WINTER OILSEED RAPE

analysis of yield formation

and crop type design for higher yield potential

Promotoren: dr.ir. R. Rabbinge,
hoogleraar in de theoretische produktie-ecologie

dr.ir. H. van Keulen,
hoogleraar in de duurzame dierlijke produktie

B. Habekotté

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The work for this thesis was conducted at The DLO-Research Institute for Agrobiology and Soil Fertility (AB-DLO) and was financed by The Netherlands Grain Centre and AB-DLO.

Stellingen

1. Een gewasgroeisimulatiemodel is een krachtig instrument voor integratie van kennis van deelaspecten van de opbrengstvorming, voor toetsing van hypothesen en voor het genereren van nieuwe onderzoeksvragen met betrekking tot de opbrengstvorming en het ontwerpen van produktievere gewastypen.

Dit proefschrift

2. De lage opbrengsten van winterkoolzaad in vergelijking met wintertarwe onder optimale teeltomstandigheden zijn toe te schrijven aan de relatief vroege afrijping, lage lichtbenuttingsefficiëntie en lage oogstindex van winterkoolzaad.

Dit proefschrift

3. Reflectie en absorptie van licht door gele kroonblaadjes hebben een negatief effect op zowel de totale biomassaproduktie als de oogstindex van winterkoolzaad.

Dit proefschrift

4. Het opbrengstpotentieel van winterkoolzaad kan het meest effectief vergroot worden door een combinatie van eigenschappen waarbij beide de source- en sinkcapaciteit voor zaadvulling worden verbeterd, met name: zo vroeg mogelijke bloei en vrijwel volledige lichtabsorptie door het blad rond volle bloei, zo laat mogelijke afrijping gekoppeld aan een lange zaadvullingsperiode, opstaande geclusterde hauwen, verkleining of afwezigheid van gele bloemblaadjes, verbetering van de zaadzetting en verhoging van de potentiële groeisnelheid van zaden.

Dit proefschrift

5. De tot de verbeelding sprekende potentiële mogelijkheden voor toepassing van gewasgroeisimulatiemodellen, zoals analyse van opbrengstvorming, het ontwerpen van produktievere gewastypen, opbrengstvoorspellingen en opbrengstverwachtingsberekeningen voor verschillende locaties en teeltmaatregelen kunnen de kritische zin ten aanzien van beschikbare modellen belemmeren.

6. Vanuit het oogpunt van duurzaamheid is de grootste uitdaging voor de komende eeuw het realiseren van een duurzame energievoorziening, waarbij het gebruiksniveau van fossiele brandstoffen niet hoger is dan het ter beschikking komen van vervangbare en/of vernieuwbare energiebronnen.

7. Koolzaadolie als basis voor de produktie van biodiesel heeft alleen toekomst voor gebruik in markt-niches.

8. Landbouwsystemen gericht op zo veel mogelijk regionaal sluiten van nutriëntenkringlopen en het zo veel mogelijk afzien van het gebruik van kunstmest en bestrijdingsmiddelen vereisen, bij een te verwachten wereldbevolking van 7.7-11.4 miljard mensen in 2040, een uitbreiding van handel in voedsel tussen wereld-regio's, hetgeen strijdig is met het uitgangspunt van regionaal sluiten van nutriëntenkringlopen.

Wetenschappelijke Raad voor het Regeringsbeleid, 1994. Duurzame risico's: een blijvend gegeven. Sdu Uitgeverij Plantijnstraat, Den Haag, 208 pp.

9. De laatste loodjes zijn niet het zwaarst.

10. Het zoeken naar 'de zin van ziek zijn' leidt tot uitwassen van het 'new age' denken waarbij men alles probeert begrijpelijk te maken, maar niet verklaart.

11. 'Vroeger' kreeg men lichamelijke klachten van te zwaar werk op het land, nu van te lang zitten achter een computer.

Stellingen behorend bij het proefschrift van Barbara Habekotté:

"Winter oilseed rape,
analysis of seed yield formation and crop type design for higher yield potential"

Wageningen, 28 mei 1996.

