

## Crop physiology and productivity

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### Abstract

This paper reviews aspects of crop physiology and productivity for selected grain legumes. Vegetative development, including phases of leaf area increase and branching are described, then, the main reproductive stages and their progression along the stem are discussed. The effects of water and nitrogen shortage on reproductive development are briefly described. A model for reproductive development along a stem is proposed and applied to several grain legumes, and effects of genetic variability are discussed. Growth, and its analysis in terms of intercepted radiation and radiation use efficiency are then reviewed. The variability of these two components is analysed according to differences due to species, genotypes (mainly characterized by different foliage structures), environmental conditions and methods of measurement. Yield is then analysed as a direct consequence of crop growth. Finally, a pattern of assimilate partitioning is described, and its consequences for reproductive structure formation, i.e. the grain number on each node of the stem, are discussed. © 1997 Elsevier Science B.V.

*Keywords:* Grain legume; Development; Growth; Assimilate partitioning; Yield determination

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### 1. Introduction

Yields of grain legumes are smaller and generally more variable than those of many other crop species. In developed countries, grain yields of legumes have not increased as rapidly as those of cereal crops. Between 1940 and 1981, for instance, winter wheat yields in the UK increased at approximately twice the rate of those for pea and faba bean (82, 44 and 31 kg ha<sup>-1</sup> year<sup>-1</sup>, respectively) (Heath and Hebblethwaite, 1985a). In France, between 1981 and 1996, yield increases were 75 kg ha<sup>-1</sup> year<sup>-1</sup> for pea and 120 for wheat (Carrouée, 1996). There is thus a need to increase the performance of pulse

crops, particularly in developing countries, where most grain legume production is for human consumption and demand is increasing due to population increase. Oram and Agcaoili (1992) estimated that yields in developing countries were only 45% of those of developed countries for pea, and 75% for faba bean and chickpea.

The agronomic problems associated with pulse crops differ between geographical areas. In the Asia–Africa–Oceania regions (Johansen et al., 1992), North America (Slinkard et al., 1992), and Europe (Monti et al., 1992), drought and biotic stresses appear to be the major limiting factors, while other stresses (such as extreme temperatures and nutrient deficiencies) have less frequent impact. Drought and biotic stresses can be alleviated in various ways, for example by breeding or crop management. Although resistance cultivars can be bred to combat diseases,

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often with time pathogens evolve to overcome the resistance. Irrigation and fungicidal sprays are not always available in developing countries to prevent drought or control foliar diseases.

Another approach is to escape stress. Damage due to drought can be reduced if the period of crop sensitivity does not fall in the period of water deficit (Ney et al., 1994). This type of approach requires an improved understanding of crop physiology and of plant responses to environment. This chapter reviews current knowledge of phenology, growth and of plant structure determination, and their consequences on yield formation.

## 2. Development

### 2.1. Vegetative development

#### 2.1.1. Plastochron

For pea and many other species, successive nodes are initiated in the apex at a constant rate throughout the crop cycle, the plastochron, calculated in cumulative degree-days (Lyndon, 1977; Dracup and Kirby, 1993; Jeuffroy, 1991; Lecoeur et al., 1995), with 0°C as a base temperature (Etévé and Derieux, 1982). Thermal time units have been widely used to describe the progress of crop development in legumes and other crops (Wilhelm and McMaster, 1995). Although other factors, such as daylength, soil compaction and nitrogen nutrition also affect the rate of leaf emergence, their influence is minor (Kirby, 1995). The end of nodal initiation varies according to the situation, but the final number of initiated nodes is, at least in the situations observed, greater than the final number of visible nodes (Lecoeur, 1994; Jeuffroy and Sebillotte, 1997).

#### 2.1.2. Phyllochron

Development of successive nodes along a stem is also constant throughout the vegetative stage in cumulative degree-days, determining the phyllochron (Leong and Ong, 1983, for peanut; Truong and Duthion, 1993, for pea). This rate is enhanced following floral initiation (Lecoeur, 1994). Variation of pea leaf appearance rate in the field is due to differences in mean temperature and plant growth rate (Truong and Duthion, 1993).

#### 2.1.3. Leaf growth and leaf area

Individual leaf area depends on cell number and cell size. The changes with time of cell number and leaf area for individual leaves of pea (*Pisum sativum* L.) show two distinct and successive phases: phase 1, during 2/3 of leaf development, involves cell division, while phase 2, during the last 1/3 of leaf development, involves cell expansion (Lecoeur et al., 1995). The effects of water deficit on leaf area have been studied at different periods in the leaf life. Early deficit during phase 1 reduces leaf area through an effect on cell number, while deficit during phase 2 reduces leaf area by reducing cell area (Lecoeur et al., 1995). These results suggest that long-term temporal analysis may be necessary to study dicot leaf expansion, whereas spatial analysis is more effective for monocot leaves. A scale was proposed by Maurer et al. (1966) to describe the macroscopic development of a pea leaf.

