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Genetics and genetic modifications of plant architecture in grain legumes: a review

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Abstract – Crop architecture may be modified to improve the adaptation of the crops to different environments and to increase the seed yield and its stability. The main peculiarities of the grain legume architecture are the indeterminate growth habit, which may lead to a prolonged growth cycle with consequences on the maturation and strong within-plant competition between the reproductive and vegetative growth and the fleshy pods. The principal reasons are presented as to why modifications of the grain legume architecture and the genetic strategies could contribute to increasing the seed yield. The main components of the crop architecture are analyzed. The flowering date is of major importance for the adaptation of a crop to the environmental conditions. The branching pattern may be directly affected independently of other architectural modifications. The leaf size and structure contribute to the leaf area index of the crop and may influence the light interception efficiency. The determinate growth habit modifies the duration of the growth cycle and the assimilate partitioning while the dwarfism may improve the adaptation to a range of environments through the reduction of the lodging risk. The pod walls may contribute to the pod photosynthesis but they account for a large proportion of the pod weight at harvest. This reduces the crop harvest index. For each of these traits, the genetic modifications that have been observed in the different grain legume species are presented as well as their genetic control. The consequences on the seed yield elaboration and the adaptation of the crops are assessed. The limitations of the architectural modifications are also investigated and the interest in combining morphogenetic and functional approaches is discussed. (© Inra/Elsevier, Paris.)

soybean / pea / lupin / faba bean / bean / cowpea / lentil / chickpea / *Glycine max* / *Pisum sativum* / *Lupinus* spp. / *Vicia faba* / *Phaseolus vulgaris* / *Vigna* spp. / *Lens culinaris* / *Cicer arietinum* / flowering date / branching / leaf structure / determinate growth habit / dwarfism / pod walls

Résumé – Modifications génétiques de l'architecture des légumineuses à grosses graines : revue bibliographique. Les modifications de l'architecture des couverts peuvent être utilisées pour améliorer l'adaptation des cultures à différents environnements et pour accroître le rendement en graines et sa stabilité. Les particularités architecturales des légumineuses à grosses graines résident dans leur croissance indéterminée et la présence de gousses présentant des parois

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épaisses. La croissance indéterminée peut conduire à un cycle de croissance prolongée avec des conséquences sur la maturation et a une forte compétition entre la croissance reproductrice et la croissance végétative pour la répartition des assimilats. Les raisons pour lesquelles les généticiens ont cherché à modifier l'architecture des légumineuses à grosses graines ainsi que les stratégies qui permettent d'améliorer le rendement en graines sont présentées. Les principales composantes de l'architecture des couverts sont analysées. La date de floraison est d'une importance majeure pour l'adaptation des cultures aux conditions environnementales. La structure des ramifications qui peut être génétiquement modifiée indépendamment d'autres modifications architecturales contribue à la mise en place de l'indice foliaire. La taille des feuilles et leur structure contribuent également à l'indice foliaire des couverts et leurs modifications peuvent influencer l'efficience d'interception du rayonnement. La croissance déterminée modifie profondément la durée du cycle de croissance et la répartition des assimilats alors que le nanisme peut améliorer l'adaptation aux conditions environnementales en réduisant les risques de verse. Enfin, les parois des gousses qui peuvent contribuer par photosynthèse à la nutrition carbonée des graines représentent à la récolte une part importante de la biomasse des gousses. Ceci réduit l'indice de récolte des couverts. Pour chacun de ces caractères, les modifications génétiques observées chez les différentes légumineuses à grosses graines sont présentées ainsi que leur déterminisme génétique. Les conséquences sur l'élaboration du rendement et l'adaptation des cultures sont analysées. Les limites des modifications architecturales sont évaluées et l'intérêt de combiner approche morphogénétique et approche fonctionnelle est discuté. (© Inra/Elsevier, Paris)

soja / pois / lupin / féverole / haricot / lentille / pois chiche / *Glycine max* / *Pisum sativum* / *Lupinus* spp / *Vicia faba* / *Phaseolus vulgaris* / *Vigna* spp / *Lens culinaris* / *Cicer arietinum* / date de floraison / ramifications / structure des feuilles / croissance déterminée / nanisme / proportion de parois dans les gousses

1. INTRODUCTION

An increasing interest is devoted to crop architecture in many species. In grain crops, the architecture is involved in the elaboration of the seed yield because of its impact on light interception [90], on the pattern of radiation interception within the canopy [167], on dry matter accumulation and on assimilate partitioning to the vegetative compartment and the reproductive growth.

The crop architecture is the three-dimensional distribution of the vegetative and reproductive organs. It is influenced by environmental conditions, mainly temperature, radiation intensity, day length and water status. The agronomic practices, such as sowing date, sowing density and use of growth regulators, also influence the crop architecture. The architecture of a canopy results from the potential structure of each individual plant and the modifications of this potential architecture because of the canopy density and the presence of neighbours. Crop architecture may be modified through genetics and breeding. Breeding can modify the structure of each individual plant but also their responses to a change in canopy density.

It must also be considered that the crop and plant architectures are highly dynamic processes in that they change with plant growth and dry matter accumulation.

In the present paper, the peculiarities of the grain legume architecture will first be analyzed as well as the reasons why breeders and geneticists have tried to genetically modify it. Then, each of the main architectural features will be examined across grain legume species. For each character, the genetics and the genetic modifications available in the different species will be presented. The consequences on the crop structure and on the yield and its elaboration will also be described.

2. THE ARCHITECTURE OF GRAIN LEGUMES

2.1. Definition of architecture

Numerous definitions of plant architecture have been given. The present paper will be based on the definition given by Ross [153] who described it as "the set of features delineating the shape, size, geometry and external structure of a plant." For the grain legumes, the growth habit of the plant must also be taken into account. Consequently, the architecture includes numerous characters such as the number of stems and branches, the structure of each stem and branch (number and length of internodes), leaf structure and the orientation of the organs. Beyond the parameters regarding each organ, the relationships between organs or groups of organs must be analyzed as emphasized by Hardwick [68] for the analysis of the modular growth of the plants. It may be debated whether the phenological stages, and especially the flowering date, should be considered as architectural features. The flowering date is not an architectural character per se, but its implications on plant architecture are very important. The flowering date determines the onset of the reproductive growth and thus the elaboration of new types of organs. In some crops, it may also determine the production time of branches and consequently the elaboration of a new group of vegetative organs. Because of these major implications on the architecture, it was chosen to include the flowering date in the present review.

Plants can also be regarded as composed of metameric units. Watson and Casper [193] defined the metameric units of *Phaseolus* as "consisting of a section of stem, a trifoliate leaf and the associated, laterally borne reproductive branch which function as internally integrated and are relatively autonomous physiological units." This metameric structure of the plants was also pointed out by Hardwick [68] and these metameric units may be identified easily in grain legumes. The plant is a continuum born from the successive production of metameric units. The modification, either genetically or environmentally induced, of the structure of each individual metamer or of their number will modify the structure of the whole plant. When genetically induced, these subsequent modifications may sometimes be considered as pleiotropic effects of the genes.

Despite the conceptual interest in considering the plant as a continuum, the modifications of plant structure in grain legumes will be analyzed according to the classical classification of the organs, as most of the available literature refers to this classification.

2.2. Peculiarities of grain legumes

The peculiarities of the architecture of grain legumes are mainly due to their indeterminate growth habit. This has always been a major concern for breeders, as very few other grain crops show this growth habit. Indeed, all grain legumes have the physiological ability to prolong indefinitely their vegetative phase after the onset of flowering. In species in which the flowers are produced at the axil of the nodes, such as peas and beans, the indeterminacy is expressed through the vegetative stage of the terminal meristem of the stem where more nodes are or may be produced. In species such as lupins, in which terminal inflorescences are produced on the stems and branches, the indeterminate growth habit is expressed through the production of new orders of branches from buds located at the axils of the top leaves of the branches of the previous order [47].

The first implication of the indeterminate growth habit is the possible competition between the vegetative and the reproductive growth for the assimilate partitioning. This may lead to a low or unstable harvest index and consequently low or unstable seed yields. The second physiological implication is the potentially long cycle and late ripening due to the prolonged vegetative phase. This is of major importance for the regions with cool and wet summers such as the United Kingdom [115]. However, it should be noted that the indeterminate growth habit is an undomesticated characteristic. It confers to the wild plant the ability to prolong its reproductive growth, maximizing the chance to breed a progeny. In the cultivated populations, it offers the ability to compensate for large variations of the stand density or to produce additional vegetative and reproductive organs to achieve an acceptable seed production when the first reproductive organs aborted or were damaged.

The second peculiarity of the grain legumes, which they share with the Brassicas, is the structure of the reproductive organs as the grains are produced in fleshy pods. The pod walls are able to photosynthesize and feed the grains [133]. At harvest, the pod walls contribute a large proportion of the biomass of the reproductive compartment. Because of this characteristic, the architecture of the reproductive organs will also be considered briefly in the present paper.