ABSTRACT

Habekotté, B., 1996. Winter oilseed rape, analysis of yield formation and crop type design for higher yield potential. Ph.D. Thesis, Wageningen Agricultural University, Wageningen, the Netherlands, 156 pp.

The study described in this thesis focuses on quantifying the seed yield formation of winter oilseed rape and on identifying crop traits and combinations of traits for increasing seed yield potential in North-West Europe, by combining experimental research with crop growth simulation. The experimental research yielded quantitative detailed data on pod formation, seed set and seed filling. Results on light absorption, light use efficiency and crop growth showed that the first two of these explain much of the variation in crop dry matter production. An empirical model was developed to describe the phenological development of the crop in relation to environmental factors. Comparison of its predictions of various developmental stages with data recorded in Germany, the Netherlands and France, showed that much of the variation in duration of the various developmental phases is attributable to the combined effect of temperature (including vernalization) and photoperiod or to the effect of temperature only. Key processes of crop growth, phenological development and partitioning of assimilates to the seeds were integrated in a simple crop growth model, whose performance was evaluated with data used for parameterization and with independent data. The model recognizably reproduced the observed variation in various crop characteristics, such as total dry matter production, pod density, seed density and seed yield resulting from different sowing dates and growing seasons. Differences between sowing dates were simulated better than differences between years. The model was used to identify options for increasing seed yield potential. Comparison with the higher-yielding reference crop, winter wheat, showed that light absorption, light use efficiency and harvest index were relatively weak yield-determining components. Crop traits and combinations of traits were identified to obtain higher values in these components. Finally, high-yielding crop types were designed and tested in simulations for various locations in North-West Europe and showed good prospects for increasing seed yield potential.

Additional keywords: *Brassica napus* L., crop growth, phenological development, seed yield, potential, increase, ideotype, model, simulation, North-West Europe

VOORWOORD

Een onderzoeker kan alleen zijn werk verrichten binnen een netwerk van personen met verschillende functies. Zo heb ik in ieder geval de rol als onderzoekster ervaren. Op deze plek wil ik dan ook graag ieder bedanken die het tot stand komen van dit proefschrift heeft mogelijk gemaakt. Het zal niet lukken iedereen daarbij bij naam te noemen.

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De eerste drie jaar van het onderzoek werden uitgevoerd in dienst van de Stichting Nederlands Graan Centrum (NGC), gedetacheerd bij het AB-DLO. Deze drie jaar volgden de leden van de door het NGC samengestelde begeleidingscommissie het onderzoek. Het waren leerzame en plezierige bijeenkomsten en ik wil dan ook graag Gerard Borm (PAGV), Jan Goudriaan (LUW-TPE), Marloes Jorna (NGC) en Matthieu Pustjens (Van der Have) bedanken voor hun bijdrage aan het onderzoek.

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CONTENTS

ACCOUNT

The Chapters 2-5 in this thesis have been included, in part or in whole, in the following publications:

CHAPTER 2	Habekotté, 1993. Quantitative analysis of pod formation, seed set and seed filling in winter oilseed rape (*Brassica napus* L.) under field conditions. Field Crops Research, 35: 21-33.
CHAPTER 3	Habekotté, 1996a. A model of the phenological development of winter oilseed rape (*Brassica napus* L.) in North-West Europe. Submitted to Field Crops Research.
CHAPTER 4	Habekotté, 1996b. Evaluation of seed yield determining factors in winter oilseed rape under potential growth conditions (*Brassica napus* L.) by means of crop growth modelling. Submitted to Field Crops Research.
CHAPTER 5	Habekotté, 1996c. Options for increasing seed yield of winter oilseed rape (*Brassica napus* L.): a simulation study. Submitted to Field Crops Research.