#### 2.1.4. Branching

Branch number in leguminous plants is highly variable, and is an important determinant of grain yield. Low plant densities can be compensated by substantial branching (Hedley and Ambrose, 1981). Plant structure varies among cultivated grain legumes. Pea and soybean branches appear mainly on the first vegetative nodes, whereas white lupin produces branches at the top of the main stem. For lupins, several orders of branches develop sequentially as described by Farrington and Greenwood (1975), but branches of the same order develop synchronously. Branching capacities vary among genotypes. Genotypes with greater branching ability generally have more determinate habits, probably because of the competition between branches in the canopy.

Branching is also strongly influenced by environmental conditions such as soil physical conditions or soil water status (Dawkins et al., 1984). Environmental conditions can modify the contributions of branches to final yield (Duthion et al., 1994, for white lupin). The potential number of branches of a given order on white lupin depends on the number of axillary buds on the stems of the previous order. The number of branches produced is linked to the plant growth rate at the beginning of branch elongation (Munier-Jolain et al., 1996a).

The branching pattern of peanut has been described by Gupton et al. (1968) and Bunting et al. (1985). The first lateral branches appear at about the time that the second true node appears on the main stem, and the rate of appearance of the other primary branches is about half that of node development on the main stem (Leong and Ong, 1983). Very high mean temperatures inhibit branching of peanut (Leong and Ong, 1983).

## 2.2. Reproductive development

### 2.2.1. The reproductive stages

The development of legume seeds has been described in several studies (Dure, 1975; Pate, 1975; Pate and Flinn, 1977). An initial phase of cell divisions is followed by a period of cell expansion, and then by an accumulation of reserve compounds in the cells. Four main stages can be defined in the life of a reproductive organ: (1) organ initiation, (2) anthesis, (3) final stage in seed abortion and (4) physiological maturity. Floral initiation is very early in the plant life (about 4–6-leaf stage). Anthesis of a flower is the time when ‘petals are opened’, according to the scale of Maurer et al. (1966) and is later than ovule fertilization by about 24 hours (Cooper, 1938; Linck, 1961). For an ovule, Pigeaire et al. (1986) demonstrated the existence of a stage after

which the probability of seed abortion is lower than 5%, called the final stage in seed abortion (FSSA). This stage corresponds to the transition between a period of active cell division and a phase of rapid dry matter accumulation in the seed (Ney et al., 1993). The first period, during which the seed enlarges rapidly, lasts about 300 degree-days after anthesis (base temperature of 0°C). At the end of this phase, the final cell number is reached in the ovule. At the pod scale, the final stage in seed abortion can be defined as the time when all the ovules of the pod have reached this stage. At FSSA, the seed number in the pod is determined. Thereafter, dry matter accumulation in the seed correlates with cumulative degree-days. Two criteria can be used to determine the time of transition between these main phases, seed number formation and seed filling. First, Duthion and Pigeaire (1991) have shown, on a great number of seeds, that there is a maximum length for aborted seeds, 8.8 mm for cultivar Solara for example. Ney et al. (1993) confirmed that, at this length, the final cell number of the embryo was reached. Second, seed water content may also be used. Ney et al. (1993) have shown that seed water content remained stable between 0.80 and 0.86 g g<sup>-1</sup> during the period of seed abortion, and decreased from 0.80 to 0.55 g g<sup>-1</sup> during the period of linear seed growth. The water content of 0.55 g g<sup>-1</sup> determines seed

Table 1  
Variation of the values determining the developmental stages and the durations of the successive phases among species

Species	Seed length FSSA (mm)	Seed water content FLO-FSSA (g · g <sup>-1</sup> )	Duration FLO-FSSA (degree-days)	Seed water content at PM (g · g <sup>-1</sup> )	Duration FSSA-PM (degree-days)	Reference
Pea	6–8.5	80–86	300	55	About 300	Duthion and Pigeaire, 1991
cv Solara			181		333–471	Ney et al., 1993
cv Finale			195		386–427	Ney and Turc, 1993
cv Frisson			234	55		Le Deunff and Rachidian, 1988
Soybean	10–12	85	250–390	60	500–620	Duthion and Pigeaire, 1991 Munier-Jolain et al., 1993
White lupin	11.5–13	85–86	600–650	65 60–65	300–400	Duthion and Pigeaire, 1991 Munier-Jolain, 1996 Noffsinger et al., 1994
Chickpea	7.6–8.7	85		60		Turc et al., 1994

physiological maturity (Le Deunff and Rachidian, 1988), and corresponds to the end of dry matter accumulation in the seed.

Analysis of the effects of short-term water deficits confirmed the existence of the FSSA (Ney et al., 1994). Water deficit after the initiation of linear seed filling at one node prevented seed abortion at this node, but seed number was lower than controls on the nodes above (which had not yet reached their FSSA).