3. WHY GENETICALLY MODIFY THE PLANT ARCHITECTURE IN GRAIN LEGUMES?

3.1. The agronomic objectives

The main agronomic reason why breeders and geneticists have tried to genetically modify plant architecture is to maximize and stabilize seed yield. The modification of crop architecture may result in a higher seed yield because of an increase of the assimilate partitioning to the reproductive compartment and a preferential allocation to the grain within the pods. The same goal may be achieved through an increase in biomass with a similar partitioning. However, as will be analyzed in the paper, most architectural modifications resulted in a reduction in the biomass production.

The second agronomic reason is to make the plant cycle best suited to the climatic conditions of a given environment, i.e. to flower when there are low risks of temperature and water stress, and to secure crop maturation. An improved resistance to diseases or to lodging will have the same result and contribute to a better yield stability.

3.2. The ideotype breeding

The definition of the optimum plant structure to reach these goals answers to the concept of ideotype defined by Donald [41] in Australia for wheat, proposed by Adams [4] for *Phaseolus vulgaris*, by Hedley and Ambrose [79] for pea and more generally assessed by Coyne [36]. In this breeding approach that combines physiological and genetic traits, the architectural characters may massively be taken into account. Indeed, even when quantitatively inherited, they are usually more heritable than the seed yield and, in some cases, they are under a mono- or oligogenic control. The selection on architectural traits is expected to be more effective than the direct selection on the seed yield and its components. This was analyzed on pea by Moot and McNeil [116]. In 1982, Adams [5] proposed a bean ideotype for high yield with a distinctly modified plant architecture which he referred to as an archetype.

It should not be concluded, however, that the only selection on the architectural traits will be sufficient to get high yielding genotypes. It should more realistically be considered that the optimum architecture is the one where the progress through breeding may be expected to be maximum. The modification of the architecture is thus an optimization of the breeding programme. Indeed, the definition of an architype and the selection for the architectural traits in the early generations of the breeding programmes make possible the use of the expensive yield trials on the best material.

3.3. Three strategies to increase seed yield through architectural modifications in grain legumes

The different architectural modifications which could contribute to a higher and more stable seed yield must be analyzed within a general scheme of seed yield elaboration. In a very basic approach, three plant compartments may be considered: the root, the vegetative (stems and leaves) and the reproductive compartments. This latter compartment is then divided into the seeds and the pod walls. The root compartment is essential because of its role in nitrogen fixation and water and nutrient uptake. It largely determines the aerial structure for a given genotype through the nitrogen [155], water [126] or phosphorus supply [117]. However, this compartment is difficult to analyze for genotypic comparisons because of a sampling error in field conditions and of its sensitivity to and possible interactions with the environment. No genetic variation for the structure of the root compartment has been reported in grain legumes.

In the present paper, we will only discuss architectural modifications of the vegetative compartment, the seeds and the pod walls.

Three major types of modifications may contribute to increase the seed yield (*figure 1*). The first one is to produce more total biomass without modification of the ratio between the reproductive and the vegetative compartments. The second one is the increase of the reproductive/vegetative ratio with a constant total biomass, contributing to an increase of the harvest index. The last one is the modification of the reproductive compartment itself with a reduction of the pod wall proportion and also an increase of the harvest index.

The increase of the total biomass is achieved with an increase of the light interception throughout the growing season. Consequently, all the architectural characters that modify the total plant leaf area during the growth cycle are potentially involved in this step. The flowering date may affect the leaf area and biomass production for species for which new branches are produced after flowering. It may also affect the conversion efficiency of the PARa (photosynthetically active radiation absorbed) into dry matter as shown on peas by Ney [126]. The branching pattern will modify the light interception, especially when branching takes place early in the cycle because of the variation in the number of leaves per plant and the modification of their three-dimensional distribution. The structure of the leaves influences the production of the biomass. The variation in the individual leaf size due to differences in its structure will result in a variation in the total leaf area and may affect the light interception efficiency. The indeterminacy of the growth habit also favours the biomass production because of a high leaf area index and, above all, a long vegetative cycle.

The pattern of assimilate partitioning between the vegetative and the reproductive compartments are modified by different architectural traits. The flowering date influences this ratio as it controls the time when the reproductive organs will be set. The growth habit shows a major impact on this feature. Indeed, the indeterminate growth habit induces a prolonged competition between the vegetative and the reproductive growth while the determinate

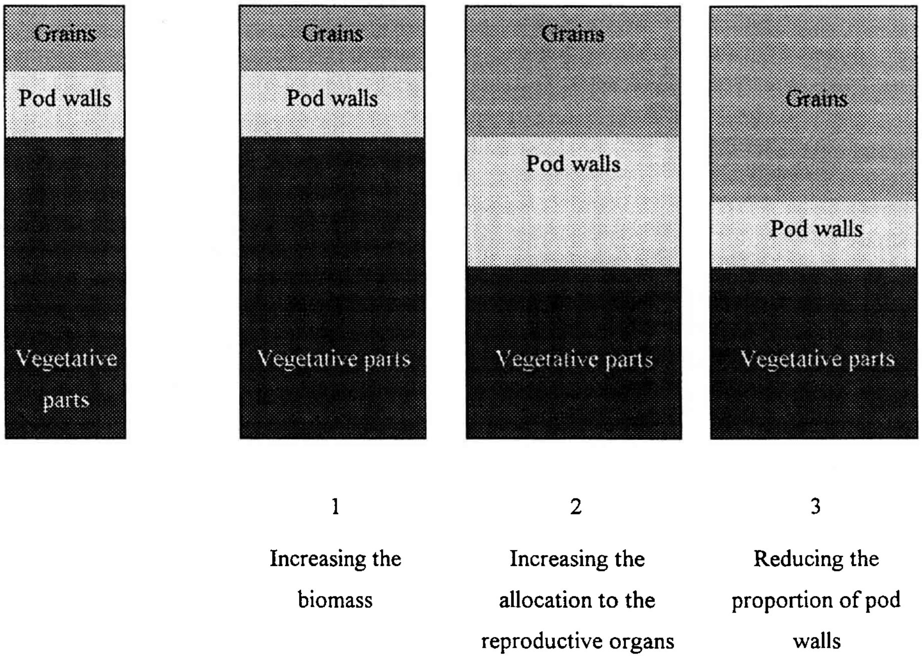

Figure 1. Different strategies to increase seed yield through modifications of the architecture (from Huyghe and Ney [85]).

growth habit, at a given time of the growth cycle, induces allocation of all the assimilates to the reproductive growth. The dwarfism may also influence the reproductive/vegetative ratio either through a modification of the pattern of resource allocation because of the reduction of the internode length or through a reduction of the canopy lodging.

The structure of the reproductive compartment has little been considered in the breeding of grain legumes. However, because of the physiological role of this compartment and the proportion of biomass which is stored in it at harvest, there is a need to examine the possible existence of a genetic variability.

4. FLOWERING DATE

The flowering of a plant is a major change in state as it induces the production of organs devoted to storage. The other phenological stages, such as the end of flowering or the maturity date, are often closely related to the flowering date. This paper will focus on the flowering date.

Genetics of flowering may be studied without consideration of the physiological basis of the flowering processes. Both qualitative and quantitative interpretations of the genetic variations have been reported. For instance, in *Arachis hypogaea*, Upadhyaya and Nigam [185] showed that the time to first flower from sowing was controlled by one single gene with additive action, whereas the rate of early accumulation of flowers could be controlled by three more independent genes with complete dominance. In spring-sown white lupin, the time to first flower was reported to be quantitatively inherited, under a highly additive inheritance [103].

4.1. The models used to explain the flowering date

Two main types of models have been developed to describe the flowering date. The first model directly relates the flowering date to the number of leaves expanded before flowering. Such relationships have been established in white lupin [92] or in pea [181]. The variations in the flowering date are related to variations in the number of leaves, whatever the genotypic or environmental sources of variation. Variations in the phyllochron have also been reported but they are usually induced by the environmental conditions because of variations in the growth rates [69, 181]. Little genotypic variations were reported for the phyllochron even if differences in leaf appearance rate were observed among pea cultivars.

The second group of model relates the rate of progression towards flowering to the temperature and day length. A relationship: $1/f = a + b\mathrm{T} + c\mathrm{P}$ was established where f is the time in days from sowing to first flowering, T and P are the respective mean preflowering values of temperature and photoperiod and a, b and c are genotypic constants [172]. This model was successfully applied on several species including grain legumes such as *Cicer arietinum* [151], *Glycine max* [66], *Lens culinaris* [172], *Lupinus angustifolius* [142], *Vicia faba* [88, 123], *Vigna radiata* [171] and *Vigna unguiculata* [65]. In all species, genetic variation was identified for the constants of the model.

Both models may be used to predict flowering. However, for an appropriate understanding and assessment of the genetic variation, there is a need to examine the responses of the different species to the different environmental parameters that may affect the flowering date as well as the genetic variation in this response. In this section, the effects of temperature and of light will be discussed.