CHAPTER 1

GENERAL INTRODUCTION

Origin, distribution and products

The terms 'oilseed rape' or 'rapeseed' refer to two Brassica species grown for oil, *Brassica napus* L. and *Brassica campestris* L. (Thompson, 1983; Weiss, 1983). *B. campestris* L. probably originates from Eurasia. The oldest known references to its cultivation come from India, China and Japan, in circa 2000 BC (Weiss, 1983). *B. napus* L. is probably a cross between the species *B. oleacea* L. and *B. campestris* L. (Bunting, 1986). The first known description of *B. napus* L. was made by Dodoens (1578) (Toxopeus, 1979; Lindemans, 1952). He described the plant as related to cabbage but grown for seed only, for the production of rape oil. Until the sixteenth century production seems to have been confined to the Netherlands. It is generally agreed that its subsequent introduction to other European countries was based on seed introduced from the Netherlands (Lindemans, 1952; Anderson, 1981). The crop is currently widely grown, in Canada, North, Central and South America, Asia, the former USSR, Oceania and Africa (FAO, 1994; Verheijen, 1995).

Oilseed rape is a crop of temperate climates. There are spring-sown and autumn-sown varieties. The autumn-sown varieties yield more than the spring sown varieties, but the latter grow where winter conditions are too severe for the autumn-sown varieties. For example, in Canada, where winters are severe, the crop is mainly grown as a spring crop, whereas in Europe, autumn-sown varieties are predominant.

Oilseed rape provides two main products: the oil (from the seeds), and meal (crushed seeds). At present the oil is mainly used for human consumption, though it is used on a small scale as a lubricant and biodiesel fuel. The meal is used as a high protein feed supplement for livestock and poultry. The advent of varieties with a low eruric acid content in the seventies has improved the quality of the oil for human consumption. The introduction of varieties with low glucosinolate content at the beginning of this decade has improved the quality of the meal for livestock and poultry.

In this thesis strategies for increasing the seed yield potential of autumn-sown varieties of *Brassica napus* L., in North-West Europe are studied.

Winter oilseed rape in perspective

World oilseed consumption has undergone a rapid increase and in the near future world demand for vegetable oils and for meal are expected to rise (Bijman, 1994; Verheijen, 1995). The major determinants for these increases in consumption are population growth, especially in China, India, South America and Africa and increases in purchasing power. Increasing prosperity is accompanied by increasing per capita consumption of vegetable oil and animal oils and fats. Moreover, per capita consumption of animal protein in meat and dairy products rises, which in turn increases the demand for oilmeal as cattle feed. In high income countries, vegetable oils are being substituted for animal oils in the diet, for health reasons. The consumption of vegetable oils is not increasing greatly in Europe (Verheijen, 1995), because the substitution of vegetable oils for animal oils and fats seems to be almost complete. The demand for oilmeal is likely to stabilize because of the stagnation of per capita consumption of animal protein, stagnation in pork production and a change in price ratio between grains and oilmeals since the EU policy reform in 1993/94. Any increase in total consumption will mainly result from a slight growth in population and from the demand for non-food purposes such as environmentally friendly lubricants and fuel. Rapeseed oil has particularly suitable qualities for this kind of use.

Oilseed rape is the most important oilseed crop of temperate climates. Its oil ranks as third most consumed oil after soybean oil and palm oil and its meal as third most consumed meal after soybean meal and cotton meal. China, EU, India and Canada are the major producers (Verheijen, 1995). Oilseed rape production, like the production of other oilseeds, will have to grow in the coming years to meet increasing demand in the world. As the possibilities to expand acreage are limited, any increased production will have to be based largely on higher productivity per ha. In the EU, the Blair House Agreement, which has limited the acreage for growing of oilseeds since 1992/93, also implies that increases in production will have to come from increased production per allowed hectare. In general, increases in production per ha^{-1} may also lead to more efficient use of other production sources, such as labour, capital, energy, nutrients and pesticides, if applied judiciously (Rabbinge, 1986; De Wit, 1992).

