Influencing Crop Canopy Development in Oilseed Rape through Genetic Variation

A.E. ARTHUR and C.L. MORGAN
Brassica and Oilseeds Research Department,
John Innes Centre, Norwich Research Park, Colney, Norwich NR4 7UH, U.K.

Oilseed rape is an untidy crop. In their chapter entitled 'Breeding and varieties' in 'Oilseed rape' (Scarisbrick and Daniels, 1986), Thompson and Hughes state that "...oilseed rape in the field still has many characteristics associated more with weeds than with a crop plant...". Whereas crops of wheat and barley are neat and tidy, with plants upright and uniform, oilseed rape shows none of these characteristics, with straggling plants of indeterminate habit and branching, all competing for available space, with some succeeding at the expense of others, resulting in a sward composed of a range of individual plant sizes, habits and maturities.

Many of these failings concern the crop canopy, the development of which, in oilseed rape, can be considered in three major stages:

1. The vegetative canopy

This canopy, lasting from seedling establishment through winter and spring until the onset of flowering, is relatively efficient, though this depends on the successful establishment of the crop, especially during and immediately following the critical period of germination. Good leaf cover and successful overwintering effectively provide an efficient base from which the crop rises to flowering in the spring.

2. The flowering canopy

The flowering canopy, from the initiation of flowering, through flowering itself and up to the cessation of petal production, is very effective at producing masses of flowers and thus provides a huge potential for pod and seed production, and hence yield. However, only a relatively small proportion of this potential is ever realised because of the innate competition both within a plant and among the individual plants forming the sward, resulting from the inefficient structure and function of the canopy.

3. The pod canopy

Covering the period from the setting of the first pods through to maturity and harvest, the canopy, as it is during flowering, is also relatively inefficient in its structure and function; thus the yield potential provided by the production of the multitude of flowers and setting of pods is not fulfilled.

So what can be done to improve the efficiency of the flowering and pod canopies? In their chapter 'Plant growth regulators for oilseed rape', Scarisbrick and Daniels (1986) list a number of defects of the crop, mostly concerned with the two later canopies, and suggest that modifications in these could lead to increases in yield or the efficiency with which a given level of yield might be achieved. Mendham et al (1991) and Thurling (1991) both attempt to address these defects through the positive approach of defining a crop ideotype for oilseed rape, listing a number of features which might be considered important in improving the yield and suitability of the oilseed rape crop for present day agriculture. These features are summarised by Mendham and Salisbury (1995) and all involve or affect the development, structure and efficiency of the crop canopy :-

1. Rapid early growth.
2. Early flowering.
3. Short sturdy stems to reduce lodging and facilitate harvesting.
4. Apetalous flowers to improve light distribution through the canopy.
5. Improved seed retention following seed maturity.
6. Fewer pods per plant to improve light penetration for pod photosynthesis.
7. Longer pods with more seeds per pod.
8. Erect pods to improve light distribution.
9. Reduced lower branching with enhanced pod production on the main stem and upper branches.

It would be reasonable to add to this list, from Daniels and Scarisbrick's (1986) discussion on defects in the crop, four other features which are likely to make significant contributions to improving the function of the crop:-

1. Increasing determinancy of flowering.

Restricting the number of flowers on individual racemes will reduce the wasteful production of the large numbers of sterile or incompletely filled pods frequently found within the canopy. Similarly, greater determinancy in branch production will limit the spread of flowering within the plant thus producing a better coordinated maturity with fewer immature green seeds remaining at harvest.

2. Increasing determinancy of branch initiation

Restricting the production of the number of primary branches and the subsequent development of secondary, tertiary and quaternary branches will also reduce unnecessary and wasteful competition between plants. It must be remembered, however, that the disadvantage of these modifications is that the plant will lose some of its plasticity of response and may, therefore, be less adaptable and responsive to adverse environmental conditions.

3. Improving the efficiency of the canopy structure and harvest index

Numerous physiological studies on the distribution of assimilate accumulation within the canopy and its subsequent effect on seed filling and on pod and embryo abortion have demonstrated that the source/sink relationships in the oilseed rape crop are poor and that the efficiency with which the plants produce their seed yield is low, thus allowing the possibility of modifying the canopy to improve this. In particular, light penetration (*e.g.* Fray, 1996) and within plant competition (*e.g.* Mendham *et al*, 1981) have been shown to be particularly important in these aspects of canopy function. The lower values of harvest index found in oilseed rape than in wheat for example (*c* 20-25% *v* 50% respectively), can, without doubt, be improved upon but it must be remembered that the oil storage product in rapeseed has a much higher energy value than the starch product of cereals and so the harvest index based simply on seed yield/biomass is inevitably lower for oilseed crops (Bhatia and Mitra (1993).

