COMPARATIVE PHYSIOLOGY OF DIVERGENT TYPES OF WINTER RAPESEED

G. Norton, P.E. Bilsborrow, P.A. Shipway

University of Nottingham (SA), Sutton Bonington
Loughborough, Leics. LE12 5RD U.K.

INTRODUCTION

The overall pattern of growth and development of winter rapeseed is well established and is qualitatively similar for a number of cultivars (Bilsborrow and Norton, 1984: Mendham *et al*, 1981a+b; Daniels *et al*, 1986:). Husbandry factors such as sowing date, plant density, fertilisation and water may modify the extent of growth and the duration of development but not the general pattern (Mendham *et al*, 1981a+b). Winter rapeseed cultivars exhibit considerable variation with respect to plant height. In recent years shorter cultivars have replaced the much taller types grown in the previous decade. While average yields have increased slightly over this period much of this increase can be attributed to improved husbandry rather than the cultivar.

This presentation will be concerned with a comparison of two rapeseed types with contrasting plant heights with respect to their detailed physiology throughout crop development and the contribution of different plant organs within the crop profile to plant development at different stages and ultimate seed yield. Such studies should eventually enable an ideal rapeseed ideotype to be proposed as an objective for plant breeders.

MATERIALS AND METHODS

The growth and development of two contrasting rapeseed cultivars, (Victor and Rafal with maximum heights of 160+ and 100 cm respectively) was investigated over a period of seven years. The undisturbed standing crop (field or experimental plots) was sampled in successive layers of 20 cm depth (area 1 x 1 m) from the top to ground level by means of a frame erected *in situ*. Harvests were usually taken at weekly intervals following the onset of spring growth until seed maturity. Destructive growth analysis was carried out on each sample in the laboratory. Radiation measurements (Total and PAR) were taken at weekly intervals throughout the growing season using tube solarimeters situated at 20 cm intervals from ground level to the top of the standing crop. Incident and reflected radiation were measured by tube solarimeters appropriately situated above the crop. Gross photosynthesis measurements of the individual plant organs within each 20 cm layer comparable with samples taken for growth analysis, were made using a $^{14}CO_2$ pulse feeding procedure (Incoll, 1975). In the case of Victor, total chlorophyll contents of individual organs comprising the respective 20 cm sampling layers were estimated and these taken as an indication of photosynthetic capacity.

RESULTS AND DISCUSSION

Detailed consideration of the results will be presented elsewhere. In this contribution only the broad outlines will be presented.

The growth and development of rapeseed can be divided into four distinct stages: 1. Vegetative; 2. Flowering and development of the reproductive framework; 3. Pod development; 4. Seed development (Bilsborrow and Norton, 1984). Each stage will be considered with respect to the two types and the significance of any differences discussed.

1. Vegetative

Maximum leaf dry matter and area in association with limited stem elongation was attained during this stage. Despite obvious variations between seasons both cultivars produced similar leaf area although leaf dry matter production was always higher for Rafal (Table 1). At the end of this developmental stage, leaf tissues accounted for in excess of 70% of the total dry matter of both cultivars. Plant size at the end of this developmental stage has been found to determine potential crop yield but the extent to which this is realised is moderated by events in subsequent growth stages.

2. Flowering and development of the reproductive framework

This stage is initiated by the onset of rapid stem elongation and flowering and ends on the completion of flowering and the reproductive framework but before any appreciable pod growth has occurred.