Increasing seed yield

Seed yields of winter oilseed rape have been increased slightly in several European countries by improved agronomic practices and breeding (Gardner, 1994). By optimizing agronomic measures, such as sowing rate, sowing date, irrigation, nutrient application, and protection against pests and diseases it has become possible to attain potential seed yields, i.e. seed yields defined by genetic characteristics of the crop and the climatic factors radiation, temperature and daylength. Breeding has resulted in higher seed yields by selecting for high-yielding lines and by eliminating constraints e.g. susceptibility to low temperatures in winter, to diseases, to lodging or to shattering of pods (Thompson and Hughes, 1986).

Despite these efforts, the seed yield increases and seed yields of winter oilseed rape are low compared to winter wheat, a widely grown autumn-sown seed crop in temperate climates, as illustrated by the seed yields of both crops recorded in the central part of the Netherlands (Fig. 1.1). As winter oilseed rape uses the same photosynthetic pathway (C3) and its growth duration is similar to that of winter wheat, similar levels of production

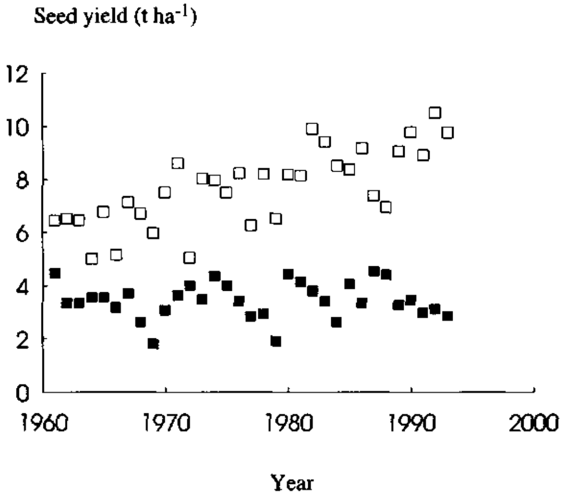

Figure 1.1 Seed yields of winter oilseed rape (solid symbols) and winter wheat (open symbols), grown under near optimal growing conditions in the central part of the Netherlands from 1961 to 1993 (Habekotté, 1989; van der Meulen, 1990a, b, 1991, 1993, 1994).

should be attainable (Daniels et al., 1986; Gosse et al., 1986). Current varieties of winter wheat in the Netherlands yield about 9 t ha^{-1} seed dry matter under near optimum growing conditions (Van der Meulen, 1990a, b, 1991, 1993, 1994). Taking into account the difference in chemical composition of the seeds of both crops (Penning de Vries et al., 1989), winter oilseed rape should yield about 5.8 t ha^{-1}, i.e. about 2.5 t ha^{-1} more than the mean seed yield currently achieved (Habekotté, 1989).

Seed yield increase has been hampered by breeding for improved seed quality, as this required backcrossing with lower-yielding spring varieties (Bunting, 1986; Bonthuis et al., 1987). Breeding for increased seed yields may be more effective if more is known about the traits the breeder should be selecting for (Thompson, 1983; Sedgley, 1991; Diepenbrock and Becker, 1992). The latter is the subject of this study.

Seed yield formation

Seed yield formation is the result of many interacting processes and their dependence on environmental factors. During the period from sowing until the onset of flowering, seed yield potential is set by the number of flower buds and leaf area index at onset of flowering (Mendham et al., 1981; Leterme, 1985). Leaf area index peaks around flowering and then declines, and stems and pods take over assimilate production (Brar and Thies, 1977; Chapman et al., 1984; Addo-Quaye et al., 1985). Conditions during flowering are particularly important for pod formation and seed set (Tayo and Morgan, 1975, 1979; Geisler and Henning, 1981; Evans, 1984; Daniels et al., 1986; Leterme, 1985; Keiller and Morgan, 1988). Seed filling is determined either by the sink capacity of the crop, governed by number of seeds and sink capacity of individual seeds, or by the source i.e. assimilate availability during seed filling (Mendham et al., 1981). Remobilization of reserve carbohydrates accumulated during earlier growth phases in roots, stems, leaves and pod hulls may also contribute to seed filling (Rood et al., 1984; Addo-Quay et al., 1985; Quilleré and Triboi, 1987).