The four stages, described here for pea, have been reported in other legumes (soybean, Pigeaire et al., 1986; Duthion and Pigeaire, 1991; Munier-Jolain et al., 1993; lupin, Pigeaire et al., 1986; Duthion and Pigeaire, 1991; Noffsinger et al., 1994; Munier-Jolain, 1996; chickpea, Turc et al., 1994). The various criteria and the duration of the two main phases vary between species (Table 1).

### 2.2.2. Progression of reproductive stages

For many legume crops, the timing of floral initiation is photoperiod and temperature dependant (Summerfield and Wien, 1980; Summerfield and Roberts, 1988), the response being different among varieties. There is a general model describing the photothermal responses of flowering, in field conditions, for soybean, cowpea, pea, chickpea, faba bean and lentil (Summerfield and Roberts, 1988; Ellis and Summerfield, 1994). A model for predicting time of pea flowering according to the leaf appearance rate and the node of first flower has been proposed (Truong and Duthion, 1993).

As for vegetative development, the sequential progression of the different reproductive developmental stages (flowering, initiation of seed filling, and physiological maturity) along the main stem has also been described by linear models (Fig. 1) based on cumulative degree-days (Acosta Gallegos and Kohashi Shibata, 1989, for dry bean; Ney and Turc, 1993, for pea; Munier-Jolain et al., 1993, for soybean; Munier-Jolain, 1996, for lupin).

Pea branches have a similar development pattern as the main stem, with similar date of flowering, rate of flowering, and date of beginning of seed filling (Jeuffroy and Sebillotte, 1997). The flowering of soybean lateral branches begins later and progresses more slowly than on the main stem (Munier-Jolain et al., 1994). The reproductive organs of soybean

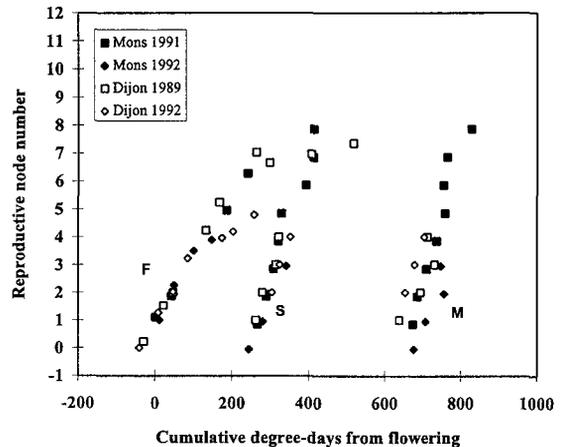


Fig. 1. Progression of flowering (F), initiation of seed filling (S), and physiological maturity (M) on the main stem of pea cv. Solara, as a function of cumulative degree-days from the start of flowering.

(Munier-Jolain et al., 1994) and lupin (Munier-Jolain, 1996) that flower simultaneously on the same plant also reach the beginning and termination of seed filling at the same time, regardless of their morphological position (nodal position, main stem, primary or secondary racemes). Moreover, the time between flowering and the beginning of seed filling and between flowering and physiological maturity are negatively correlated with the time of flowering.

Vegetative and reproductive development of a stem ends after a variable number of nodes. At this stage, there are still initiated nodes in the apex of a pea plant, which will never develop. Thus, the end of production of new nodes on a stem is due to the early halt of development or growth of already initiated nodes (Lecoeur, 1994; Jeuffroy and Sebillotte, 1997). Hormonal and nutritional models have been proposed to explain the determinism of the end of development (Hardwick, 1985). On soybean, leaf emergence ceased when a pod reached 5 mm long on the node situated just above the last fully developed node (Sinclair, 1984a). Thus actively growing seeds at the top node of the stem may inhibit the emergence of a new leaf.

The duration of seed filling varies greatly according to field conditions. In indeterminate soybean, termination of seed filling has been described as the result of the 'self-destruction' of the plant, due to the

remobilization of large amounts of nitrogen (Sinclair and de Wit, 1976). In different environmental conditions, seed filling has been shown to end when nitrogen available in the plant for remobilization was exhausted (Munier-Jolain et al., 1996b), except in the situations where seeds had reached their potential size, which depends on seed cell number.

### 2.2.3. Effects of water stress and nitrogen deficiency

In glasshouse and field experiments, short-term water stresses did not change the rate of progression of flowering, or the beginning of seed filling and physiological maturity in pea (Ney et al., 1994). They did not change the length of either the period between flowering and beginning of seed filling or the period between the beginning of seed filling and physiological maturity. The main effect was an earlier cessation of flowering, and thus a smaller number of flowering nodes, which potentially bear pods

and seeds. These results are consistent with the effect of water stress on other indeterminate species, such as dry bean (Acosta Gallegos and Kohashi Shibata, 1989). The beginning and end of seed filling are earlier under long-term water stress compared with control conditions (Turc, 1995), from 30 to 50 degree-days and from 50 to 100 degree-days respectively for the first node, resulting in a shorter period of seed filling. The duration of soybean seed filling is affected by water deficit (Sionit and Kramer, 1977; Korte et al., 1983).