4.2. Genetic variation in the response to temperature

The variations in leaf number of the stem are the main sources of variations in the flowering date in white lupin and are mainly temperature-driven. The number of mainstem leaves varies significantly with the environment (location, sowing date, year) [84]. These variations may be explained through the processes of leaf primordia production which is affected by the thermal time and the initial seed size [83] and vernalization [82]. Quantitative genetic variations for the vernalization requirements were identified and proved to be mainly additively inherited. It was also shown that there was an early phase of the apex development, a juvenility period, when the apex was unable to respond to the vernalization stimulus. The duration of this phase was shown to be genetically variable [135]. The vernalization requirements may be genetically reduced to zero. Such genotypes then behave as thermoneutral as their structure is constant whatever the temperature during the early seedling stages [30]. In *Lupinus angustifolius*, both quantitative and qualitative variations were found [100]. The qualitative variations were associated with the induced mutant recessive gene *efl* in which vernalization hastened flowering but did not appear to be essential, or the spontaneous dominant mutation *Ku* which suppressed the vernalization requirement [58]. Such a hastening of the flowering after seed vernalization with low temperatures was also observed in faba bean [46].

It should be noted that the physiological basis of the response to low temperatures for the transition of the apices from the vegetative stage to the floral stage has not been elucidated. Similarly, the receptors of the low temperature signals have not been identified.

In cowpea, after floral initiation, floral bud development may be suppressed by a combination of high night temperatures and long photoperiods [134]. Hall [67] showed that tolerance to heat-induced floral bud suppression was controlled by a single recessive nuclear gene.

4.3. Genetic variation in the response to light

Light massively influences the time of flowering and the expression of the floral stage. Three components must be distinguished.

The first component of the effect of the light is the amount of radiation which, through the photosynthesis, controls the production of assimilates and the growth. A reduction of the growth rate may slow down the rate of leaf appearance and then delay flowering. Such a reduction may be due to environmental conditions but also to modifications either genetically or environmentally induced of the leaf area.

The second component of the light which affects flowering is day length and most grain legumes species show a response to this parameter (*table I*). The species in which flowering is hastened by long day length are called long-days species.

The genetic control of the photoperiod response has been extensively studied in pea, a long-days species. Murfet [121] and Murfet and Reid [122] developed a stimulus model. Three genes, *Sn*, *Dne* and *Ppd*, confer a photoperiodic requirement (needs for long days) through the synthesis of a graft-transmissible signal while two other genes, *E* and *hr*, condition the expression of *Sn*, *Dne* and *Ppd*. On short days, this system acts as a floral inhibitor. In contrast, the gene *gigas* (*Gi*) in its dominant form acts as a floral promotor while its recessive allele

Table I. Grain legume species for which a photoperiod response of the flowering date have been identified.

Species	Type of response to photoperiod	Type of genetic variation	References
Arachis hypogaea	short-days	quantitative	[129, 204]
Cajanus cajan	short-days	quantitative	[111]
Cicer arietinum	long-days	quantitative	[151]
Glycine max	short-days	oligogenic	[81]
Lens culinaris	long-days	quantitative	[172]
Lupinus angustifolius	long-days	quantitative	[143]
Phaseolus vulgaris	short-days	quantitative	[191]
Pisum sativum	long-days	oligogenic	[121]
Vigna radiata	short-days	quantitative	[171]
Vigna subterranea	short-days		[106]
Vigna unguiculata	short-days	quantitative	[45]

induces an extreme delay in flowering. This gene could control the production of a flowering stimulus and show a strong response to vernalization. The recessive *fsd* mutant also delays flowering on long days but does not show response to vernalization. The balance between the floral promotor and inhibitor controls the floral signal. Flowering is provoked if this floral signal is higher than the stimulus level necessary for the apex to turn floral. The level of stimulus is controlled by the gene *Lf* for which a series of alleles (*Lf*^{d}, *Lf*, *lf*, *lf*^{a}) modifies the position of the first flowering node (15, 11, 8 and 5, for the allelic series) [120]. This model is illustrated in *figure 2*. Another gene, *Veg-1*, was shown to block a step before the floral initiation [146] as the mutant produces vegetative lateral branches at axillary sites occupied by inflorescences with flowers in the wild type. Two mutants behaving as *veg-1* were shown to be affected at another locus, *veg-2* [122].

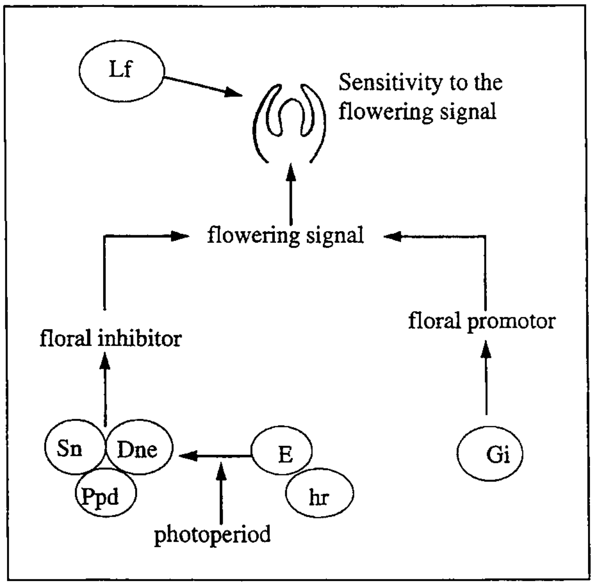

Figure 2. The major genes controlling the sensitivity of floral initiation and flowering to photoperiod in pea (from Lejeune-Hénaut [102]).

The effect of the photoperiod has also been studied in soybean, a short-days species. Five loci have been reported to control time to flowering and to maturity in soybean: E_1 and E_2 [11], E_3 [23], E_4 [24] and E_5 [110]. In all these loci, the dominant allele delayed the flowering and the maturity. Cober et al. [32] quantified the effect of the different alleles in near-isogenic lines and showed that, under a natural day length, which reached a maximum of 15.4 h in their experiments, E_3 and E_4 delayed flowering for 5 days and E_1 delayed flowering for 16 days. The delays are values when compared with the alternative early-flowering alleles. Under controlled conditions, Upadhyay et al. [183] reported that E_2 induced a response to photoperiod similar to that of E_3. These genes seem to affect the duration of the phase of photoperiod sensitivity which is longer with the dominant alleles.

These genes also have an effect on the duration of the pre-inductive period which is photoperiod insensitive [184]. A longer period of photoperiod insensitivity will delay flowering. On four genotypes, Collinson et al. [35] observed a variation in the duration of the insensitivity phase from 11 to 33 days at constant temperatures conditions of 30/20 °C day/night. Besides this continuous variation, a long-juvenile trait was also evidenced in soybean. It was shown to be controlled by a single recessive gene [141]. The possible interactions with the genes affecting the response to photoperiod have not yet been reported.

Common bean, *Phaseolus vulgaris*, was first shown to respond to short day length by Garner and Allard [55]. However, the genetics of the photoperiodic response was a matter for debate. The primary dominant gene responsible for sensitivity to photoperiod was named *Ppd* by Wallace et al. [192]. Some genotypes with the dominant allele *Ppd* show an increased sensitivity as a consequence of the presence of a second dominant gene which was assigned the symbol *Hr* by Gu [63]. However, the *Hr* allele little affects the flowering time in *ppd/ppd* plants [64]. White et al. [199] suggested the presence of a third gene called *Tip*, which could be allelic to either *Ppd* or *Hr* loci.

In *Vigna radiata*, the response to photoperiod was shown to be controlled by one dominant or partially dominant gene [175]. In *Vigna subterranea*, Linnemann [106] observed an effect of the photoperiod on the flowering time and Linnemann and Craufurd [107] revealed differences between genotypes, as only one among the three genotypes analyzed was responsive to photoperiod. Brink [22] found that the flowering time only depended on the temperature but that the time to podding was affected by the photoperiod. This post-flowering effect of the photoperiod was also observed on soybean [62] and groundnut [52]. Nevertheless, no information is available on a possible genetic variation for the response to photoperiod after flowering in these species.

It was further demonstrated that the genes controlling the response to photoperiod in soybean also showed different responses to light quality. Under a low ratio of red to far-red (R:FR) and long days, the flowering was delayed compared with normal light. E_1 was more sensitive than E_3, with E_4 in an intermediate position [33]. This would indicate that these genes, or some of them, could be part of the phytochrome family of genes.