Insight into the relative importance of yield-determining processes and crop characters requires quantitative analyses of components of yield formation in relation to crop physiological, phenological and morphological characters and the environmental factors radiation, temperature and daylength, followed by integrated analysis at crop level. This could result in a model that includes the key processes of yield formation and explains yield variation under varying environmental conditions.

Identification of yield-determining processes and crop characters

The development of the ideotype concept (Donald, 1968; Thompson, 1983; Sedgley, 1991, Rasmusson, 1991) has led to breeding, plant and crop physiology research focusing on identifying of simple crop characters which influence the physiological processes determining final seed yield (Thompson, 1983; Daniels et al., 1986; Thurling, 1974; Thurling, 1991). For example, crop biomass at flowering has been suggested as a criterion of yield potential (Mendham et al., 1981, 1984; Grosse et al., 1992a), smaller petals or apetalous flowers may improve light absorption and dry matter production by the green canopy (Mendham et al., 1981; Yates and Steven, 1987; Rao et al., 1991) and an increase in yield components, pods m^{-2} or seeds per pod may increase the sink capacity and the partitioning of assimilates to the seeds (Mendham et al., 1981; 1984). However, some of the strategies proposed are conflicting, the quantitative effects of crop traits on seed yield were often not clearly identified, and physiological and genetic interactions between characters often remained unclear (Diepenbrock and Becker, 1992; M.J.J. Pustjens, Van der Have, pers. comm., 1995; A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995). Moreover, the recording of some of the proposed characters in breeding programmes is sometimes considered to be too laborious and expensive (Diepenbrock and Becker, 1992; F. Grosse, Saaten-Union, pers. comm., 1995). Improvement in these aspects may enhance the effectiveness of breeding programmes and thus lead to increases in seed yields of winter oilseed rape.

Important crop physiological processes and crop characters for seed yield have mainly been identified on the basis of studies correlating crop characters with seed yield, by using different varieties in experiments in different growing seasons per location (Thurling, 1974; Grosse, 1989; Grosse et al., 1992a, b), on comparative crop growth analyses among varieties and environments (Rao et al., 1991; Mendham et al., 1981, Mendham et al., 1984) and on crop physiology research focusing on different aspects of seed yield formation.

In correlation studies the effects of various factors and their interactions can be studied by using statistical methods and experimental layouts. The results are defined by the genetic material used and by prevailing environmental conditions. Causal relationships based on underlying interacting processes of crop growth and development and their relationships with the environment often remain unclear and limit extrapolation of the results to other growing seasons and locations. The effects of crop characters on seed yield are difficult to quantify experimentally by comparative crop growth analyses between varieties, as many characters are involved, with their own- often different- responses to environmental factors. Studies on one variety in different environments are hampered by the influence of environmental conditions. Plant and crop physiology research has improved understanding of different aspects of yield formation and provides starting points for yield increase. However, there is a lack of studies that analyse the different aspects of yield formation in an integrated way.

Production ecology research may combine the objectives of the approaches mentioned above and may contribute to these approaches too. It aims at investigating the crop processes that determine yield and at integrated analyses of these processes in relation to the environment (Rabbinge, 1986). Models are needed to analyse the effects of various processes and crop traits on seed yield because yield is the outcome of the interaction between these processes and their dependence on the environment. Crop growth modelling also provides the opportunity to design high-yielding crop types. Their effect on final seed yield may be evaluated under different environmental conditions defined by agronomic measures, years and locations (Loomis et al., 1979; Spitters and Schapendonk, 1990; Lawn and Imrie, 1991; van Oijen, 1991; Hunt, 1993; Kropff et al., 1994; Aggarwal, 1995; Kooman, 1995).

Objectives and approach of the thesis

The main objectives of the study described in this thesis were:

I: To integrate existing knowledge on seed yield formation of winter oilseed rape, and to identify and fill in important gaps in this knowledge in order to explain seed yield formation in relation to environmental factors under potential growth conditions.

II: To quantitatively identify crop traits and combinations of traits for increasing seed yield potential of winter oilseed rape in North-West Europe.