Flowering is accompanied by the production of the reproductive framework and the attainment of maximum plant height but with little pod development. Certain features of this stage deserve amplification. Dry matter accumulation increased rapidly whereas the green area index remained constant (Table 1). The contribution of leaf tissues to the green area (and total dry matter) declined throughout this stage. This was due to leaf losses beginning at the lowest level in the crop profile and gradually progressing upwards. Leaf losses were more severe in Rafal than Victor. Loss of leaf green area was compensated for by the production of stems and branches. Total stem and branch green area and dry matter were comparable in both types. Thus at the end of this developmental stage the newly formed pods were restricted to the top 60 cm of the crop profile in both cultivars. The flower and later pod bearing layers were composed almost entirely of stems and branches with some leaf tissue in the lower pod bearing strata. Leaf tissue was concentrated in the lower horizons of the crop profile (20 - 100 cm in Victor and 20 - 60 cm in Rafal). No leaf tissue remained below 20 cm in either cultivar. Attenuation of incident radiation (Total and PAR) was especially marked in the top 60 cm of the crop with around 70 - 80% of the incident PAR being absorbed by this region in both cultivars. Between 50 and 20% of the total incoming radiation and PAR respectively were reflected by Rafal (No measurements available for Victor). Notwithstanding the high absorption of incident radiation by the flower bearing layers, the photosynthetic capacity of the component tissues was found to be low (Rafal). The contribution of the leaf bearing layers lower down the crop profile was small due to the low intensity of radiation penetrating to this depth in the crop. Throughout this stage the developing reproductive structure represented the major sink for assimilates produced mainly by leaf tissue and to a lesser extent the stems and branches themselves (Bilsborrow and Norton, 1987; Chapman *et al*, 1984; Rood *et al*, 1984). The intense competition for assimilates between the developing reproductive structure and newly formed pods resulted in the loss of between 20 - 25% of the 15000 potential pods m^{-2} in both cultivars at the end of this stage. Factors other than the availability of assimilates may also be involved in loss of potential pods.

The major physiological differences between the two cultivars during this stage were:

(a) Rapid loss of leaf area by Rafal (50%) compared with Victor (30%).

(b) Flowers and later pods, pod bearing branches and stems were restricted to a 60 cm layer at the top of the crop. Leaf tissue accounted for 20% and 10% of the total green area of the pod bearing layers of Victor and Rafal respectively at the end of this stage.

3. Pod development

Maximum pod area and hull dry weight was achieved during this stage with the formation of a dense pod canopy 60 cm deep at the top of the crop. In all but exceptional years the reproductive framework of Rafal was strong enough to maintain a fully erect growth habit to plant maturity. Victor lodged badly, long before pod development was completed so that the pod bearing layers were concentrated between 60 and 120 cm. Leaf senescence continued to proceed rapidly and leaf area amounted to around 5% of the total green area of Rafal (0.25 out of 3.65) by the end of this development stage. Victor retained its leaf tissue longer with about 30% of the total green area (1.85 out of 5.1) accounted for as leaf when maximum pod area was attained. All this leaf tissue was located in the lower part of the pod layer and immediately below and its contribution to total plant photosynthesis would have been small. 80% of the incident radiation and almost all the PAR was attenuated by the pod bearing layer. Thus the stems and branches, pods and some bract-like leaves lower down the pod bearing layer constituted the major photosynthetic tissues during this stage. The photosynthetic efficiency of the pod and stem tissue was found to be inferior to that of leaf tissue on an equivalent area basis (Rafal). It was concluded that there were insufficient assimilates to maintain the continued development of all the pods and seeds contained therein. Pod and seed losses were progressively more severe in the lower regions of the pod canopy presumably due to mutual shading from above. Losses amounted to 40% of the potential pods in both cultivars by the end of this stage.

Thus the major differences between the two cultivars on the completion of pod development were: a. The taller cultivar lodged badly before the completion of pod development whereas the shorter cultivar generally remained erect. b. Leaf retention was more prolonged in Victor resulting in this cultivar having a proportionately higher green area (5.1) compared with Rafal (3.65). c. The effectivity of this additional green area in photosynthesis is doubtful since dry matter accumulation overall and pod growth (area and weight) were almost identical in both types. d. Victor retained slightly more pods than Rafal.