4.4. Consequences on yield elaboration

The first possible consequence of the genetic variation in the time of flowering is the adaptation of the flowering date of a cultivar to the conditions of a region. It is important to start to flower when the weather conditions are optimum for the reproductive growth. This is why the manipulation of the flowering genes is so important in the adaptation of the soybean to different latitudes. The long-juvenility trait has been incorporated into soybean for adaptation to short-day conditions. In this respect, the genes controlling the response to day length and the juvenility phases show a much higher potential for an optimum tuning to a given environment and also for a reduced answer to the sowing date. Parvez and Gardner [132] demonstrated that, in a range of sowing dates at Gainesville, Florida, USA, or a range of day lengths under controlled conditions, the plant height and the number of nodes were more constant in the presence of the 'juvenile' trait. The effect of the trait also depended on the Maturity Group of the material as well as on the agronomic practices. The duration of the period from flowering to pod set was lengthened in Maturity Group IV while it was shortened in Maturity Group VI. The effect was more severe under early sowings (short day lengths) than under late sowings (long day lengths) in South Carolina (USA). The effect on the seed yield was highly significant with an increase of more than 40 % under early sowings for Maturity Group IV [179].

Changes in phenology have major impacts on the plant morphology and consequently on the yield elaboration. Through the study of isogenic lines which differed in flowering and maturity genes, Wilcox et al. [202] showed, in soybean, that the late flowering isolines had more leaves and were taller than the early flowering isolines but had similar stem growth and leaf initiation rates. As a result of their late maturity, the late flowering isolines had more reproductive nodes. Their branches contributed more to the total seed yield than those of the early flowering material (25 % versus 10 %).

In pea, Biarnès-Dumoulin et al. [17] reported that the early flowering expressed by the first flowering node was the main genotypic covariate that explained the genotype * environment interactions for seed yield in a trial with 10 genotypes and 12 environmental conditions. Variations in soil water availability during the flowering and the pod set may induce differential response of the genotypes to environmental conditions depending on their time of flowering.

In faba bean over 2 years and across a wide range of genetic variations for flowering time, Nachi and Le Guen [124] showed that the early flowering types were producing more biomass in the early parts of the cycle. There was no relationship for the end of the growth cycle.

5. BRANCHING PATTERN

The production of branches have been studied in most grain legumes. This trait is affected both by the genetics and by the environmental conditions during growth. It is very sensitive to the plant density.

5.1. Nutritional modifications of the branching pattern

In white lupin, for a given genotype, it was shown that the number of first-order branches was related to the number of mainstem leaves [86]. Munier-Jolain et al. [119] demonstrated that the number of branches of a given order was related to the plant growth rate at the beginning of the elongation of the pointed branch order. A similar effect may be due to a modification of the assimilate partitioning either induced by a modification of the structure of other plant compartments, following massive abortion of flowers or young pods or by the neighbourhood effect. This latter effect may be observed for a given genotype when changing crop density. The same physiological mechanisms may explain the variation in the branch number in the pea plant when manipulating the genes regulating the flowering time or the dwarfing genes [7]. It was also observed on some occasions that the contribution of the mainstem to the seed yield may be negatively correlated to the contribution of the branches [87].

5.2. Genetic modifications of the branching pattern

Besides these nutritional effects, some genes that directly modify the pattern of branching have been identified in grain legumes.

In pea, numerous *ramosus* mutants were found [7]. The loci *ram, rms1*, *rms2*, *rms3*, *rms4* and *rms5*, with several alleles for some of them, were identified and located on the different chromosomes [122]. In all cases, the recessive forms lead to more branches, produced either at the bottom of the stems or from the nodes all along the stems. Even when the mutants show similar branching patterns, they differ in their levels of production of growth regulators. Thus, *rms1* and *rms4* are characterized by low levels of root-sap zeatin riboside, while *rms1* and *rms2* show high levels of shoot auxins [16]. The *rms1* and *rms2* mutants increase branching through a graft-transmissible signal while the *rms4* mutation appears to promote branching by controlling physiological processes within the buds [15, 16].

In soybean, two independent genes, *Br1* and *Br2*, which modify the branching pattern, have been identified [125]. The dominant alleles induce the production of more branches at the upper positions, and their effect is more important in the determinate genetic background.

In white lupin, the number of first-order branches is modified by the presence of the gene controlling determinacy (see later) [92]. In the presence of the determinacy gene, less leaves are produced on the first-order branch compartment.

6. LEAF SIZE, STRUCTURE AND SHAPE

The size of each individual leaf influences the total leaf area and, therefore, is likely to influence the light interception efficiency of a canopy.

6.1. Genetic modifications of the leaf structure

Numerous mutants for the leaf form and structure were reported on pea and reviewed by Marx [109]. Some are monogenic homeotic mutations for leaf morphology. The afila recessive mutation (*afaf*) induces the transformation of the leaflets into tendrils, these types being called semi-leafless. In the stipuless recessive mutant (*stst*), the stipules are reduced to a vestigial structure similar to bracts [78]. The combination of the *af* and *st* mutations leads to the leafless structure. In the *acacia* mutation (*tltl*), leaflets occur at all leaflet positions on the leaf. This mutation was first described by Vilmorin and Bateson [189]. Villani and DeMason [188] demonstrated that the leaves of the double mutant (*afaftltl*) had less and smaller cells than the wild-type plants and that most phenotypic differences can be attributed to differential timing of major developmental events during leaf development. The tendrilled-acacia allele (*tac*) at the *uni* locus (named uni^{tac} by Murfet and Reid [122]) restores small leaflets to the tendrils of the *af* plants [158]. Goldman and Gritton [59] evidenced that the expression of the *tac* gene, in the semi-leafless genetic context, varied during the plant development as the *tac* leaflets contributed much more to the total leaf area above the first pod-bearing node than below this node (80 % versus 27 %). At the same *uni* locus, the allele *uni* reduces the leaf down to two stipules and one leaflet [122].

More mutations that affect the leaf structure have been observed in pea. The *rogue* mutation modifies the structure of the leaflets which are more narrow than on the wild type, both leaflets and stipules being in an upright position. The *coch* mutation modifies the structure of the stipules while the leaflets of the *apu* mutation are inserted on stalks [122].

In soybean, several genetic modifications of the leaf structure have been reported. The shape of the leaflet is modified with two genes, either to a narrow (*ln*) or to an oval (*lo*) shape. The soybeans have normally trifoliolate leaves. The number of leaflets may be genetically increased to five (Lf_1) or seven (lf_2) [49]. The combination of these two independent genetic systems leads to a high number of leaflets, up to 15. Genetic modifications affecting the pubescence were observed on soybean. The Pd_1 allele conditions dense pubescence (three to four times the normal number of trichomes) and is dominant over normal pubescence density, pd_1 [14]. The pubescence colour is conditioned by the *T* locus with *T* (tawny) dominant over *t* (grey) [131]. The *T* locus was shown to be associated with the E_1 locus involved in the control of flowering and maturity [34]. Takahashi and Asanuma [176] also reported an association between tawny pubescence and chilling tolerance, either because of a linkage between the *T* locus and a gene-controlling chilling tolerance or a pleiotropic effect of the *T* allele.

Modifications in leaf structure and size were also reported in *Cicer arietinum*. Argikar [6] reported on the monogenic recessive *alternifolia* mutant in which the number of leaflets was reduced to 5 to 9 compared with 11 to 15 in the wild type, the leaflets being in an alternate position. Pundir and Reddy [139] also found a similar mutation, the mean leaf area being reduced by 22 %.

In white lupin, Plarre [138] reported a mutant gene *mirus* which affected a group of characters. Among those characters, there is a modification of the leaf structure on the first leaves of the branches. The leaves are reduced down to a small bract but the internode structure is not modified.

6.2. Agronomic consequences of the leaf structure modifications

Following the variation in structure, the leaflets, stipules and tendrils contribute differently to the total leaf area depending on the foliage type. Goldman and Gritton [60] reported that at harvest in a normal foliage of pea, the stipules and the tendrils contributed 43 % and 15 % of the total leaf area, respectively, while in the isogenic *afila* they contributed 60 % and 40 %, respectively. These percentages were variable throughout the season. These authors also confirmed that the mean stipule area was larger in the *afila*-type foliage. When comparing leafless, semi-leafless and normal leafed pea in a non-isogenic context, Heath and Hebblethwaite [77] observed no difference in the attenuation coefficient of light interception between the different canopies, nor in the photosynthetic efficiency. In both dry and normal conditions, the photosynthetic area index (PAI) was reduced in the semi-leafless material (*afaf*) and even more in the leafless genotype (*afafstst*) (*figure 3*). In dry conditions, the leafless pea intercepted less light and produced less biomass because of a severely limited leaf area. In contrast, in the condition with a normal water supply, reduction of the leaf area with the *af* gene did not reduce the radiation interception efficiency. Consequently, in climatic conditions with risks of large plant development, the reduction of the leaf area with the *af* and *st* genes may reduce lodging and disease incidence and thus contribute to a higher seed yield.