Nitrogen deficiency induces an early end of pea flowering (Sagan et al., 1993; Jeuffroy and Sebillotte, 1997). The rate of progression of flowering along the stem is not modified. Nitrogen deficiency for various periods in the cycle have been studied. Cessation of flowering is only affected if the deficiency starts before the onset of flowering on the stem and if it has a long duration (Jeuffroy and

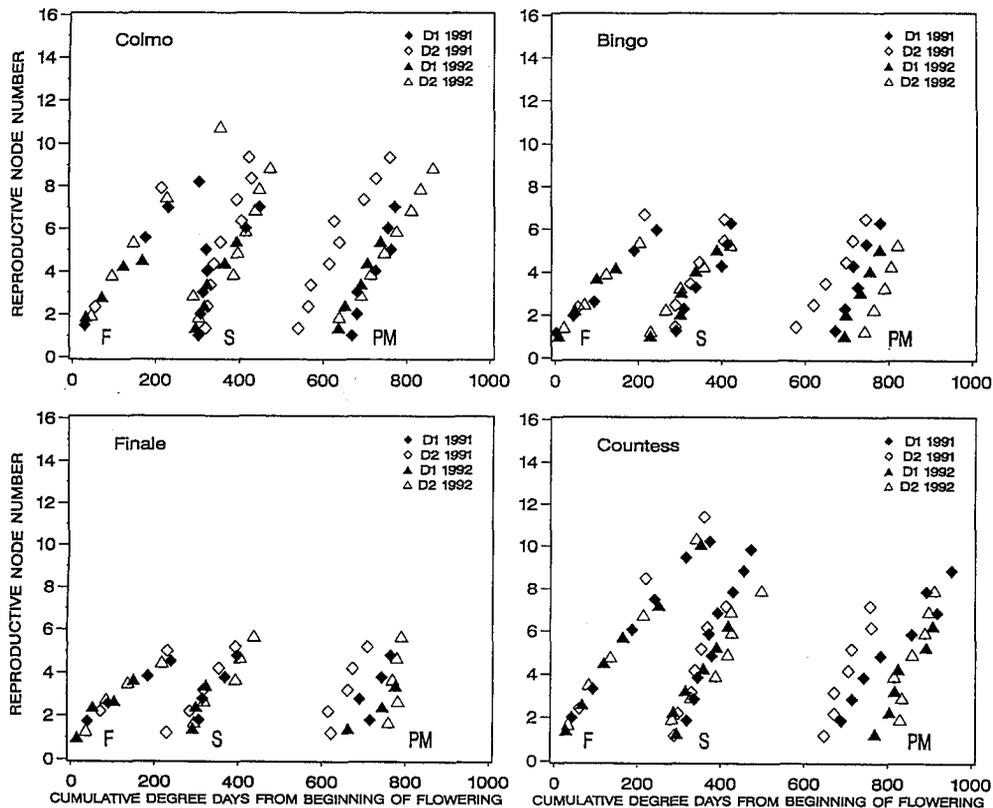


Fig. 2. Genotypic variability of progression of flowering (F), beginning of seed filling (S), and physiological maturity (PM) on the main stem of pea, as a function of cumulative degree-days from the start of flowering, for four genotypes in different environments.

Sebillotte, 1997). Truong and Duthion (1993), examining the deviations from their model for predicting the time of flowering, observed that deficient nitrogen nutrition (characterized by a low nitrogen concentration of aerial parts at flowering) promoted flowering. Although grain legumes can fix  $N_2$  in symbiosis with rhizobia, nitrogen deficiencies have often been observed in pea fields (Doré, 1992). In these situations, there are always few branches per plant.

#### 2.2.4. Genetic variability

In ten genotypes of pea, varying in their seed size, foliage type and number of branches (Dumoulin et al., 1994), the progression of flowering, beginning of seed filling, and physiological maturity were linearly correlated to cumulative degree-days since the beginning of flowering. Significant genotypic differences were observed in the rates of progression of flowering and of beginning of seed filling (Fig. 2). The time between flowering and beginning of seed filling at the first node and the duration of seed filling were very similar in all genotypes, despite differences in seed size.