4. Improving the resistance to pod shatter.

Between 10 and 15% of the seed yield is commonly lost through the crop's propensity to pod shatter, and in severe cases this can be as high as 50%. This results in loss of yield and increases the amount of volunteer plants occurring as weeds in subsequent crops in succeeding years. The seed shed may remain dormant in the soil for many years, making crop rotation less effective in dealing with the problem. This is more than simply a problem of weeds and may result in the genetic contamination of the crop seed and is particularly important when subsequent crops are grown for different seed products, for instance contamination may be seriously damaging if a double-low rape crop grown for food production follows a crop grown for high erucic acid. Little variation for resistance to shattering is available to breeders from within the *Brassica napus* breeding pool but it can be found in related species and amongst lines of rapeseed resynthesised from the diploid parents of *B. napus*, viz *B. rapa* and *B. oleracea*.

Breeders have succeeded in raising the yield and quality of oilseed rape steadily over the past 20 years and, with the advent of hybrid and genetically modified (GMOs) varieties, further improvements can be expected in the near future. However, breeders have paid little direct attention to the defects listed earlier as long as they have been able to select new varieties with improved yield from amongst existing gene pools, and have given only slight consideration to producing a more efficient canopy. Further improvements to the crop, once variation in the existing gene pool has been exhausted, will require the coordinated use of many of the canopy features described above. Most of the attention to canopy development and matters of efficient substrate and photosynthate utilisation, and conversion into seed yield, has come from physiologists endeavouring to understand source/sink relations and modifications to canopy structure and development through the use of plant growth regulators (see eg Child 1984). Indeed, many of the defects of the crop listed here can be influenced to some extent by the use of plant growth regulators such as chlormequat (CCC). This work on plant growth regulators and their potential to modify characteristics contributing to inefficiencies in the crop canopy has been reviewed by Daniels and Scarisbrick (1986) .

However, whilst plant growth regulators can make a valuable contribution to physiological studies on canopy development by providing a means to effect modifications to canopy structure, form and function, their use in an agricultural context will be limited by expense. Changes resulting from the use of plant growth regulators can also be found as genetic variants amongst breeding and research populations, and germplasm accessions. Valuable mutants expressing characteristics potentially useful for modifying the crop canopy have been observed, described and utilised in work at the John Innes Centre, notably lines with reduced petal numbers and erect pods. The value of these two novel traits in modifying canopy structure and improving photosynthetic efficiency has been demonstrated in work carried out jointly between the John Innes Centre and the University of Newcastle-upon-Tyne (Fray et al 1996). During flowering, normal canopies absorb around 80% of the incident light at peak flowering, allowing only 22% to penetrate to the lower, earlier formed pods photosynthesising deep in the canopy. Canopies with the apetalous morphology, however, allow around 40% of the incident light to reach the deeper regions of the canopy; thus, apetalous canopies have a 70% higher light transmission through the canopy with the potential to greatly reduce pod and seed abortion and consequently increase yields. Similarly, canopies with erect pods allow some 25-30% more light to penetrate to basal pods during the pod-forming stages compared to more conventional horizontal podded canopies (Fray, 1995).

There are a number of important practical advantages to being able to modify the canopy through the use of genetic variation rather than growth regulators. Once progress towards understanding the genetic control of the particular trait has been made and the genes involved or at least the regions in which they occur have been mapped, marker-assisted technologies can be used to rapidly introgress the genes (or the regions in which they occur) into commercially useful backgrounds to provide breeders with ready access to the novel traits. It will also facilitate the production of genetic stocks of near-isogenic lines of the trait in which a standard genetic background has small regions of the genome containing the genes of interest introduced into it. This allows direct comparison of the standard, conventional line with pre-determined forms of itself modified to express particular novel traits so that further progress may be made in the development of the most appropriate ideotype for a specified agronomic condition.

Near-isogenic lines are an extremely effective way of assessing the contribution made by a novel trait; indeed, comparisons of lines with modified phenotypes with conventional lines is likely to be fraught with difficulty and mis-interpretation because, unless the background genes are the same in the lines being compared, differences found in any such comparisons may be due to effects from the differing background genes rather than, or in addition to, the genes or traits under investigation. Sets of near-isogenic lines, with a common genetic background and varying only in the expression of the trait of interest, thus provide an extremely valuable tool for physiologists, geneticists and breeders. Such lines are reproducible and can be replicated extensively to allow investigations to be repeated on genetically identical material over time and locations by providing reliable pure-line genetic stocks which can be re-sampled as required. Indeed, a fine example of their application in studies on modified canopies is well demonstrated in the work on the apetalous and erectophile pod characters conducted by Fray et al (1996).

