THE APETALOUS FLOWER CHARACTER AS A COMPONENT OF A HIGH YIELDING IDEOTYPE

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The concept of an ideotype, or model crop plant for breeders to strive for, has been explored in a range of annual seed crops (Donald and Hamblin 1983). Certain features are common in a diversity of cereal, legume, oilseed and cotton crops. These include good performance at high plant density, strict annual habit, short strong stems, an efficient canopy of leaves, high harvest index and (generally) early flowering and maturity. Rapeseed is no exception, and breeders have been working (consciously or unconsciously) towards a type combining these morphological features with proven physiological advantages. Other breeding objectives, such as improved quality and disease resistance, may sometimes take precedence, but in the longer term, crops of higher yield and greater efficiency must be sought. This paper aims to review some of the work done by the authors and others which helps to point towards an efficient crop type for rapeseed.

Inefficiency During Flowering and Pod Set

Rapeseed has particular problems in producing a photosynthetically efficient canopy, especially during and after flowering. Among the major field crops, it is unique in producing a mass of brightly coloured flowers at the top of the crop for an extended period. This is particularly apparent in European winter crops, where plants are sown early, grow to a large size and produce enormous numbers of flowers. In studies in the United Kingdom (Mendham et al. 1981), the 25,000 or so flowers per m^2 reflected or absorbed up to 60% of incoming solar radiation, but only half or less survived to produce pods with seeds (Table 1).

Table 1. Yields and components of representative crops, United Kingdom (Mendham et al. 1981)

Crop	Sowing date	Seed yield t/ha	No. of pods $10^3/m^2$	No. of seeds /pod	Mean seed wt mg	Harvest index %
Typical early sowing	12 Aug 1972	3.58	12.2	5.7	5.72	18
Poor late sowing	2 Oct 1969	1.23	3.9	7.1	4.45	21
Moderate late sowing	1 Oct 1971	3.20	6.6	11.5	5.04	27
Excellent late sowing	3 Nov 1976	4.54	4.3	20.1	4.53	38

Most leaves senesced soon after flowering commenced, leaving green pods and stems as the source of photoassimilate. On average, only 6 seeds per pod survived, with an extremely low harvest index (seed as a proportion of above ground dry weight). As a result, none of the early sown crops exceeded about 3.6 t/ha, characteristic of the better commercial crops at that time.

Later sowings, on the other hand, varied widely (Table 1) between very low yields and those which considerably exceeded the best of the early sowings. Fewer flowers and pods were produced on the late sown plants, the variation in yield and harvest index being largely accounted for by changing numbers of seeds per pod, retained through the phase just after flowering when abortion is likely. The better late sowings were shown to have intercepted more radiation and hence made more growth in spring than the poorer ones, but then produced no more pods. This resulted in a sparse but efficient canopy of green pods and also better retention of green leaves underneath. Oil content did not vary greatly from about 40% in all sowings, so oil yields reflected seed yields. The question from this work was, how to reliably combine adequate vegetative growth for full interception of radiation with an efficient canopy of pods?

The Importance of Seed Survival

Breeders in Europe and elsewhere have conventionally associated many pods with high yield, as indeed they are often correlated. However, some of the Australian breeders have pursued a different approach, and made substantial advances by incorporating Japanese material into their programmes. Very high yields were shown to be possible (Table 2) from new cultivars such as Marnoo in comparison with an existing Canadian cultivar (Mendham et al. 1984).

Table 2. Yields and components of Australian cultivars compared to the Canadian Midas, sown 20 May 1981, Gretna, Tasmania (Mendham et al. 1984)

	No. of days to flower	Seed yield t/ha	No. of pods $10^3/m^2$	No. of seeds /pod	Mean seed wt mg	Oil content % d.m.
Unirrigated						
Midas	133	3.18	5.32	19.0	4.17	49.9
Marnoo	131	3.68	5.24	28.2	3.22	47.9
RU1	123	3.63	4.48	30.7	3.29	41.9
Irrigated						
Midas	134	4.62	7.18	16.9	4.34	46.1
Marnoo	133	5.53	8.24	19.7	3.27	46.1
RU1	123	5.35	8.74	22.0	3.78	40.6

The most consistent feature was very high rates of seed survival, up to near the potential of about 30 per pod in crops without irrigation. Mild water stress in that case restricted the number of pods set, but subsequent rainfall allowed most seeds to be retained. Seed size and oil content were reduced under stress conditions in the Australian cultivars compared to Midas, which appeared to have been bred for large seeds of high oil content, to the detriment of seed numbers and hence yield potential. With irrigation, many more pods were formed and hence numbers of seeds per pod reduced, but the differences between cultivars were still clear. The very early flowering RU1 performed nearly as well as Marnoo, except that oil content was low. Subsequent cultivars released in Victoria and New South Wales have combined the early flowering and good seed retention of these lines with disease resistance and good product quality.