In isogenic lines, the modification of foliage with the *af* gene affects the yield and the yield components depending on the genetic background, while the *st* gene seems to have a detrimental effect on seed yield [98], possibly due to a too extreme reduction of the leaf area index and thus a reduction of the light interception efficiency. In an isogenic

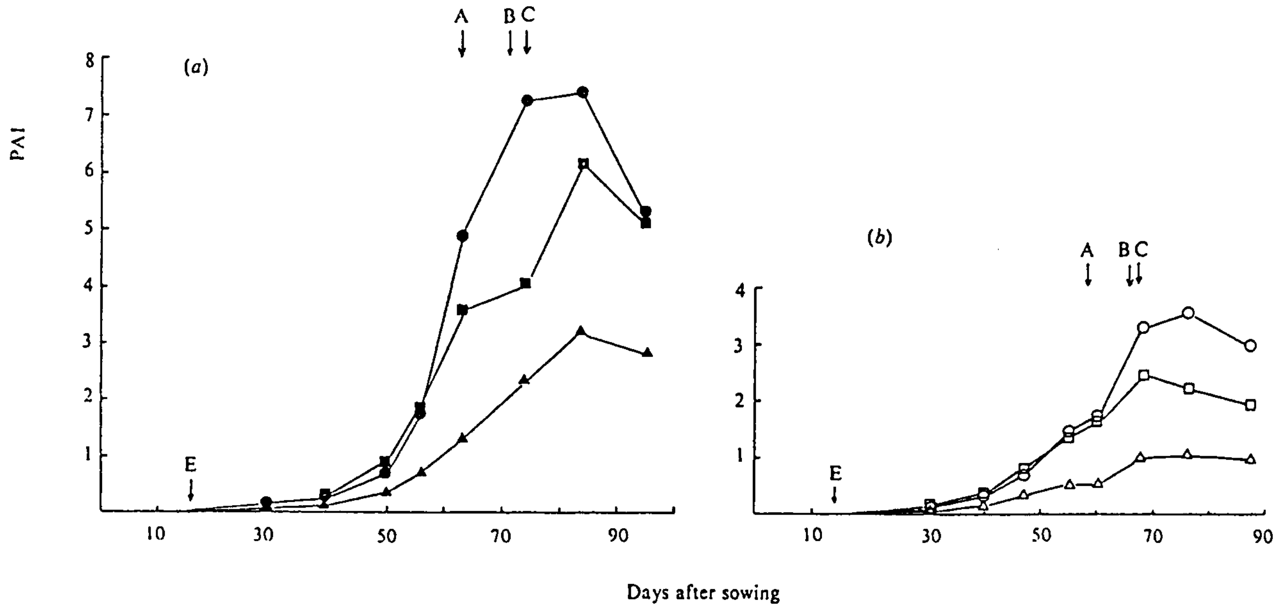

Figure 3. Photosynthetic area index (PAI) of pea crop canopies under normal water supply (*a*: Sutton Bonington, UK, 1983) and moisture stress (*b*: Bunny Park, UK, 1983). Genotypes with three foliage types were grown: leafed (Birte), ●, ○; semi-leafless (BS3), ■, □; leafless (Filby), ▲, △; E: emergence; A: flowering of BS3; B: flowering of Birte; C: flowering of Filby (from Heath and Hebblethwaite [77]).

context, under spaced plants grown in pots, Cardi et al. [27] showed that the number of seeds and pods per plant was higher for the structure with a larger leaf area, for instance *AfAf* was superior to *Afaf* and *afaf*. This ranking is likely to disappear in a dense canopy situation. Nevertheless, it should be noted that the harvest index was variable, and that the highest index was obtained with the *AfAf* genetic system. In field conditions, Moot and McNeil [116] demonstrated that modification of the leaf structure (leafed versus semi-leafless) had no significant effect on the seed yield response of the genotypes to variations in plant density. Both types were similarly highly susceptible to a strong increase in density. However, a selection for a different response to increasing density was possible in both types.

In soybean, the modification of the leaflet shape with the *ln* allele improved the light penetration into the canopy [80] but none of the modifications obtained with the alleles *ln* and *lo* had an effect on the seed yield [71]. However, increases in the number of leaflets to five (Lf_1) or to seven (lf_2) had a consistently negative effect on the seed yield whatever the genetic background [71].

7. DETERMINATE GROWTH HABIT

The determinate growth habit is a spectacular architectural modification in grain legumes. The word 'determinate' covers different situations. In the lupin species, it is expressed by the condition that, at a given time of the reproductive cycle, all the vegetative buds become floral, thus preventing further vegetative growth through the production of additional branch orders. It contributes to separate the vegetative and the reproductive phases during the plant cycle. In soybean, faba bean, bean and pea, the determinate growth habit is expressed by the floral stage of the stems. This may then induce the production of branches at different locations along the stems. As a result, the vegetative stage may become longer than in the indeterminates. The determinate mutation has been found in most grain legumes, either after spontaneous mutations or after induced mutagenesis.

7.1. The genetics of the determinate growth habit

In soybean, two genes are involved in the control of the determinate growth habit. The gene pair *Dt1dt1* was first identified by Woodworth in 1933 [203]. Bernard [12] when studying intermediate stem type, proved that a second gene, *dt2*, was also involved. The dominant allele of *Dt2* conditions a semi-determinate growth habit. The locus *dt1* is epistatic to *Dt2*, with *Dt2* only expressed in the presence of *Dt1*, and masked in the presence of the homozygous *dt1dt1*. Thompson et al. [178] found a third allele at the *Dt1* locus, named *dt1-t*, which reduced the number of nodes less severely than the allele *dt1*: 16.9, 11.5 and 20.3 for *dt1-t, dt1* and *Dt1* in isogenic lines, respectively.

In faba bean var. *minor*, determinate mutations *ti-1* and *ti-2* were reported by Sjödin [168]. These mutations dramatically reduced the number of flowering nodes after the onset of flowering and are often referred to as topless mutations. A determinate mutation, under recessive monogenic control, was reported in *Vicia faba* var. *major* by Filipetti [50]. There is no report whether this mutation is similar to one of those reported by Sjödin [168].

In pea, Swiecicki [174] reported that the gene *det* confers a determinate growth habit and also appears to force a more precocious development of the flower buds into mature flowers. However, the *det* plants were shown not to be determinate in the botanical sense since the so-called terminal inflorescence arises from the development of an axillary bud rather than the terminal meristem, which ceases to grow [162].

In the different lupin species, many determinate mutants were reported either from spontaneous mutations or from induced mutation programmes. In *L. albus*, Mikolaczyk et al. [114] reported a monogenic recessive mutation, *epl*, in an early flowering spring-sown genotype. The mutant had no branches, a flower or a small inflorescence being produced at the axil of the last leaves. This mutation was transferred by crosses into an autumn-sown genetic background. The plant structure was then very different, with numerous short primary branches. The plants became determinate after the production of one or two orders of branches. In the presence of the determinate allele, the upper first-order branch carried no leaf [92].

Similarly, monogenic recessive mutations for determinate growth habit were detected in *L. mutabilis* [152] and *L. luteus* [180]. In *L. angustifolius*, several mutations were detected, controlled by either a monogenic recessive or monogenic dominant gene [113]. A determinate type which was selected by Forbes in the United States in 1965 resulted from a natural mutation that appeared to be incompletely dominant [57].

In *Phaseolus vulgaris*, three distinct plant growth habits have been described by Singh [164]. According to this classification, type I refers to a determinate growth habit. In this species, the determinate growth habit has been reported to be controlled by a single recessive gene [9].

In chickpea, a determinate growth habit was first reported by van Rheenen et al. [187] after a mutagenesis programme. The determinate character was under a digenic control.

7.2. Agronomic consequences of the determinate growth

Because of its major impact on the growth, a lot of effort has been devoted to the analysis of the impact of this architectural modification on the yield. However, the analysis of the results is not always easy. The study of the effect of the determinate growth habit in isogenic lines may be misleading for the agronomic potential of the determinate character. Indeed, the genetic background or phenological characteristics may be optimum for the indeterminate growth habit and suboptimum for the determinate growth. Similarly, the optimum agronomic practices for one type of architecture may not be optimum for the other.

7.2.1. Effect on canopy structure and crop maturation

The determinate growth habit leads to a severe reduction of the plant growth with a reduction in the number of nodes and leaves and in plant height.

The determinate growth habit also makes possible an earlier maturation. Milford et al. [115] observed that a determinate autumn-sown genotype of white lupin matured up to 6 weeks before an autumn-sown indeterminate genotype. On *Phaseolus vulgaris*, White et al. [198] reported a 4 to 5 day earlier maturation for the determinate genotypes for trials carried out at three locations with different elevations in Colombia. In soyabean Green et al. [61] showed that the semi-determinate types, based on the *dt2* allele, matured, on average, 2 days earlier than their indeterminate counterparts.

In the case of white lupin, the determinacy strongly modified the distribution of the leaves on the first-order branches [92] as well as the relationship between the structure of the mainstem and of the first-order branches [86]. In faba bean, Singh and Schroeder [166] demonstrated that the determinate forms produced more tillers than their indeterminate counterparts.