#### 2.2.5. A model for reproductive development

Ney and Turc (1993) proposed a general description of reproductive development on the main stem of a pea plant. Reproductive development can be entirely defined by the start, the end and the rate of progression of each stage along the stem: flowering, beginning of seed filling, and physiological maturity (Fig. 3). This general pattern of development has been successfully applied to soybean (Munier-Jolain et al., 1993) and lupin (Munier-Jolain, 1996). As some of the parameters in this model are constant or easily calculated, the characterization of the whole reproductive development requires only a few observations. Thus, this model can be used to determine precisely the developmental stages of each reproductive organ on a plant, all along the cycle. It also allows the period of seed formation to be determined, during which time abortions can occur: it begins with the flowering of the first reproductive node and ends when the last reproductive node reaches the beginning of the seed filling stage. The period of seed filling, for an individual plant, lasts between the beginning of seed filling of the first

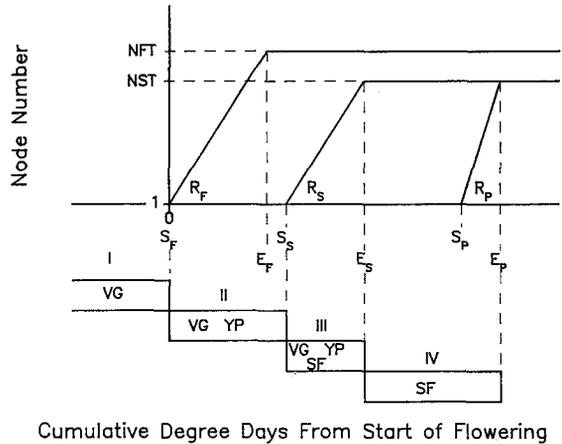


Fig. 3. A general description of pea reproductive development.  $S_F$ ,  $S_S$  and  $S_P$  are the start of flowering, seed filling, and physiological maturity;  $R_F$ ,  $R_S$  and  $R_P$  are the rates of progression of the three stages along the stem;  $E_F$ ,  $E_S$  and  $E_P$  are the ends of the stages. NFT and NST are the highest flowering and fruiting nodes.

reproductive node and physiological maturity of the last. Thus, the periods of seed formation and seed filling overlap between the beginning of seed filling of the first and of the last reproductive nodes. This description allows analysis of the effects of limiting factors: for example a drought period can have an effect on seed number or on mean weight per seed, depending on which period is affected (Ney et al., 1994).

### 3. Growth

#### 3.1. Radiation interception

As for other species, dry matter accumulation in legume crops can be analysed according to radiation interception and photosynthesis of the canopy. There has been much effort to model radiation interception by canopies of grain legumes. Generally, the fraction of incident radiation which is intercepted by the canopy,  $I/I_0$ , is calculated as a function of the leaf area index (LAI) as:

$$I/I_0 = 1 - \exp(-k \times LAI) \quad (1)$$

where  $k$  is the extinction coefficient of the canopy. In some studies, LAI is directly correlated with time

expressed in cumulative degree days (for instance for alfalfa (*Medicago sativa*): Lemaire and Allirand, 1993). Some other authors calculate LAI from the product of leaf area per plant and plant density. Leaf area per plant was related by Sinclair (1984b), Sinclair (1986) to the plastochron index, hypothesizing that both variables are dependent on temperature if there is no drought. This model was used by Sinclair et al. (1987) to simulate LAI of cowpea (*Vigna unguiculata*) and black gram (*Vigna mungo*) and more recently by Hammer et al. (1995) for peanut (*Arachis hypogea* L.).

Very different extinction coefficients have been reported for a given species as reviewed by Varlet-

Grancher et al. (1989). These variations are due to the differences in methods of measurements and to the environmental conditions. Solar radiation balance is calculated as the difference between the radiation received (incident and soil-reflected radiation) and lost (crop-reflected and transmitted radiation) by the canopy. Methods differ by the type of radiation measured (total radiation or photosynthetically active radiation, PAR, measured as energy flux or photon flux) and also by the calculation of the balance. Some authors calculate absorbed radiation and others intercepted radiation (in this case, reflected radiation by soil and canopy are neglected). Variation in reported extinction coefficients also results from ef-

Table 2

Extinction coefficient  $k$  reported by various authors, and methods of calculation of radiation balance (absorbed and intercepted) and type of radiation measured

Species	Absorbed		Intercepted				Reference	
	Tot. R.	EPAR	QPAR	Total Rad.	EPAR	QPAR		Other <sup>a</sup>
Glycine max							0.88 0.60	Shibles and Weber (1965) Sinclair (1986)
Phaseolus vulgaris						0.4		Gardiner et al. (1979)
Cajanus cajan			0.38				0.90	Natarajan and Willey (1985) Sivakumar and Virmani (1984) Hugues et al. (1981)
Medicago sativa	0.88						0.97	Gosse et al. (1982) Fuess and Tesar (1968)
Vigna unguiculata	0.93				0.62			Varlet-Grancher and Bonhomme (1974) Littleton et al. (1979)
Vigna mungo					0.95			Muchow and Charles-Edwards (1982)
Lupinus albus			0.83					Varlet-Grancher et al. (1989)
Cicer arietinum							0.47–0.61	Hugues et al. (1987)
Arachis hypogea							0.50	Hammer et al. (1995)
Pisum sativum leafed				0.33/0.49			0.33	Heath and Hebblethwaite (1985b) Martin et al. (1994) Ney (unpublished)
Pisum sativum semi-leafless			0.49	0.33–0.49 cor. $\pi/2$			0.33 cor. $\pi/2$	Heath and Hebblethwaite (1985b) Martin et al. (1994) Ney (unpublished)
Pisum sativum leafless			0.46	0.55/0.75 cor. $\pi/2$				Heath and Hebblethwaite (1985b)