The Apetalous Flower Character

Following discussions with breeders on the problems the dense flower canopy causes in rapeseed, and the potential benefits of removing it, Buzza (1983) produced an apetalous line, i.e. without the usual bright yellow flower petals. The character apparently requires recessive alleles of two genes for its expression, although there may be modifiers acting as well. There is a certain amount of instability towards the end of the flowering period when some petals may be produced. This character was produced in a line closely related to Marnoo, with which it has been compared (Rao and Mendham 1987, with more detailed papers having since been submitted for publication).

The apetalous plants were of similar type to Marnoo, but the remaining flower parts were somewhat larger, including calyx, anthers, stigma and ovary. Pods were longer and wider than in Marnoo. There did not appear to be any problems in pollination, with bees visiting in similar numbers to Marnoo flowers. There was a major difference in the amount of solar radiation transmitted through the flower canopy, with about 30% more radiation reaching the leaves below. In Marnoo, the proportion of radiation reaching the base of the inflorescence declined from 84% at the beginning of flowering to 40% at full flower, whereas in apetalous it was still 70% at that time. Leaves persisted, remaining green and active until close to pod maturity, and fewer pods aborted or lost their seeds.

These features have generally been translated into a substantial yield advantage, for example in an experiment with irrigation treatments (Table 3).

Table 3. Yields and components of an apetalous line compared to Marnoo, sown 10 June 1986, Cambridge, Tasmania (Rao and Mendham 1987).

	Seed yield t/ha	No. of pods $10^3/m^2$	No. of seeds /pod	Mean seed wt mg	Harvest index %
Unirrigated					
Marnoo	3.39	7.47	14.5	3.47	30
Apetalous	5.01	7.34	18.9	3.70	39
Irrigated					
Marnoo	4.04	7.70	18.6	3.75	30
Apetalous	5.59	7.54	21.6	4.14	42

On crops with similar vegetative growth and number of pods, apetalous produced more seeds per pod, larger seeds, higher harvest index and about 40% higher yield. The difference was larger without irrigation, where neutron moisture meter measurements showed that apetalous extracted more water from lower in the soil profile. It may be that the longer active leaf life also promotes root activity, as rapeseed crops generally show little increase in root weight after flowering commences. Apetalous maintained a consistently higher stomatal conductance than Marnoo, but also a higher leaf turgor at lower osmotic potentials, indicating possibly greater drought tolerance. While it is difficult to believe that all these characteristics are a result of removal of petals, the potential effects through the plant and crop could be widespread.

The apetalous character is being transferred to different backgrounds, including European winter types where it may be particularly useful. Clearly, if it can help raise harvest index from about 20% (Table 1) to 40%, major increases in yield are possible. In Canada, interest has been shown in its ability to limit spread of Sclerotinia disease, which can build up on dead petals lodged in the leaf axils of conventional plants. There may be other means of eliminating or reducing petals as, for example, in plants with cytoplasmic male sterility, but there it is only expressed in the female parent lines, not in the final hybrid.

Pod Characteristics

Apart from ability to retain seeds, some of the available morphological variants in pod type may be useful in an ideotype. By analogy to the erect leaved character in cereals such as rice, an erect pod habit instead of the usual near horizontal arrangement on the plant stems and branches may allow better distribution of radiation through the canopy. One such type is Chinoli (Brassica campestris), produced by Professor N. Thurling, University of Western Australia. This was incorporated in comparisons with other B. campestris and B. napus lines (Rao and Mendham 1985, and in a paper since submitted for publication). The erect pod characteristic was unable to be expressed in better seed set and yield, due to lodging and possible infertility due to the wide cross used to produce Chinoli. However, where lodging was prevented, there were indications of higher efficiency of conversion of intercepted solar radiation to dry matter during pod growth.

There is also a "long pod" type found in B. napus (Chay and Thurling 1989) which may be advantageous under some conditions, such as at lower plant density where increased numbers of seeds per pod were not offset by reduced numbers of pods per plant.

Towards an Ideotype for Rapeseed

Evidence has been presented that, as well as the characteristics common to ideotypes in other annual crops, a more efficient crop canopy during flowering and pod production is desirable and attainable. Vigorous vegetative growth to achieve near full light interception should be followed by as early flowering as possible given environmental constraints such as frost. A moderate number of flowers, preferably without petals to aid distribution of radiation, should give a more efficient canopy of pods. Selection for high rates of seed retention, as found in many Japanese lines and new Australian cultivars, should complement the apetalous character. Other characteristics, such as erect and/or long pods, may further improve efficiency of photosynthesis by pods and remaining leaves.

Thurling (1991) has suggested how some of the characteristics listed above, plus others relating to resistance to pod shattering and disease, and improved product quality, could be combined into an ideotype. Production of dihaploid lines from crosses involving the separate characteristics could be the quickest method.

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