Because of the modifications in the number of leaves and nodes, the leaf area index is generally much lower in the determinate genotypes. This was observed in the faba bean by Pilbeam et al. [137] even if, at its maximum, the leaf area index made it possible to intercept all the incident light. However, whatever the plant density, the threshold for intercepting all the incident light was generally reached later and the duration of maximum interception shorter. As a consequence, the total biomass is generally lower in determinate canopies than in indeterminate canopies for both the faba bean and white lupin [94, 124, 137]. Besides modifying the total light interception, the determinacy also modifies the penetration of light into the canopies. This may lead to a variation in the photosynthetic activities of the different organs. Koscielniak et al. [96] reported, in field conditions, a larger contribution of the pods to the total photosynthesis in the determinate types of faba bean than in the indeterminate types (13 % versus 6 %).

7.2.2. Effects on yield, yield stability and seed composition

Numerous papers have reported results of yield trials comparing the performance of determinate and indeterminate genotypes. *Table II* summarizes the data on four grain legumes. The location, type of material under comparison and seed yield as well as the significance of the differences are given.

There is no general trend to conclude an advantage of one type over the other. In the United States, the indeterminate early flowering genotypes tend to perform better in the northern areas with short-growing season, whereas the determinate late flowering genotypes tend to yield better in the long growing season of the south. The poor performance of the determinates in the short season is associated with their very short stature, which is likely to result in the low height of the lowest pods and thus difficulties at the harvest as well as plants with a limited vegetative development. However, Cober and Tanner [31] noted that the tall determinate selected in early maturing material may outyield their indeterminate counterparts, depending on the environment. Thus, the genetic background as well as the other architectural features must be adapted to get the optimum expression of the determinacy.

In addition to the level of yield, yield stability is a major agronomic component. In autumn-sown white lupin, Julier et al. [94] found that, over a wide range of agronomic conditions, the determinate genotype under study tended to show a more stable seed yield than the indeterminate genotype. In *Phaseolus vulgaris*, Kelly et al. [95] showed that the determinate types were more unstable than the indeterminate cultivars while White et al. [198] reported that on isogenic lines that the determinates were more stable. According to the behaviour of additional genotypes in White's experiments, the stability seems to be genotype-dependent more than architectural type-dependent.

Table II. Seed yield (t·ha^{-1}) comparison between determinate and indeterminate genotypes in grain legumes.

Plant material	Yield			Location	Reference
	I	SD	D		
Glycine max					
Early flowering material					
15 I and 15 D in 3 crosses	3.4		2.9*	Ohio (USA)	[1]
2 D, 2 SD, and 2 I	4.0	3.8	4.2	Ontaria (C)	[2]
21 I and 21 D in 3 crosses	2.6		2.5	Minnesota (USA)	[53]
8 D, 3 SD and 8 I	3.0	3.0	3.0	Illinois (USA)	[10]
3 D and 3 I	3.3		3.7	Toulouse (France)	[19]
1 pair of isogenic lines	2.3		3.5*	Toulouse (France)	[177]
1 D, 1 SD and 1 I	4.8	4.7	4.6	Toulouse (France)	[26]
35 pairs of near-isolines	2.2		2.2	Ontario (C)	[31]
Intermediate flowering					
40 SD and 40 I in 3 crosses	3.9	3.7		Indiana (USA)	[200]
3 pairs of isogenic lines	4.8 [a]		4.7 [a]	Maryland (USA)	[195]
114 pairs of isogenic lines	3.3		3.3	Iowa (USA)	[28]
Late flowering material					
2 D and 2 I	2.6		3.0*	Alabama (USA)	[194]
Lupinus sp.					
1 D and 1 I (*L. angustif.*)	1.2		1.5	Australia	[18]
1 D and 1 I (*L. albus*)	3.0		3.3	France and UK	[94]
Phaseolus vulgaris	I		II or III		
4 D and 8 I	1.7		1.5	Colombia	[138]
5 pairs of isogenic lines	1.4		1.4	Colombia	[198]
14 D and 14 I	2.5		2.1*	Michigan (USA)	[95]
Vicia faba					
51 D, SD and I	3.7 [a]	6.4 [a]	7.1 [a]	Germany	[166]
1 D and 1 I	5.5		3.1*	UK	[136]
1 D and 1 I	5.5		3.8*	Germany	[170]
3 D and 4 I	3.3		2.8*	Syria	[161]

The numbers of genotypes upon which the comparisons are based are given. D: determinate genotype; I: indeterminate genotype; SD: semi-determinate; for *Phaseolus vulgaris*: I: determinate; II: erect indeterminate; III: prostrate indeterminate. * Significant difference ($P < 0.05$). [a] Seed yield calculated from yield per plant and plant density.

The difference in seed yield elaboration must be investigated, especially because of the modification of the within-plant competition. Julier et al. [93] observed that in white lupin while in the indeterminate genotype, the whole reproductive phase was simultaneous to vegetative growth, the period of competition was extremely short in the determinate genotype (*figure 4*). Egli and Leggett [44] noted that, at the beginning of flowering, a determinate soybean line produced more of its total vegetative material than the indeterminate genotype. This also illustrates a reduced competition between the vegetative and the reproductive growths in the determinate line. When the use of the determinacy results in plants with a very restricted vegetative phase, the potential of biomass production after the onset of

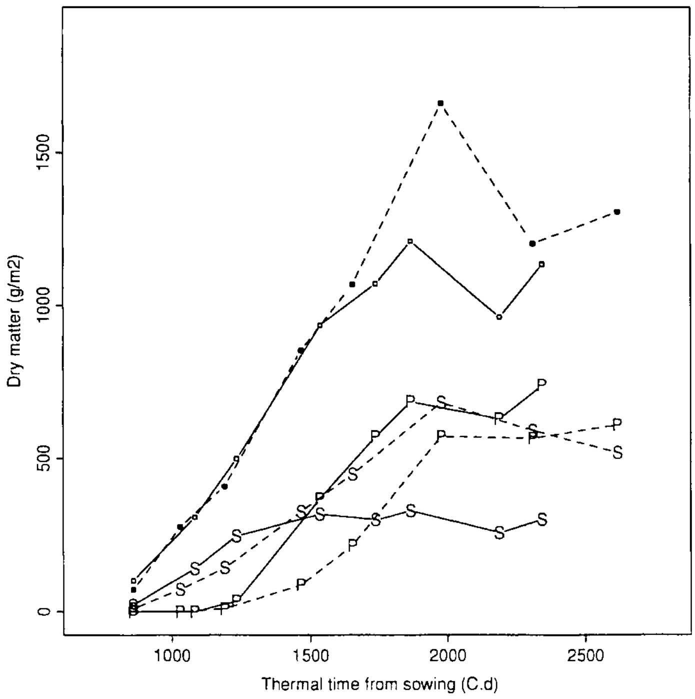

Figure 4. Overall (□, ●), pod (P) and stem (S) dry matter during the growing season in a determinate genotype (—□—) and an indeterminate genotype (----●----) of autumn-sown white lupin (from Julier et al. [93]).

flowering is too low to achieve high yield. This holds true for most grain legumes and may explain the differential response of the determinates and indeterminates to different planting pattern. Indeed, the vegetative development of the determinate soybean genotypes will better valorize equidistant planting patterns as this will allow the production of biomass to be maximum at or soon after flowering [43].

The effect of the determinacy on the grain composition has been investigated in soybean. Wilcox and Guodong [201] demonstrated that the seed protein concentration of the grains were similar in the determinate and indeterminate populations selected in two crosses. While there was no significant relationship between seed yield and seed protein concentration among the determinate lines, this relationship was negative among the indeterminate lines.

8. DWARFISM

Dwarfing genes are commonly used in numerous grain crops and particularly in cereals. Architectural modifications due to dwarfing genes have been reported in different species of grain legumes.

8.1. Genetics of dwarfism

In pea, 15 loci with more than two alleles for some of them are involved in internode length (*table III*). Mutations at 11 of these loci result in short internodes [97]. Some of these mutants have short internodes because of a deficiency in the level of endogenous gibberellic acid (GA): *le*, *na*, *lh*, *ls*. They are called synthesis mutants [145]. In those mutants, the application of exogenous GA restores the normal internode length. In such cases, the different expression of dwarfism due to different alleles correlates with

Table III. The different genes which modify the internode length in pea in chronological order.

Genes	Gene action	References
Le	GA synthesis	[112]
La	GA response	[39]
Cry	GA response	[140]
Lm	GA response	[105]
Na	GA synthesis	[196]
Lh	GA synthesis	[144]
Lk	GA response	[144]
Ls	GA synthesis	[144]
Lw	Photomorphogenic	[91]
Lv	Photomorphogenic	[147]
Lka	GA response	[148]
Lkb	GA response	[148]
Lkc	GA response	[149]
Lkd	GA response	[37]
Sln	GA synthesis	[150]
Lip1	Photomorphogenic	[54]
Igr	GA response	[122]

GA: gibberellic acid.

endogenous GA_1 levels but not with the overall GAs present in the plant [88]. This is the case for the alleles *lh* and lh^i [173] and for *le* and le^{5839} [154]. The *Le* gene was shown to encode a gibberellin 3β-hydroxylase which converts GA_{20} to the bioreactive GA_1. The reduced activity in the *le* mutant was associated with an alanine to threonine substitution in the amino acid sequence of the enzyme [104]. The sites of action associated with the *ls*, *lh* and *na* genes on the GA biosynthesis pathway were also identified [145].