<sup>a</sup> Other methods (for example photometric units) or not specified.

fects of differences in environmental conditions on the canopy (e.g. leaf angle can be affected by drought), spatial distribution of the leaves (plant densities and row spacing), and variation in their optical properties, which may result from variation in nitrogen content. These sources of variation are not generally taken into account. Table 2 summarizes the variations of  $k$  among experiments for grain legume crops. For pea crops, the estimation of  $k$  is difficult because of the transformation of leaves into tendrils for semi-leafless (leaflets transformed into tendrils) or leafless (absence of stipules) genotypes. As tendrils and petioles are cylindrical, some authors multiply their projected area by a correction factor of  $\pi/2$  (Heath and Hebblethwaite, 1985b; Martin et al., 1994). No difference was found in coefficient  $k$  between leafed and semi-leafless genotypes although a leafless genotype was found to have a higher  $k$ . Heath and Hebblethwaite (1985b) suggested that comparisons of leafed, semileafless and leafless genotypes with respect to radiation interception should be interpreted with caution, because nothing is known about the proportion of the area of tendrils involved in radiation absorption. However, no significant difference was found in PAR absorption during the crop cycle between isogenic lines of pea differing in foliage structure (Finale, leafed, and Solara, semi-leafless) (Fig. 4). The results obtained by Heath and Hebblethwaite (1985b), Pyke and Hedley (1985), and Martin et al. (1994) confirm the small differ-

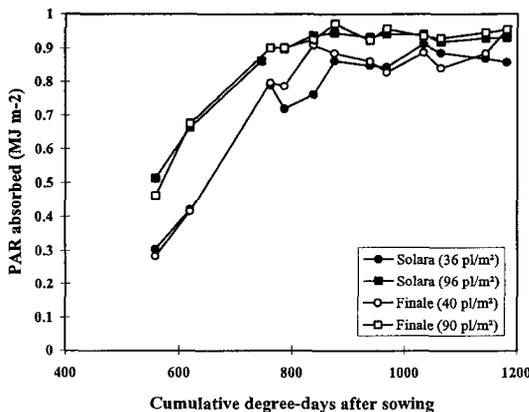


Fig. 4. Photosynthetically active radiation (PAR) absorbed by two isogenic genotypes (Solara: semi-leafless; Finale: leafed) in Dijon in 1988.

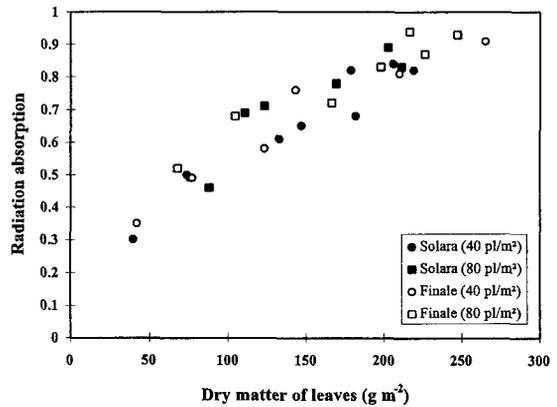


Fig. 5. Relationship between leaf dry matter and radiation absorption for two isogenic genotypes of pea (Solara: semi-leafless; Finale: leafed) in 1989 in Dijon.

ences observed in  $k$  between leafed and semi-leafless genotypes at least until flowering. Conversely, the leafless genotypes, characterized by the absence of stipules, absorbed less PAR during the cycle (Heath and Hebblethwaite, 1985b). Thus the transformation of leaflets into tendrils is not detrimental to PAR absorption. The ratio PAR absorbed: g leaf dry matter, for Solara and Finale grown at 40 and 80 plants m<sup>-2</sup>, shows that the same leaf dry matter was needed to absorb the same PAR (Fig. 5). However, PAR is more uniformly distributed within the canopy of the semi-leafless genotype than the leafed genotype (Fig. 6). The greater PAR penetration and standing ability due to tendrils has led to increased use of

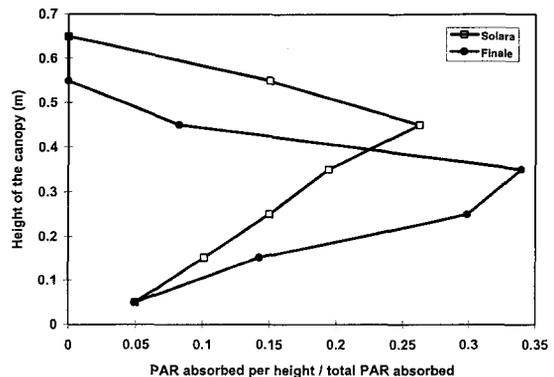


Fig. 6. PAR absorption in canopies of two isogenic genotypes of pea (Solara: semi-leafless; Finale: leafed) at the beginning of seed filling, in Dijon in 1989 (plant density = 80 plants m<sup>-2</sup>).

this trait in new varieties of pea during the last ten years.