The study focused on quantifying the general trends in potential seed yield formation of winter oilseed grown in North-West Europe, in relation to environmental factors, and on identifying the options for breaking these general trends in order to increase the seed yield. It may be expected that varieties adapted to a certain geographical region, such as North-West Europe, respond similarly to agronomic measures, environmental conditions (Mendham et al., 1981) and changes in crop characters. For example, later sowing generally results in reduced seed yields, whereas low temperatures in spring or summer retard the phenological development of the crop, and reduced seed set is generally partly compensated by increased mean seed weight, but ultimately leads to depressed seed yields. Therefore, quantification of the key processes of yield formation may be based on a reference crop, which in this study was the variety Jet Neuf. The options for increasing seed yield will not refer to relatively small differences in strategies of seed yield formation among existing varieties, but to more drastic changes in crop traits and combinations of traits. When the options are being identified, the measurability of crop characters and the genetic variability of these crop characters are borne in mind. Analysis of seed yield formation in the reference crop and of options to increase its seed yield potential may also form a reference frame for interpretating the yield formation strategies of different existing varieties.

In the study, field experiments were combined with simulations. Field experiments were carried out to answer questions about key processes of crop growth and seed yield formation such as light absorption, light use efficiency for total dry matter production, pod and seed set, seed filling and formation and relocation of reserve carbohydrates. These processes were quantified in relation to crop physiological and phenological characteristics and the environmental factors temperature and radiation. A simulation model was used to quantify crop phenological development in relation to temperature and photoperiod. Key processes of crop growth and phenological development were integrated in a crop growth model to explain seed yield variation under potential growth conditions. The model was used to identify weak and strong yield determining components of winter oilseed rape compared to winter wheat as high-yielding reference crop and for evaluating various crop traits and combinations of traits for increasing seed yield. Finally, the model was used to design and test crop types with increased seed yield potential in North-West Europe.

Outline of the thesis

Pod formation, seed set and seed filling are important aspects of the seed yield formation of winter oilseed rape and are studied experimentally in Chapter 2. Questions were addressed concerning 1) the period and extent of pod and seed abortion, 2) the effect of position in the canopy, defined by branch order and height, and time of pod initiation on pod and seed set, 3) the relation between pod and seed set and assimilate availability during relevant periods, 4) the potential growth rates of individual seeds and 5) the contribution of reserve carbohydrates to seed filling. Pod formation, seed set, seed filling and formation and relocation of reserve carbohydrates of winter oilseed rape, are analysed and described quantitatively.

In Chapter 3 experimental data of crop phenology recorded at different locations in North-West Europe are used to develop and test a sub-model to predict the emergence, onset and end of flowering and maturity of winter oilseed rape in relation to temperature and photoperiod.

In Chapter 4, light absorption, light use efficiency and total dry matter production were analysed experimentally. A crop growth model is used to integrate the key processes of crop growth, phenological development, pod and seed set and seed filling. The performance of the model is evaluated with experimental data used for parameterization, described in Chapters 2 and 4, and with experimental data derived from literature. Seed yield variation among sowing dates and years is analysed by using the model.

In Chapter 5, seed yield formation of winter oilseed rape is compared with that of the higher-yielding reference crop winter wheat, in terms of light absorption, light use efficiency and harvest index, to identify strong and weak yield-determining components. Options for seed yield increase, partly derived from previous chapters and from literature were evaluated quantitatively, by using the model introduced in Chapter 4. Finally, ideotypes for higher seed yield potential are designed and tested for different locations in North-West Europe.

The thesis concludes with a general discussion in which the methodology of the study, its scientific achievements, its usefulness for breeding and the implications of the findings for the cultivation of winter oilseed rape are evaluated (Chapter 6).