4. Seed Development

Seed development proceeded after the attainment of maximum pod area and hull weight. Throughout this period stem including branches and hull dry weight and area remained constant. Pod losses were relatively small throughout this period but Victor retained many pods that were devoid of seed (3000 m^{-2}). Thus at maturity approximately 60% of the potential pods were retained by both cultivars. Only 30% of the potential seeds attained maturity in both cultivars. In Rafal, all yield components (pod numbers, seed numbers per pod, seed weight) declined down the profile. Since the location of the pods in the crop canopy changed when Victor lodged no conclusions could be made with respect to yield components. Rafal was almost devoid of leaf tissue throughout pod filling whereas a significant amount of leaf tissue persisted in Victor (approximately 20% total green area) until seed maturity. This was all located in the pod bearing layer. Stem and pod green areas were similar for both cultivars and remained constant throughout. Because of the leaf retention by Victor, the total green area of this cultivar was 25% greater than Rafal. In excess of 70% total incident radiation was absorbed by the pod bearing layer of both cultivars. PAR absorption (measured only in Rafal) by the pod layer was 90%. 95% of the gross photosynthesis of Rafal took place in the pod layer. (Gross photosynthesis measurements were not determined with Victor). Gross photosynthesis of Rafal declined throughout pod filling to around 38% of the maximum attained just before peak flowering. This decline in photosynthetic capacity could not be attributed to a proportional loss of green area but to a less efficient photosynthesis of stem and pod tissue compared with leaf tissue. Remobilisation of dry matter within the plant did not contribute to seed development. In both cultivars it would appear that ultimate seed yield is determined by the photosynthetic capacity of the pods, stems and branches in Rafal with an additional small contribution from residual leaf tissue in Victor. The gross photosynthetic capacity of these layers would be moderated by the density of the pod bearing layers as affected by lodging. Thus Rafal outyielded Victor (442 compared with 320 $g.m^{-2}$) notwithstanding a more favourable green area index from the latter (5.1 - 4.1) compared with the former (3.65 - 3.2). Differences in total biomass production could be attributed to differences in seed yield. Final harvest indices were 0.35 and 0.27 for Rafal and Victor respectively. Lodging reduced the effective photosynthetic capacity of Victor during stages 3 and 4, thus pod retention was reduced dramatically and a considerable proportion of those retained did not contribute to crop yield (empty pods). Had Victor retained an erect growth habit final seed yield would probably have been comparable with that of Rafal.

CONCLUSIONS

The major conclusions from this comparative study are:

(1) Leaf area indices were similar for both cultivars during the vegetative stage but leaf dry matter production was much higher in Rafal.

(2) Leaf retention was markedly different for the two cultivars. Rafal was almost completely defoliated at pod development whereas Victor retained appreciable leaf tissue until maturity.

(3) Pod development in the erect pod canopy was similar but lodging adversely affected pod retention and the capacity of these to support seed development. Lodging would adversely affect the photosynthetic capacity of pod bearing layers with the consequent reduction in seed yield compared with erect types.

(4) Seed yield was determined by the photosynthetic capacity of the pods, stems and branches plus residual leaf. Pod, stems and branches were inefficient in photosynthesis compared with leaf tissue and it is clear that this is the major factor determining the yield of any rapeseed cultivar.

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Table 1. Summary of physiological data for two rapeseed cultivars

Rafal

Maximum Plant height (cm): 100+

Dry matter production g m^{-2}

Developmental stage	Total	Leaf	Stem	Pod	Seed
1 end	230	180	50	-	-
2 end	630	90	460	70	-
3 end	1040	10	520	490	-
4 end	1270	-	480	750	440

Victor

Maximum Plant height (cm): 160+

Dry matter production g m^{-2}

Development stage	Total	Leaf	Stem	Pod	Seed
1 end	145	105	40	-	-
2 end	745	127	485	35	-
3 end	1000	70	520	390	40
4 end	1180	20	470	650	320

Green area — Rafal

Developmental stage	Total	Leaf	Stem	Pod
1 end	4.15	3.45	0.8	-
2 end	4.25	2.10	1.60	0.40
3 end	3.65	0.25	1.70	1.70
4 end	3.20	0.00	1.60	1.60

Green area — Victor

Developmental stage	Total	Leaf	Stem	Pod
1 end	4.95	4.1	0.85	-
2 end	4.50	2.80	1.35	-
3 end	5.10	1.85	1.50	1.85
4 end	4.10	0.80	1.60	1.70

	Rafal	Victor
Pod numbers m^{-2}		
Potential	13,260	15,000
Harvested	7,600	8,300*
Seeds pod^{-1}		
Potential	30	28
Harvested	11	10
Harvest index	0.35	0.27

* Including 3000 empty pods