### 3.2. Radiation use efficiency

Numerous studies have addressed photosynthesis in legume crops. Radiation use efficiency (RUE), i.e. the ratio aerial dry matter produced to PAR absorbed, was found to be widely variable for a given species. In pea for instance, Heath and Hebblethwaite (1985b) found 0.96 to 1.46 g aerial dry matter per MJ of total radiation intercepted depending on the experimental location; Pyke and Hedley (1985) 1.25 g DM MJ<sup>-1</sup> total radiation intercepted; Martin et al. (1994) 1.43 g DM MJ<sup>-1</sup> PAR intercepted under drought conditions, and Wilson et al. (1985) 2.36 g DM MJ<sup>-1</sup> PAR intercepted. One reason for this wide variability is the large effects of environmental conditions. Reductions in RUE under drought have been recorded in many studies for grain legumes including faba bean (Green et al., 1985), pigeon pea (*Cajanus cajan* L.) (Hughes and Keatinge, 1983) or pea (Keatinge et al., 1985). RUE is sensitive to minimum temperature (Bell et al., 1992, for peanut (*Arachis hypogea* L.)) and nitrogen nutrition (Sinclair and Horie, 1989).

RUE also varies along the crop cycle. As RUE depends on the relationship between sources and sinks (Shibles et al., 1987), it increases with pod growth and then declines when seeds are filling, as shown for pea (Fig. 7).

Finally, numerous studies (Boerma and Ashley, 1988; Ashley and Boerma, 1989; see Shibles et al., 1987 for a review) have reported genetic variability in canopy apparent photosynthesis for soybean. In our experiments for three years in Dijon (France) with pea, RUE ranged from 1.55 to 2.05 g aerial dry matter MJ<sup>-1</sup> PAR absorbed for 6 genotypes of pea before flowering. On the other hand, no significant difference was found between genotypes differing only in their leaf structure (Heath and Hebblethwaite, 1985b; Pyke and Hedley, 1985).

### 3.3. Growth and yield determination

A positive relationship has been found between canopy apparent photosynthesis (CAP) during the reproductive period and yield in soybean (review by

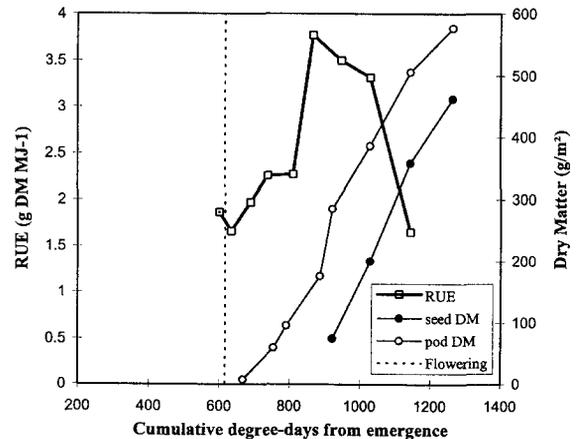


Fig. 7. Variations of radiation use efficiency (RUE) with time in relation to growth of pods and seeds for pea (Solara, Dijon, 1989).

Ashley and Boerma, 1989). For some of these studies, such as those involving source–sink manipulations, the results must be interpreted with caution: if CAP during reproductive development is influenced by sinks, it is obvious that CAP will correlate with yield.

Other authors have related yield or yield components directly to the production of assimilates by the canopy. Jiang and Egli (1995) found a linear relationship for soybean between seed number, the most predictive component of yield, and crop growth rate during flowering and pod set.

## 4. Assimilate partitioning and structure determination

### 4.1. Assimilate partitioning

There is little knowledge of processes involved in carbon partitioning to the various organs of a plant (Whisler et al., 1986). Assimilate partitioning is thus the main weak point of current crop simulation models. Usually, carbon is translocated from a mature leaf to the nearest actively growing region, but this general pattern can be changed if leaves are removed or shaded or depending on sink requirements (Shibles et al., 1987).

In pea, the presence of a sink and a source on the same reproductive node led some authors to study

the possible preferential relationship between them. At a node scale, the assimilates allocated to the pods come mainly from the leaf of the node, and to a lesser extent from the hull of the node (Flinn and Pate, 1970). However, translocation of assimilates between nodes can occur (Harvey, 1973; Szykier, 1974; Jeuffroy and Warembourg, 1991). In pea and soybean, during the reproductive phase, carbon is preferentially exported to pods on the same node and, secondarily, to pods two nodes below or above (Shibles et al., 1987), according to the vascularisation of the plant (see review of Pate, 1975).

