PHYSIOLOGICAL BASIS OF SEED YIELD AND QUALITY IN OILSEED RAPE

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ABSTRACT

This paper identifies the key events in development and growth of the rapeseed crop, and how environmental factors interact with them to produce seed yield and quality. Production of an efficient canopy of leaves before flowering at an appropriate time for the environment is a requirement for all crops to set up an high yield potential. The specific characteristics of rapeseed during flowering, when active photosynthetic surfaces change from leaves to pods and stems while much of the radiation is reflected or absorbed by flowers, make subsequent events critical to the achievement of that potential.

INTRODUCTION

This review concentrates on *Brassica napus*, with contrasts made where appropriate with other oilseed *Brassica* species. It is a summary of a full review to be published shortly (Mendham and Salisbury, 1995). The aim is to give an overview of current understanding of the physiology of crop development and growth, and how these processes interact with environmental factors to produce the final yield and quality. This is to set the scene for the following papers to advance the subject further in specific aspects.

DEVELOPMENT

Development, or the progress of the crop through its life cycle, should be distinguished from growth, or the increase in area, size and particularly weight of individual organs, whole plants and the whole crop or community. Keys of development stages for field use (eg Sylvester-Bradley and Makepeace, 1984) include stages of leaf, stem, flower, pod and seed development, but these need to be supplemented with more detailed recording of, for instance, inflorescence initiation or ovule development (both usually requiring dissection) for more critical studies.

The basic factor affecting rate of development (usually expressed as inverse of number of days to complete a stage or the whole life cycle) is temperature, as for all plants. There will normally be a linear response above a base temperature, about 5°C (Morrison *et al* 1989), although development proceeds slowly above 0°C and some authors use degree-days (°C d) above zero as a measure of thermal time. From sowing to emergence may therefore take around 140°C d, or 9 days at 15°C. Each leaf may take 20-60°C d to initiate (plastochron) from the apex or growing point, and 60-120°C d to emergence (phyllochron) (eg Smith and Scarisbrick,1990), depending on other factors such as water supply, nutrition and spacing. Later leaves produced during stem extension have a shorter phyllochron. Each cultivar will have a minimum number of leaves which it must produce before inflorescence initiation, ranging from about 6 to 12.

Responses to vernalization and photoperiod will often mean that more than the minimum number of leaves will be produced, hence delaying flowering and producing a potentially larger leaf area and yield. One or both of these responses, which are governed by up to 4 genes, are found in most cultivars, giving a range of flowering and maturity times. European winter cultivars show a strong response to both, Australian cultivars are intermediate, and Canadian cultivars show least response (Salisbury and Green, 1991). The duration of the stem extension phase, from inflorescence initiation to flowering, may

be of at least as much significance to final yield as the length of the pre-initiation phase. While mainly controlled by temperature and daylength, vernalization may also operate (Thurling and Kaveeta, 1992). *B. rapa* normally flowers much earlier than *B. napus*, hence restricting its yield potential, but genes are available within the species or in crosses with *B. napus* to modify the lengths of the pre-flowering phases.The final phase, from flowering to maturity, is mainly controlled by temperature. A range of sowings of a European winter cultivar, for example, took about 700°C d above 4.2°C (60-90 days) (Mendham *et al* 1981) whereas a Canadian cultivar took about 580°C d above 5°C (Morrison *et al* 1989).

CROP GROWTH TO FLOWERING

Root growth, including laying down of reserves principally in the taproot, continues until reaching a maximum late in the flowering phase, when water and nutrients may be extracted from as deep as 1-1.5 m by up to 2 Km length of roots/m^2 , of surface area $5m^2/m^2$ (Kjellstrom, 1991). *B.rapa* has a restricted root system as a result of its earlier flowering,

Expansion of individual leaves to form the canopy for radiation interception is again temperature-controlled, but modified by nitrogen nutrition and water supply in particular. A larger leaf area index (L) can be produced by delaying flowering or increasing leaf expansion rates, for which genetic variation is available, but L of about 4 at flowering appears to be optimal (Mendham *et al* 1981) as about 90% of radiation is intercepted and more leaf may be wasteful. Extended leaf area duration, for example by early autumn sowing, may be of value in building up reserves, but the photosynthetic role of leaves is mainly lost after flowering. The efficiency of pre-flowering growth is about 1.2-1.5 g/MJ total solar radiation during active spring growth, but may be as low as 0.4 g/MJ at low temperatures or under water stress.

