giving prostrate and GhGh giving erect plants (Muehlbauer et al., 1995). Erect lentils are easier to harvest than lodged plants and lodging increases losses of both seed and straw. The tendency for plants to lodge is related to stem diameter and probably stem lignification (Erskine et al., 1988). Variability in stem height is continuous and pods can be placed in the range 3 -30 cm from the base, allowing for selection for suitability for mechanized harvesting, which requires a clearance of about 12 cm. Advantageous and positive correlations have been found between plant height and yield in lentil. An increased height often ensures a large vegetative frame on which many reproductive nodes can develop. However, deleterious correlations have been reported between plant height and both time of maturity and tendency to lodge (Erskine et al., 1988). Growth habit can also affect the severity of diseases (W. Erskine and T.W. Bretag, personal communication) as infection by *Sclerotinia sclerotiorum* (Lib.) de Bary is often enhanced when the plant tops touch the ground after lodging.

#### **Reproductive structures**

Reproductive nodes commonly carry one to three flowered racemes per peduncle. A single gene determines the difference between double and triple flowered genotypes but up to seven flowers per peduncle have been recorded for plants grown in a glasshouse. The effect of the multi-podded habit on yield needs further investigation (Erskine et al., 1988, Muehlbauer et al., 1995). Pod length was found to have a direct positive effect on yield (Muehlbauer et al., 1995). Problems with pod drop account for 65% of losses in mechanical harvesting under dry conditions, and pod dehiscence contributes to the remainder. Excellent resistance to pod dehiscence has been found; a single recessive gene pi controls pod indehiscence. The wild progenitor, *L. culinaris ssp. orientalis* has *PiPi* and cultivated *L. culinaris spp. culinaris* has *pipi*. Variability for shattering occurs in the cultivated type even in the presence of *pi*, which indicates the presence of modifier genes. Genetic variation for pod drop may be limited (Erskine et al., 1988; Muehlbauer et al., 1995).

Path coefficient analyses and positive correlations of grain yield with a range of morphological and physiological traits have been discussed by Verma et al. (1993) and Muehlbauer et al. (1995). Breeding for increased harvest index has been advocated in lentils (Erskine et al., 1988). In Middle Eastern countries however, lentil straw is still a valuable commodity and requires a large biological yield rather than a high harvest index. Prolonged leaflet retention may also contribute to a larger forage yield.

#### Effects of seed size on yield

Seed size is highly heritable (Erskine et al., 1988; Muehlbauer et al., 1995) and has been studied for its relation with yield. Correlations of seed size with yield differ between studies, with positive and negative values having been found (Singh and Singh, 1969; Verma et al., 1993; Muehlbauer et al., 1995).

Seed size was positively correlated with pod size and leaf size among bold seeded genotypes. Correlations between pod size and leaf size were also demonstrated, leading to the suggestion leaf size may be a fairly reliable selection index for seed size in segregating populations, even at the seedling stage (Sharma et al., 1993). However, seeds per pod is negatively correlated with 1000 grain weight, pod size and leaf area in bold-seeded lentils in India (Sharma et al., 1993).

Some of the contradictory associations reported for seed size are worth considering in the context of varying environments and diverse gene pools. Of interest are the studies of Erskine (1996), who examined adaptation to temperature and rainfall in Syria, Turkey and Lebanon among accessions and breeding lines of two seed-size groups represented by largeseeded, yellow cotyledon lentils and by small-seeded red cotyledon lentils (seed mass < and > 4.5 g/100 seeds or seed diameter < and > 6 mm respectively). West Asia historically has been the only lentil growing area in the world where both types are largely grown by farmers.

The large seeded material had a longer reproductive growth period than the small-seeded group (2.8 days longer). An extended period is considered to be required to fill the greater seed mass per pod among the yellow-cotyledon types, which also produces taller plants and more straw. The germplasm with large seeds was less susceptible to winter cold. The group also had an advantage in yield over the small-seeded types in average temperatures <10 °C, with the converse being true at higher temperatures.

Allied to the higher cold tolerance of the large-seeded group was their response to cool conditions throughout the season. They showed an advantage in yield at the two wetter sites, with the cool and wet seasons allowing a protracted period for vegetative and reproductive growth, whereas the small-seeded group was better adapted to dry environments. To cope with dry warm environments, drought escape through early flowering and early maturity is important (Erskine, 1996). Selection among the large-seeded lentils should be for early flowering, as an extended reproductive period may be required by all large-seeded lentils.

The environment, acting as an evolutionary force creating and preserving genetic variation useful for lentil improvement, should not be underestimated (Erskine et al., 1989). The obvious discrimination is in seed size (Muehlbauer et al., 1995) as macrosperma types are common in the Mediterranean basin and Western Hemisphere, while microsperma are dominant on the Indian subcontinent.