Marker-assisted technologies, such as marker-assisted backcrossing and selection in which molecular markers are used to greatly improve the efficiency and reduce the time scales in the production of genetic stocks, offer exciting possibilities in the effective production of near-isogenic lines for a wide range of traits. Such lines, as described above, can provide a most valuable approach to the physiological and genetic studies of canopy development through the provision of genetic stocks specifically designed for such investigations. The improved efficiency and reduced timescales offered by marker-assisted technologies in the production of near-isogenic lines thus open up new avenues for such investigations.

Furthermore, research in recent years on the comparison of the *Brassica* genomes, including oilseed rape, with the geneticists' model plant, *Arabidopsis thaliana*, has revealed that there are significant similarities in the organisation of the genomes amongst these related species. Extensive molecular studies on the relatively small genome of *Arabidopsis* have provided genetic maps with many molecular markers, providing very detailed coverage of the genome. These, in turn, have formed the basis of extensive mapping studies to locate genes controlling, or at least involved in the control of, a wide range of characteristics, including morphological variation. Whilst everyone recognises and accepts the limitations of the geneticists' model plant for the expression of crop, sward and yield characteristics, the similarity of its genome to those of the crop brassicas offers new and exciting potential for the mapping and application of marker-assisted technologies to the improvement of the *Brassica* crops, including oilseed rape. Traits identified as being important for the improvement of the crop, such as those concerned with canopy development, can be investigated and mapped in the model plant to link genetic markers with the particular genes needed for the modification of a desired trait. This information can then be transferred to the rape crop where it can form the basis of targeted mapping studies by exploiting the similarities in genome organisation. This greatly increases the chances of locating the genes and, in turn, for employing the highly efficient procedures provided by marker-assisted breeding and selection for *Brassica* crop improvement, or for the development of near-isogenic lines and other genetic stocks.

Studies on canopy development are dependent on the ability to provide modifications to canopy structure and assess the effects of the alterations, through physiological investigations of light penetration, photosynthetic efficiency, nutrient uptake and utilisation. As mentioned, plant growth regulators can and have been used extensively to effect the changes needed to form the basis of comparative and investigative studies. However, their effects can be unpredictable and sometimes difficult to reproduce depending on weather conditions and crop age and stage, and are always likely to be expensive and difficult to apply on anything but an experimental basis (Daniels and Scarisbrick, 1986; Pouzet, 1995). A realistic alternative is the production and use of specially constructed genetic stocks exhibiting a range of characteristics ideally suited to studies on canopy development. Two examples have already been discussed as the apetalous and erectophile pod characters, but many other traits with potential in studies on modified canopy structure have been observed at the John Innes Centre amongst doubled haploid populations derived from crosses involving resynthesised *Brassica napus* produced by the hybridisation of various forms of its diploid parents, *B. rapa* and *B. oleracea*.

Amongst these lines, extensive variation exists for a wide range of characters influencing morphology and canopy structure, such as branch number, branch angle, branch length and position up the stem, the extent of development of primary, secondary, tertiary and further branches, pod length, position and number of pods, number of seeds per pod and size of those seeds, expressions of determinancy through restricted flower and branch number, and more easily penetrated open canopy structures as opposed to dense, closed structures, variation for stem thickness and strength of support to reduce lodging. Indeed, genetic variation exists amongst the resynthesised lines for most plant characters but most notably for those associated with the canopy ideotypes identified and described by Mendham et al (1991) and Thurling (1991), as referred to earlier.

Thus, traits of particular interest can be identified and the genes involved or at least those causing significant effects mapped. Then, with the aid of marker-assisted technologies, near-isogenic lines for the targeted traits can be produced and used for detailed physiological assessment of their effects in modifying the canopy. In this way, genetic stocks of near-isogenic lines can form the basis of such studies by providing a range of material, genetically stable and reproducible, easily and readily replicated, and varying for the traits relevant to the ideotype trait being investigated.

To summarise, therefore, the large and rapid increase in the cultivation of oilseed rape is a relatively recent phenomenon, particularly in relation to many of the cereal crops such as wheat, barley and oats, and as a result is relatively young in breeding terms. This means that it still retains many of the features of its wild ancestors which leads to plants having an inefficient canopy structure when grown as a crop. Additionally, the physiological functioning of the crop is poorly understood so that suitable ideotypes are not available on which to base research and breeding programmes. The absence of this knowledge, which is basic to our understanding of the crop's form and function, and fundamental to its effective and efficient improvement, needs to be remedied before significant further progress can be achieved. To this end, it is necessary to generate variation within the crop so that changes in crop architecture may be assessed for their usefulness in improving the agronomic characteristics of the crop. The wild ancestors of oilseed rape are a most valuable source of this variation and can now be readily incorporated into cultivated oilseed rape through the use of modern technologies to enable researchers and plant breeders to a) explore the plant ideotype and b) improve the crop agronomically. Research into assessing and understanding the genetic basis of this variation is currently being undertaken at the John Innes Research Centre in Norwich, UK.

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