GROWTH AND DEVELOPMENT: FLOWERING TO MATURITY

Yield components are often measured at harvest to try to understand how experimental treatments have affected yield. This may be misleading, however, if the way in which they are developed, and the timing, are not understood. There is often substantial compensation between them, for example a crop which has set few pods may have many seeds per pod or may fill the seeds to a large size if subsequent conditions are favourable. The number of seeds retained per pod has been shown to be closely related to the capacity of the crop to carry them, as determined by growth up to flowering and expressed as crop dry matter per pod (Mendham *et al* ,1984).

While *B. napus* and the other two amphidiploid species, *B. juncea* and *B. carinata* are self-fertile, bees or other vectors may increase the rate of seed set and allow crops to finish flowering sooner. Yields are often not increased, however, suggesting that pollination does not normally limit yield.

Determination of the yield components

Pods begin rapid growth in length and then weight within a few days of anthesis, whereas rapid seed growth is delayed for about 20 days (Hocking and Mason, 1993). During this time seeds are most likely to abort, as competition for assimilate becomes intense within the developing pod canopy. At this time, stem and branch growth are nearly complete, and leaf area is declining rapidly as shade from the flowers and pods increases. There is thus a clear sequence of growth in which leaves are followed by stems, pod walls, and then seeds (Mendham *et al*, 1981).

The first of the yield components to be determined, number of pods/m^2 overlaps to some extent in timing with the second, number of seeds per pod, and similar factors affect both. A substantial proportion (often more than half) of the potential pod sites (flower buds

and flowers) do not carry pods to maturity. Losses are greater on lower and secondary branches, towards the end of flowering, and not only represent a wasted resource but are a deleterious factor as the flower layer may reflect or absorb around 60% of incoming radiation.The success rate of flowers in forming pods has been shown to be related to the amount of radiation intercepted by the crop canopy (per flower), during and shortly after the flowering period, as well as to supply of water and nitrogen (Leterme, 1988).

The prescence of a critical phase for seed abortion, established by dissection of young pods (Mendham *et al*, 1981), was confirmed by *in situ* studies using X-rays (Pechan and Morgan, 1985). The phase, corresponding to the lag phase before active seed growth begins, lasts for 200-300°C d (Leterme, 1988). In most field situations this means about 19-25 days (300°C d at 15-12°C respectively), whereas at higher temperatures, eg 20°C in a glasshouse (Pechan and Morgan, 1985) the process may take only 10 days (200°C d) because growth in pod length is curtailed as seeds abort. The number of seeds per pod which survived this phase was shown to be related to the amount of radiation intercepted by each pod over the critical period (Mendham *et al*, 1981), although the relationship differed between dense canopies in early sown crops and lighter canopies in later sown crops. Water stress during this time will cause greater seed abortion. The greater water use efficiency of *B. juncea* may be due to osmoregulation maintaining turgor during the abortion phase, resulting in more seeds per pod (Wright *et al*, in press).

The end of the seed abortion phase and the beginning of the next phase, that of active seed growth, can be estimated by plotting seed growth against time, fitting a linear approximation to the main period of seed growth, and extrapolating it back to zero weight on the x-axis. The seed growth phase can then be described in terms of duration (related mainly to temperature) and rate of growth, related to assimilate supply.

Sources of assimilate for pod and seed growth

As noted above, the amount of solar radiation intercepted by crops during and just after flowering has a direct effect on number of both pods and seeds. This appears to be particularly important in rapeseed due to the changing nature of the photosynthetic surfaces, and the loss of the radiation absorbed or reflected by flowers, both happening at the critical time for the main mass of earlier formed pods. The changed spectral composition of the radiation under the flower layer is also less favourable for photosynthesis (Yates and Steven, 1987). Removal of the yellow petals in an experimental "apetalous" line (Rao *et al*, 1991) allowed much more radiation to penetrate to leaves and young pods, and increased seed numbers per pod and yield. Even water extraction appeared to be increased, as activity of roots as well as leaves was prolonged.

While all green surfaces of the crop contain stomata, they are most frequent on leaves and least on stems, with pod surfaces intermediate (Major, 1975). All have been shown to be photosynthetically active (eg Norton *et al*, 1991), with efficiency roughly in proportion to stomatal frequency. Pods may also be important in fixing respired CO_2 from growing seeds as well as external CO_2 uptake. At the time when walls are growing rapidly and seeds are likely to abort, however, they may still be "heterotrophic" (Leterme, 1988), or dependent on assimilate from elsewhere in the plant. By the time pods had attained maximum hull weight and area, Norton *et al* showed that pods and stems were responsible for 95% of the crop gross photosynthesis, due to their position in the crop and loss of most of the leaf area by then.