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CHAPTER 2

QUANTITATIVE ANALYSIS OF POD FORMATION, SEED SET AND SEED FILLING IN WINTER OILSEED RAPE (*BRASSICA NAPUS* L.) UNDER FIELD CONDITIONS

ABSTRACT

Pod formation, seed set and seed filling of winter oilseed rape (*Brassica napus* L.) were studied in two field experiments with the variety Jet Neuf. Variations in total dry matter production (source size) and pod density (sink size) were established by varying seed rate, plant density, sowing date and the application of shading. Pod formation and seed set per pod were recorded on different branches, at various heights in the canopy and on pods initiated at different times during flowering.

Pod density and seed density appear to be fully determined just after the end of flowering. The potential number of pods (i.e. the number of flower buds) did not appear to be a limiting factor, as at all positions in the canopy it was much higher than the number attained. Averaged over the whole canopy, pod set varied between 43 and 58 %. Potential and actual pod density were linearly related to cumulative dry matter production of the crop until the onset of flowering and until the end of flowering, respectively, i.e. to total assimilate availability over that period. The number of seeds per pod did not vary with height in the canopy. Primary branch number and the moment of pod initiation during flowering had some effect on the number of seeds per pod; however, this had little influence on the overall mean number of seeds per pod of the whole canopy and did not affect the differences among treatments. A linear relationship was found between seed density and dry matter production of the crop during flowering. Individual seed weight followed a sigmoid pattern when plotted against the temperature sum from the onset of flowering per flower bud until maturity. The pod hulls were the only competing sink during early seed fill and remobilization of reserve carbohydrates contributed at most 12 % to final seed yield.

INTRODUCTION

The area under oilseed rape has increased significantly in the EC in recent decades (Eurostat, 1975-87, 1991). Increased seed yields have been obtained by breeding and improved agronomic practices; however, they are moderate compared to winter wheat (Leterme, 1985; Daniels et al., 1986). A simple calculation of the theoretical potential seed yield of winter oilseed rape, compared to that of winter wheat of 11.4 t ha^{-1} (dry matter), and accounting for the higher energy content of the oilseeds, showed there was scope for improving yield up to 6.9 t ha^{-1} (Daniels et al., 1986), about 3.5 t ha^{-1} higher than current mean seed yields under near-ideal growing conditions in the Netherlands (Habekotté, 1989). It is a challenge for agronomists and breeders to identify the constraints to yield improvement and to suggest ways to realize higher seed yields.

Seed yield is the product of pod density, seeds per pod and mean seed weight. Growth before floral initiation already influences the potential number of pods through the number of leaves and consequently the potential sites for flowering branches in the leaf axils (Mendham and Scott, 1975). Flower buds start to develop at flower initiation just before or during winter, or early in spring (Mendham et al., 1981; Tittonel, 1988). Pods are initiated during flowering, and pod abortion and reduction in the potential number of seeds per pod occur during flowering and to some extent during the subsequent pod development phase. Losses of pods and seeds per pod seem to be heavier in the more shaded, lower parts of the canopy, especially in dense crops (Mendham et al., 1981). As branch order increases, fewer flowers form a pod and seed number per pod decreases (Tayo and Morgan, 1975; Geisler and Henning, 1981). The moment of pod initiation may also influence pod set and seed number per pod (Tayo and Morgan, 1975, 1979).

Experiments involving leaf removal, shading before and during flowering (i.e. varying source size) and varying the number of pods (sink size) have indicated that assimilate supply is an important factor determining pod formation and seed set (Tayo and Morgan, 1979; Evans, 1984; Leterme, 1985; Inaga et al., 1986; Keiller and Morgan, 1988b).

Generally, mean seed weight varies less than pod density and number of seeds per pod (Mendham et al., 1981; Sierts et al., 1987; Grosse, 1989). Growth rate of the seeds appears to be determined either by assimilate availability during seed filling and the number of competing seeds or by the maximum growth rate of the seeds (Mendham et al., 1981). Remobilization of reserve carbohydrates accumulated during earlier growth phases in roots, stems, leaves and pod hulls may contribute to seed filling (Rood et al., 1984; Addo-Quay et al., 1985). Quilleré and Triboi (1987) reported a contribution of at most 17.5 % to final seed yield under field conditions.