Another group of mutants, *lk*, *lka*, *lkb*, *lkc* and *lkd*, does not appear to be deficient in GA but shows a reduced response to applied GA. The mutations in these five loci impair some functions in the stem elongation transduction pathway. They are called sensitivity mutants. Three more mutants, *lw*, *lv* and *lip1*, demonstrated a photomorphogenic response for the internode elongation [122].

In soybean, six genetic systems which affect internode length have been reported: *df1* by Stewart [169], *df2* selected from the variety Lincoln, *df3* selected from the variety Adams [25], *df4* selected from the variety Hark [49], *df5* [130] and *df6* [197]. While in the first five the allele for dwarfism is recessive, the allele for dwarfism at the *df6* locus is codominant. An allelic series (*S*, *s*, *s-t*) which modifies plant height by altering internode length without modification of the internode number was also reported by Bernard [13]. Besides these genetic systems which are referred to as dwarf, other mutants which show modifications in the internode length but without modifications of the leaf area have been described in soybean. The 'brachytic' mutation was noted by Boerma and Jones [20] to be controlled by two independent recessive genes, *sb1* and *sb2*.

In white lupin, Harzic [72] reported two different types of mutants. In XA100, the dwarf progenitor obtained in the autumn-sown genetic background after a mutagenesis programme, the dwarf character is under the genetic control of two recessive genes. This mutant was shown to be a synthesis mutant [75]. In a spring-sown spontaneous mutant, a monogenic recessive control was observed.

In *Vicia faba* var. *minor*, four different genes were reported to induce dwarfism: *dw1* found by Bond in the cultivar Compacta, *dw2* a spontaneous mutation found at Svalof (Sweden), *dw3* a spontaneous mutation found in the line HG115C and *dw4* found in the cultivar Fribo after mutagenesis [29]. The *dw1* mutant is responsive to the application of exogenous GA [186]. An induced dwarf mutant was found by Filipetti [51] in *Vicia faba* var. *major*. No information exists whether this mutation is similar to one of those reported in var. *minor*.

In *Phaseolus vulgaris*, dwarfism was observed at the hybrid level after crosses between the Andean and Mesoamerican gene pools. This dwarfism affects the internode length as well as the structure of the reproductive organs. It was shown to be controlled by two complementary dominant genes *DL1* and *DL2* [165]. This dwarf-lethal incompatibility in intergene pool crosses was later confirmed by Mumba and Galwey [118].

Different dwarf mutants were reported in lentil after mutagenesis treatment by Sharma and Sharma [159], Dixit and Dubey [40] and Tyagi and Gupta [182]. The inheritance of these mutations have not been analyzed. In all cases, the mutants showed a very poor fertility.

Dwarfism was reported in chickpea by Athwal et al. [8] and Singh and Dahiya [163]. Sandhu et al. [156] after mutagenesis found a dwarf mutant different from the previously reported mutations and controlled by a single recessive gene, *pt*. This genetic control was in agreement with the report from Dahiya et al. [38].

Dwarf mutants were also found in pigeon pea (*Cajanus cajan* (L.) Millsp.). Saxena et al. [157] observed that one locus was involved in the control of dwarfism and evidenced two alleles inducing dwarfism at this locus.

Internode length may be affected by the pleiotropic effect of other genetic systems. Thus, Ismail and Hall [89] showed on cowpea that the heat-tolerance genes had a progressive dwarfing effect due to shorter mainstem internodes and this involved a reduced shoot biomass production.

8.2. Agronomic effect of dwarfism

8.2.1. Effects on the canopy structure

The first impact of the dwarfing genes is the reduction of plant height. It is especially important in pea, where, in the absence of dwarfing genes, the intensive cultivation of peas for grain production would be impossible. However, little information is available on the agronomic effects of the different genes found in *Pisum sativum*.

Dwarfing genes were often reported to have a pleiotropic effect on other characters than the internode length. They may influence the branching pattern because of modifications in the assimilate partitioning, as reported in peas by Arumingtyas et al. [7] for the genes *le* and *na* which increase the numbers of branches.

In soybean, whatever the genetic system, except the *s* system, the dwarfism also affects the internode length as well as the leaf size. For instance, with the *df6* system, the individual leaf size is reduced by 80 % due to a 76 % reduction in the individual cell size. The internodes were also 55 % shorter [197]. The subsequent effects on seed yield per plant and mean seed weight may be attributed to a severe reduction in the plant leaf area. With the ‘brachytic’ mutation, the internode length is reduced by 37 % and the number of nodes is only reduced by 5 % [101].

In white lupin, it was shown that the presence of the dwarfing genes from the mutant XA100 reduced the internode length by 41 % on the mainstem and by 22 % on the primary branches [73]. However, this form of dwarfism does not modify the number of leaves on the different organs nor the individual leaf size. Consequently, the efficiency of radiation interception throughout the growth cycle was not affected by the presence of dwarfism.

In faba bean, in the presence of the *dw1* mutation, the internodes were 50 % shorter than those of the wild type [186].

In lentil, the dwarf mutants had their internode length reduced by 62 to 67 % [40, 182].

8.2.2. Effect on seed yield

In soybean, the seed yield is very negatively affected for the *df* genetic systems which severely reduce the individual cell size. Lee et al. [101] showed that the ‘brachytic’ mutation had no negative effect on the seed yield even if the yield stability of the ‘brachytic’ lines seems to be reduced in conditions that were not prone to lodging.

In white lupin, the pattern of assimilate partitioning was modified by the presence of dwarfism. In the dwarf mutant, Harzic et al. [74] demonstrated that more assimilates were allocated to the pods and less to the stems than in the nondwarf control, both types being indeterminate autumn-sown genotypes (*figure* 5). The difference in the allocation pattern between the dwarf and the nondwarf was consistent over years but small. No difference in seed yield was observed at the harvest. This was further confirmed by the similar seed yield measured on seven near isogenic pairs in the autumn-sown genetic background [73]. However, when studying a wide range of dwarf genotypes, Harzic et al. [76] found that the seed yield may become negatively affected if the plant height is too severely restricted.

In faba bean, the effect of the dwarfing gene *dw1* was analyzed. Along with a positive effect on the lodging tolerance, the dwarf lines had a seed yield 15 to 18 % higher than the control and also a higher protein content [186]. However, there has been little use for this mutation in breeding since then, possibly because the effect on the plant structure was too dramatic.

9. MODIFICATION OF THE STRUCTURE OF THE PODS

The pods of the grain legumes are very fleshy. They are able to photosynthesize when fully exposed to light. This feature was reported on white lupin [133], pea [108] and chickpea [160]. Most of the assimilated carbon was rapidly exported to the seeds. However, this feature contributes little to seed carbon nutrition because the fruits are shaded into the grain legumes canopies. The thick pod