The beginning of active seed growth on the first-formed pods on the mainstem coincides with the apparently coordinated cessation of flowering in apical regions of all inflorescences on the plant. Keiller and Morgan (1988) showed that, prior to this time, the apical regions are stronger sinks for assimilate, and hence receive priority over young pods and their seeds, which are thus more likely to abort than once they are receiving a strong flow of assimilate. Flowers and pods can synthesise their own phytohormones (Bouttier and Morgan, 1992), which do not appear to be important factors in lack of sink strength

and hence liability to abort, which is more a function of assimilate, water and nutrient supply.

Within the crop canopy the mainstem and first-formed upper branches have priority for assimilate. When pods were prevented from forming on these by daily removal of stigmata and anthers (Tommey and Evans, 1992), the lower branches produced more pods and seeds, although not enough to make up for the loss.The experimental technique was designed to minimize damage to the flower canopy and hence radiation profile. Removal of stigmata on lower branches actually increased yield, with better pod and seed survival and growth on mainstem and upper branches, indicating that a more determinate habit may improve yield under most conditions. Other changes which could improve light relationships within the canopy include the apetalous character, more upright pods, and possibly longer but fewer pods each with more seeds.

Assimilate reserves built up pre-anthesis do not appear to contribute significantly to pod and seed growth, probably representing less than 10% except under conditions of severe water stress.

QUALITY CHANGES DURING SEED DEVELOPMENT

Droplets of storage oil first appear in cotyledons of the embryo at about 18 days after pollination, and then increase in size and number between 20 and 30 days, corresponding to the beginning of rapid growth of the seed. Oil percentage then reaches a plateau at physiological maturity (Hocking and Mason, 1993). Factors which accelerate or arrest maturity such as high temperature, water stress or frost (Daun *et al*,1985) tend to reduce final oil content, whereas lower temperatures or irrigation may increase it. Fatty acid composition (Romero, 1991) follows a pattern reflecting the change from saturated acids to the main unsaturated acid storage components, oleic and linoleic acids, with erucic acid in older cultivars. Linolenic acid content decreased from an initially high value to that characteristic of the mature seed. Again, factors which curtail development will alter the final balance of fatty acids, for example high temperatures will reduce linoleic or erucic acids by curtailing desaturation or extension of the oleic acid molecule respectively. Frost damaged seed may contain more saturated fatty acids than normal seed.

Protein content as a percentage is high in the early stages of seed development, but the laying down of substantial quantities of storage protein takes place during the main seed growth phase, as for oil (Hocking and Mason, 1993). Factors which decrease oil content such as high temperature tend to increase protein content, as does increased nitrogen availability.

Glucosinolates, the mainly undesirable components of seed meal after oil extraction, also accumulate in the seed during growth, after synthesis in pods and elsewhere in the plant (de March *et al* , 1989). In high glucosinolate cultivars, Bilsborrow *et al* 1993 showed that a peak was reached in the pod walls at 400-600°C d from pollination. A rapid decline in pod wall glucosinolates then occurred during the active seed growth phase, when seed glucosinolates increased at a rate of about 8μmol per 100°C d. In low glucosinolate cultivars, an earlier and lower peak was reached in the pod walls at 300°C d, followed by a slow increase in seed glucosinolates at about 1μmol per day until maturity. While frost may reduce glucosinolate levels in the mature seed by halting development, levels may be increased by water stress, high temperatures, disease or sulphur application.

High seed chlorophyll is another quality problem, and is associated with immaturity, either where crops are cut prematurely, when seasons are not long enough or when frost intervenes (Daun *et al*,1985).

REFERENCES

Bilsborrow, P.E., Evans, E.J., Murray, F. and Zhao, F.J. (1993) Glucosinolate changes in developing pods of single and double low varieties of autumn-sown oilseed rape (*B.napus*) . *Annals of Applied Biology* 122, 135-143.

Bouttier, C. and Morgan, D.G. (1992) Development of oilseed rape buds, flowers and pods *in vitro*. *Journal of Experimental Botany* 43, 1089-1096.

Daun, J.K., Clear, K.M. and Mills, J.T. (1985) Effect of frost damage on the quality of canola (*B. napus*). *Journal of the American Oil Chemists Society* 62, 715-719.

De March, G., McGregor, D.I. and Seguin-Schwartz, G. (1989) Glucosinolate content of maturing pods and seeds of high and low glucosinolate summer rape. *Canadian Journal of Plant Science* 69, 929-932.

Hocking, P.J. and Mason, L. (1993) Accumulation, distribution and redistribution of dry matter and mineral nutrients in fruits of canola (oilseed rape), and the effects of nitrogen fertilizer and windrowing. *Australian Journal of Agricultural Research* 44, 1377-1388.