Promising results were obtained for yield improvement in Bangladesh by introducing genes for larger seed size (>2.5 g/100 seeds) from macrosperma into a locally-adapted microsperma variety (1.3-1.5g/100) (Sarker et al., 1992). The lentils in South Asia are of a specific ecotype (*pilosae*), characterized by the pubescent trait and by their short plant height and small seed. They are thought to have been derived from a small founding population as they show a lack of variability compared to lentils in other regions (Erskine et al., 1996). The lack of variability is seen as a bottle-neck to genetic improvement and much progress is expected to come from hybridization with "exotic" germplasm.

# Quality

Quality factors such as seed size and seed thickness affect the processing and cooking quality and seem to be strongly heritable. Cooking time is more related to seed size (r=0.92) than to environment (Muehlbauer et al., 1995). Seed coat colour, which is important in determining market potential is controlled by several genes and pleiotropic action is likely for epicotyl and flower colour, with parallels in *Cicer* and *Pisum* (Muehlbauer et al., 1995). Five alleles have been identified for the *Scp* gene which controls the trait of spotted seed coat; the nonspotted genotype is *scp scp*. Background colour, while the dominant *Tgc* produces a tan ground colour. When both are present (*Ggc Tgc*) a brown seed coat is produced. The double recessive (*ggc tgc*) has a green seed. A recessive gene *tan* for zero tannin in the coat is thinner and more fragile, making the seed more susceptible to rot. Two loci are involved in determining the colour of lentil cotyledon, with dominant red colour (*Yc*-) epistatic to both yellow (*I*-) and green (*ii*) (Muehlbauer et al., 1995).

A small but positive correlation (r=0.26) has been reported between protein content and seed weight (Sharma et al., 1993) and between seed size and protein per seed (r=0.31) suggesting that breeding for larger grain does not necessarily cause a decline in protein content.

# LUPINS

# **Plant architecture**

In lupins (Lupinus spp.) pod set and growth on the main shoot, thickening of the main stem and vigorous growth of the first-order lateral branches all occur at the same time (Gladstones, 1994). This is likely to generate competition for resources. In addition, the branches grow above the main shoot and shade its leaves and inflorescence. The competitive effects of these branches have been demonstrated by cutting them off at an early stage. The main shoot then sets more pods and produces a greater yield. As often happens, more pods are set than will fill seeds. As a result of this perceived wasteful process, genotypes of narrow-leaf lupins (Lupinus angustifolius L.) with less branching have been developed and have given promising yields in the short-season environments of Western Australia (Hamblin et al., 1986). However, interest in reduced-branching lost favour among breeders for a number of years because of problems associated with high alkaloid levels, insufficient *Phomopsis* resistance, and small seed size (Gladstones, 1994). Reduction in branching and the late production of new leaves were also considered to enhance susceptibility to brown leaf spot (Pleiochaeta setosa [Kirchn.] Hughes). A single incompletely dominant gene, Det, controls reduced branching. In plants carrying Det or similar genes, enhanced pod set appears to be achieved indirectly through suppression of competing branch growth. The Det genotypes lack the capacity for new leaf development after initial setting regardless of when it occurs. Therefore, new leaves may be able to function later in the season, when older leaves have senesced and/or fallen down. It is this part which makes reduced-branching lupins so vulnerable to brown leaf spot as it causes premature loss of older leaves. More recent comparisons have shown restricted-branching types have the potential for higher yields than and normal types of narrow-leafed lupins and albus lupins when compared in otherwise similar genetic backgrounds (Dracup and Kirby, 1996).

# **CONCLUDING REMARKS**

There is a scarcity of genetic resistance to the many foliar diseases of the cool-season pulses. Morphological characters, which can create microenvironments less favourable to the development of epidemics, can have significant effects on yield and quality.

The economic value of the variation in morphological traits available in germplasm of the pulses still remains largely unexploited. A reason for this is that the underlying physiological factors interact and are complex to understand. Their study requires an interdisciplinary and global approach. Collaboration between diverse disciplines to widen our knowledge is a recent trend not yet fully exploited.

Computer models, which can simulate plant development and growth (Jeuffroy and Ney, 1997) will enhance our understanding of crop physiology and the effect of plant morphology on yield, disease resistance and quality. They will help in dealing appropriately with the complex interrelationships.

When using morphological variation, it is important to be mindful of the specificity of the cropping system and of the environment in which this variation will be exploited. Strategies for the genetic improvement of low input systems in tropical areas should be different from those aimed at high input European systems. This applies particularly where the option exists for disease control by means of morphological traits rather than the application of chemicals. Techniques developed recently, such as positional cloning, can help overcome limitations in genetic improvement, where traits depend on complex interactions between genes, gene products and the environment.

The expression of many morphological traits may vary with the genetic background of the individual plant. New traits may also upset the balance among other factors which have evolved in the species and still influence performance. Genetic improvement aimed at achieving an "equilibrium" are, therefore more likely to succeed than those where a reputedly "positive" trait is over-emphasised.

International cooperation has, and should continue to have, an important role in collecting, characterising and maintaining germplasm collections. Finally, a large variability also exists among wild relatives of several legume species. Joint international and national efforts are needed to save this variability for present and future exploitation.

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