In a  $^{14}\text{C}$ -labelling experiment, with plants growing under two different radiation intensities, Jeuffroy and Warembourg (1991) showed that there was no priority among the sinks in the plant during the period of seed formation. When the amount of assimilates produced by the whole plant was severely reduced, the amount of  $^{14}\text{C}$  allocated to each individual organ was proportionally reduced. This led to a model for assimilate partitioning between the organs on a stem, at different dates during this period. In the model, the assimilates produced by the stem during a time interval are allocated to each pod in proportion to its demand. This demand is linked to the initial amount of dry matter of the pod before its final stage in seed abortion, and to the seed number of the pod

after this stage (Jeuffroy and Devienne, 1995). Partitioning between reproductive and vegetative organs is dependent on the plant growth during the two preceding phyllochrons (Jeuffroy, 1994a). This model was tested in various field conditions (Jeuffroy and Devienne, 1995), with good accordance between observed and simulated growth of the different organs, i.e. pods of each node and vegetative parts. However, in situations with water stress, the growth rate of seeds which had begun to fill before the beginning of the stress remained stable, while abortions occurred on pods which had not yet reached this stage (Ney et al., 1994). This suggests that filling pods have priority over young pods in assimilate partitioning. In soybean, defoliation reducing the supply of assimilates did not also modify seed growth after the beginning of the linear growth phase of the seed (Munier-Jolain, 1994). This observation could be used in a general model of assimilate partitioning.

#### 4.2. Relationship between assimilate partitioning and structure formation

At the pod scale, seed number can be predicted from pod growth dynamics during the first 120 degree-days after anthesis (Jeuffroy and Chabanet, 1994). Thus, the pattern of assimilate partitioning (see above) and the relationship between early pod growth rate and seed number per pod have been used to construct a model for seed number production on each node of a pea stem (Jeuffroy, 1992; Jeuffroy, 1994b). The inputs of the model are the development parameters (as presented above), the growth rate of the whole stem during the period of seed formation, and the climatic data (mean daily temperature). When tested in various field conditions (Jeuffroy, 1994b), this model gave a good account of the variability in seed number partitioning among the nodes of the stems (Fig. 8). This model requires measurements of the assimilate demand of the filling seeds. In soybean (Munier-Jolain, 1994) and pea (Munier-Jolain and Ney, 1995), the potential seed growth rate is determined by seed cell number, which is fixed at the beginning of seed filling. Thus, if the cell number is low at this stage, the accumulation of reserves in the seed until physiological maturity can be limited even if assimilate sources are large. The rela-

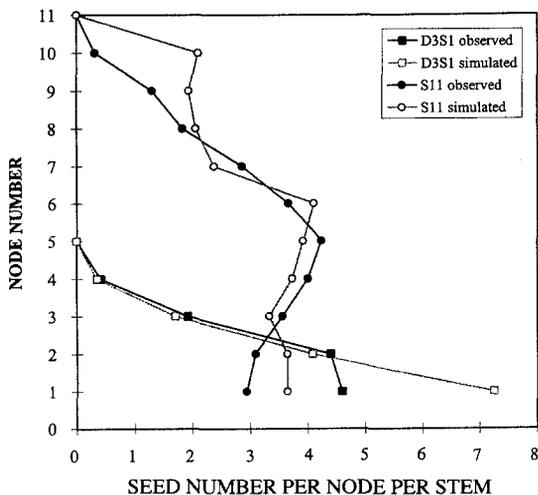


Fig. 8. Comparison of observed seed numbers per node observed and values simulated with the model of Jeuffroy (1994b), from two field locations (D3S1 = Chartres, sown 14/03/89, 257 stems  $\text{m}^{-2}$ ; S11 = Grignon, sown 24/02/92, 97 stems  $\text{m}^{-2}$ ).

tionship between seed growth rate and cell number does not seem to differ between genotypes, even with substantial differences in individual seed weight.

## 5. Conclusion

Recent work has substantially improved understanding of the functioning of legume crops. This allows better definition of the various improvements that are possible in production, yield stability, and seed quality of these crops. The more precise characterisation of the developmental stages along the cycle, and the determination of sensitive periods may make possible the avoidance of stresses. For example in pea, water stresses (Ney et al., 1994) or high temperatures (Jeuffroy et al., 1990) affect yield reducing seed number when they occur before the final stage in seed abortion. The later the stress, the smaller the decrease in yield. Concerning growth, there is genetic variability for radiation interception and radiation use efficiency. Little increase is to be expected in potential RUE, but genotypes with low RUE must be eliminated. The partitioning of growth into harvested yield also could be improved. Harvest index (HI) remains widely variable on some species. Determinate types have, in some conditions, more stable HI, but these types are not available for all grain legume species. For some species, it is necessary to understand the reproductive structure formation in relation to environmental conditions. Recent studies have shown, as described in this chapter, that plant structure can be simulated from plant sequential development and growth.

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