Keiller, D.R. and Morgan, D.G. (1988) Effect of pod removal and plant growth regulators on the growth, development and carbon assimilate distribution in oilseed rape (*Brassica napus* L.). *Journal of Agricultural Science, Cambridge* 111,357-362.

Kjellstrom, C. (1991) Growth and distribution of the root system in *Brassica napus*. In: McGregor, D.I. (ed) *Proceedings GCIRC Eighth International Rapeseed Congress*, Saskatoon, Canada, pp. 722-726.

Leterme, P. (1988) Modélisation du fonctionnement du peuplement de colza d'hiver en fin de cycle: élaboration des composantes finales du rendement. In: *Colza: Physiologie et Elaboration du Rendement* CETIOM, Paris, pp. 124-129.

Major, D.J. (1975) Stomatal frequency and distribution in rape. *Canadian Journal of Plant Science* 55, 1077-1078.

Mendham, N.J. and Salisbury, P.A. (1995) Physiology - crop development, growth and yield. In: Kimber, D.S. and McGregor, D.I. (eds) *Production and Utilization of Brassica Oilseeds* . CAB International, Oxford. (due September).

Mendham, N.J., Shipway, P.A. and Scott, R.K. (1981) The effects of delayed sowing and weather on growth, development and yield of winter oil-seed rape (*Brassica napus*). *Journal of Agricultural Science, Cambridge* 96, 389-416.

Mendham, N.J., Russell, J. and Buzza, G.C. (1984) The contribution of seed survival to yield in new Australian cultivars of oil-seed rape (*Brassica napus*). *Journal of Agricultural Science, Cambridge* 103, 303-316.

Morrison, M.J., McVetty, P.B.E. and Shaykewich, C.F. (1989) The determination and verification of a baseline temperature for the growth of Westar summer rape. *Canadian Journal of Plant Science* 69, 455-464.

Norton, G., Bilsborrow, P.E. and Shipway, P.A. (1991) Comparative physiology of divergent types of winter rapeseed. In: McGregor, D.I. (ed) *Proceedings GCIRC Eighth International Rapeseed Congress*, Saskatoon, Canada, pp. 578-582.

Pechan, P.A. and Morgan, D.G. (1985) Defoliation and its effects on pod and seed development in oil seed rape (*Brassica napus* L.). *Journal of Experimental Botany* 36, 458-468.

Rao, M.S.S., Mendham, N.J. and Buzza, G.C. (1991) Effect of the apetalous flower character on radiation distribution in the crop canopy, yield and its components in oilseed rape (*Brassica napus*). *Journal of Agricultural Science, Cambridge* 117,189-196.

Romero, J.E. (1991) Fatty acid composition of the triacylglycerol fraction in developing *Brassica rapa* seeds. In: McGregor, D.I. (ed) *Proceedings GCIRC Eighth International Rapeseed Congress*, Saskatoon, Canada, pp. 1826-1830.

Salisbury, P.A. and Green, A.G. (1991) Developmental responses in spring canola cultivars. In: McGregor, D.I. (ed) *Proceedings GCIRC Eighth International Rapeseed Congress*, Saskatoon, Canada, pp. 1769-1774.

Smith, L.J. and Scarisbrick, D.H. (1990) Reproductive development in oilseed rape (*Brassica napus* cv. Bienvenu). *Annals of Botany* 65, 205-212.

Sylvester-Bradley, R. and Makepeace, R.J. (1984) A code for stages of development in oilseed rape (*Brassica napus* L.). *Aspects of Applied Biology* 6, 399-419.

Thurling, N. and Kaveeta, R. (1992) Yield improvement of oilseed rape (*Brassica napus* L.) in a low rainfall environment. I. Utilization of genes for early flowering in primary and secondary gene pools. *Australian Journal of Agricultural Research* 43, 609-622.

Tommey, A.M. and Evans, E.J. (1992) Analysis of post-flowering compensatory growth in winter oilseed rape (*Brassica napus*). *Journal of Agricultural Science, Cambridge* 118,301-308.

Wright, P.R., Morgan, J.M., Jessop, R.S. and Cass, A. (in press) Comparative adaptation of canola (*Brassica napus*) and mustard (*B. juncea*) to soil water deficits: yield and yield components. *Field Crops Research.*

Yates, D.J. and Steven, M.D. (1987) Reflexion and absorption of solar radiation by flowering canopies of oil-seed rape (*Brassica napus* L.) *Journal of Agricultural Science, Cambridge* 109, 495-502.