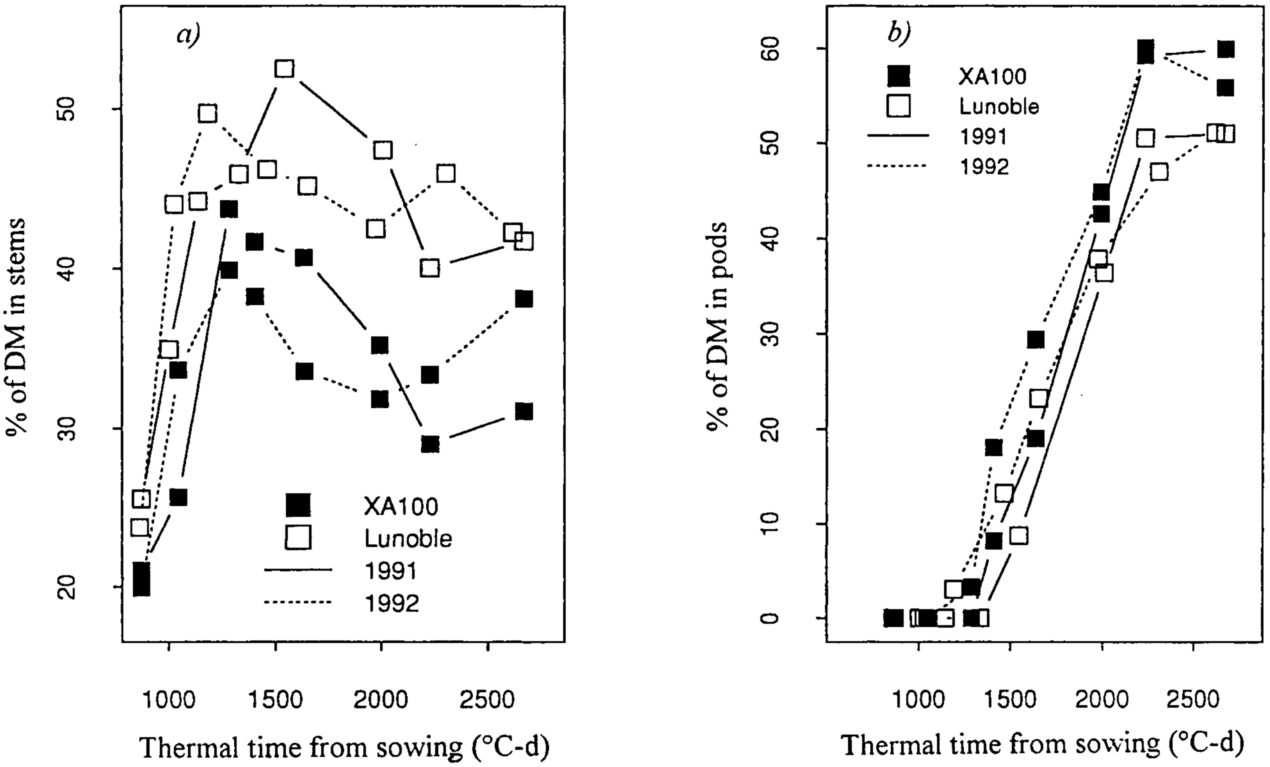

Figure 5. Proportion of dry matter in stems (*a*) and pods (*b*) of a dwarf (■) and a nondwarf (□) autumn-sown white lupin genotypes over 2 experimental years (from Harzic et al. [74]).

walls may contribute to the C and N metabolisms of the pod and the grains through reallocation during the seed filling. However, at maturity, a large amount of the reproductive biomass may be stored in the pod walls. Consequently, the harvest index of the crop may be low because of the low harvest index of the reproductive compartment itself. Despite its metabolic importance and possible impact on the harvest index, little attention has been paid to the structure of the pod walls and pod wall proportion in grain legumes.

9.1. Genetic variation in pod wall proportion

The different grain legume species behaved very differently in regard to gene variation in pod wall production. *Table IV* summarizes the data on the pod wall proportion observed on the different species of grain legumes. The lowest proportions were observed for peas, with the highest being for *Lupinus mutabilis*.

Few papers have investigated the possible genetic variation in the pod wall proportion. Wallace and Munger [191] noted that, in *Phaseolus vulgaris*, there were differences between genotypes for the pod wall proportion, from 20 to 27 % of the pod biomass at harvest, and that this variation was associated with seed yield variation, the highest yielding variety showing the lowest pod wall proportion. A much larger variation was observed on *Lupinus angustifolius* (23 to 38 % among 83 cultivated lines [142]) and on *Lupinus albus* (20 to 43 % among 365 accessions; Lagunes-Espinoza, unpublished data). It may be expected that a large genetic variation exists in most grain legumes species and that it has

Table IV. Proportion of pod walls observed in different grain legumes.

Species	Proportion of pod walls (% pod biomass)	References
Cicer arietinum	24	Lagunes-Espinoza (pers. comm.)
Glycine max	25.8	[56]
Lathyrus sativus	32	Lagunes-Espinoza (pers. comm.)
Lens culinaris	31	Lagunes-Espinoza (pers. comm.)
Lupinus albus	33	[142]
Lupinus angustifolius	34.5	[42]
Lupinus luteus	46	[142]
Lupinus mutabilis	45–51	[70]
Phaseolus vulgaris	20–27	[190]
Pisum sativum	13	[142]
Vicia faba	19	[21]
Vigna unguiculata	31	Lagunes-Espinoza (pers. comm.)

little been exploited in breeding. The case of pea may be different because of the low proportion of pod walls in the presently available cultivars. This may be the result of a long process of human selection for grain production.

9.2. Possible consequences on seed yield

Beyond a direct modification of the yield because of a modification of the reallocation pattern within the pods, it may be speculated that a reduction of the pod wall proportion through breeding could modify the early growth of the pods. In the early growth of the pods, the pod walls contribute to a large proportion of the pod weight. They reach their maximum dry weight at the time when the growth rate of the pod is maximum, thus when the number of pods that a plant can feed is minimum. It must be noted that this time also corresponds to the stage identified as the final stage of seed abortion. If the reduction of the pod wall proportion ends in a reduction of their dry weight throughout the pod cycle, the number of pods which the plant can feed could be increased. This could substantially contribute to an increase of the seed yield potential. Among the white lupin material under breeding, this trait was shown to be genetically correlated to the seed yield ($r = -0.59$), was heritable and showed little genotype * environment interaction [99].

The association between low pod wall proportion and high seed yield reported by Wallace and Munger [191] should be handled with care in *Phaseolus vulgaris* as, in this species as well as in pea, there has been a selection for the proportion of pod wall when these grain legumes were bred for the production of green pulses eaten as vegetables. However, the selection for high seed yield has likely contributed to a reduction of the pod wall proportion in the varieties used for grain production. It would be necessary, however, to investigate the possible consequences on the seed quality and especially the protein content of the grains, which is the main interest of the grain legume crops.

The genetic modification of the pod wall proportion through a modification of the pod structure offers new prospects for the increase of the seed yield because of modification of the plant structure. This may be potentially more important for species with large pod walls.

10. CONCLUSION

In many species, the genetic manipulation of the crop architecture either through the modification of the structure of plants or of the phenological stages was effective in improving the yield potential and the adaptation to a given type of environment. Architectural characters may also be combined to achieve this goal. Dwarf determinate in white lupins or combinations between determinacy and flowering genes in soybean are examples of such combinations. The approach mainly applied on the vegetative structure may now be extended to the reproductive compartment where major prospects for genetic modifications and improvements exist. Consequently, both yield potential and stability may be improved with modifications in crop architecture. These modifications create a new genetic background where the selection may take place. The breeding programmes must then be designed to increase the genetic variability within the optimized architecture and then to carry out a selection for the targeted agronomic objectives in this material.

The architectural modifications may, in most cases, contribute to reduce the vegetative development of the crops and increase the assimilate partitioning towards the reproductive growth and the grains. In this sense, the architectural modifications contribute to a further domestication of the grain legumes. The reduction of the vegetative development also leads to a reduction for the plant to compensate for low plant density or heterogeneous spatial distribution. It is then essential to optimize agronomic practices (sowing date, sowing density, row spacing, but also weed and disease control).

Some of the architectural modifications have been tagged with molecular markers, random amplified polymorphic deoxyribonucleic acids or restriction fragment length polymorphism. In the species for which a genomic map has been developed, some of the genes have been located. However, a lot of work remains to be done in the molecular biology of the architectural modifications. It would first be necessary to achieve a better understanding of the physiological pathways involved in these modifications. This is currently done for the characters such as dwarfism. A species such as pea is a model plant for the understanding of this character because of the number of mutants identified for the internode length. The physiological and molecular basis of the determinacy is still questioned, however. It would also be of interest to analyze the similarity among species of the genetic systems involved in a given architectural modification, as well as the similarity of the genome localization of the mutations.

All the research carried out on the modifications of crop architecture are based on the hypothesis that the change in structure is prevalent to the intensity of the function. For instance, modification of leaf size has more effect on leaf photosynthesis than that of the photosynthetic activity per unit of leaf area. This heavy assumption is likely true for the massive modifications, such as those which discard one of the plant compartments. However, it is not always so clear. It could be questioned whether modifications of the functions could result in architectural modifications. Two examples may illustrate this question. We recently found among the dwarf determinate autumn-sown white lupin material a genotype which behaves like the determinate, i.e. it stops its vegetative growth after one or two orders of branches, but does not carry the determinacy gene. Either an unknown architectural modification contributes to this feature or some of its physiological functions make it impossible for its vegetative structure to develop beyond those two orders of branch. Another example is the modification of the profile of pod distribution along the stem of the pea crops. Breeding for higher yields has resulted in genotypes for which, under a dense canopy, a higher proportion of seed yield is obtained on the first nodes. This also results in an architectural modification, as the number of nodes produced on the plant is reduced. The identification and manipulation of the physiological functions could be beneficial for an increased rate of genetic gain. However, the major difficulty of this approach is to identify the physiological functions that are involved. If the architectural modifications are in most cases discrete, the physiological functions are in most cases quantitative and show a continuous range of variation. There are few experimental results presently available.

Genetic modification of the crop architecture can then be considered as a first step in the optimization of the plant – possibly the easiest step since it uses highly heritable traits as selection criteria. The next step for the breeders will then be to combine both architectural and physiological criteria in the breeding programmes. An example of such a combination was given by Acosta-Gallegos and White [3] in *Phaseolus vulgaris,* who identified plasticity for the flowering date under a range of sowing dates. This plasticity, which was genotype-dependent, may be combined with genetic control for response to photoperiod.

The screening for physiological response will require the development of new screening strategies. However, this approach combined with the architectural modifications will make it possible to finely tune the plants for their responses to the environment and the agronomic practices in order to maximize the adaptation, the seed yield as well as grain quality. This approach will be facilitated by a better understanding of the processes and intense collaboration between the different disciplines of plant research.

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