The aim of this study was to describe quantitatively the seed production process as a basis for developing a simple mechanistic crop growth model of winter oilseed rape. Such a model may then be used to determine the eco-physiological characteristics of the crop that limit seed yield, and to identify possibilities for yield improvement (Habekotté, 1996a, b; Chapters 4 and 5). The available basic information on the formation of yield components in oilseed rape partly refers to experiments on individual plants of summer and winter rape varieties, grown under controlled conditions, and partly needs to be further quantified for modelling purposes. Therefore, to increase quantitative insight in pod formation, seed set and seed filling in winter oilseed rape under field conditions, the following questions were addressed: 1) When and to what extent are pods and seeds aborted ? 2) What is the effect of position in the canopy (branch order and height) and moment of pod initiation on pod and seed set ? 3) Can potential and actual pod and seed density be explained in terms of cumulative assimilate supply during the formation period ? 4) What is the pattern of source- and sink-limited growth of individual seeds when related to the temperature sum from the onset of flowering ? 5) Do other sinks compete with seeds during seed filling and what do remobilized reserve carbohydrates contribute to final seed yield ?

MATERIALS AND METHODS

Two sets of field experiments were carried out in 1989 (sown in autumn 1988; experiment 1) and 1990 (sown in autumn 1989; experiment 2), respectively with variety Jet Neuf on a heavy clay soil near Wageningen, the Netherlands (5° 40' E, 51° 58' N). The experiments were laid out in a split plot design, with treatments as the main plots and harvest dates as sub-plots. Treatments were applied to establish variation in total dry matter production and pod density (number of pods per unit area) through varying seed rate, plant density, sowing date, removal of side branches and application of shading. The first experiment comprised four treatments and five replicates (Table 2.1). Low plant density was obtained by thinning by hand in autumn and again in early spring. Experiment 2 comprised four treatments with four replicates, except for treatment 1, having eight replicates. Shading was effected with black plastic netting, from the first week of flowering until final harvest, intercepting 60 % of the light.

Fertilization followed the current recommendations and pest and diseases were controlled such that crop damage was negligible in both years (Table 2.1). From early spring onwards, moisture content of the top soil (0-20 and 20-40 cm depth) and depth of the water table were measured periodically to estimate water availability to the crop. Irrigation was applied in 1989 to avoid drought stress. Daily maximum and minimum temperatures were recorded at the meteorological station in Wageningen, about 10 km from the experimental site. In experiment 1, temperature was recorded continuously in the open air and below the netting.

Crop development was recorded weekly from early spring until final harvest, using the phenological scale of Habekotté (1978). Gross sub-plot size was 8.64 m^2 of which 1.92 m^2 (net) was harvested periodically from early spring until early July to record total aboveground dry weight and the number of plants per m^2. Dry weight was determined after drying for 24 hours at 105 °C. At each harvest five plants per plot were randomly selected to determine weight of roots, green leaves, yellow leaves, main stem, side branches, flower buds, flowers, pod hulls, seeds and mean seed weight. In these samples data were also collected on pods with seeds, seedless pods (aborted pods still attached to the plant), peduncles (aborted flower buds, flowers or pods), and open pods (shattered or damaged by birds). Potential number of pods was defined as the sum of pods, aborted pods, peduncles and open pods. Potential and actual pod density were calculated as potential or actual number of pods per five plants divided by the weight of pods per five plants, multiplied by total pod weight per m^2. Seed density was derived from total seed weight and mean seed weight, and the number of seeds per pod from pod density and seed density.

Table 2.1 Details of the field experiments.

Detail		Experiment 1	Experiment 2
Treatments (tr.):		1) Low plant density (lpd)	1) Low seed rate (lsr)
		2) High plant density (hpd)	2) High seed rate (hsr)
		3) Low plant density and removal at flowering of all side branches except the highest (rsb)	3) Low seed rate and later sowing (lso)
		4) Low plant density and shading, leaving 40 percent of full light from the first week of flowering till final harvest (sha)	4) Low seed rate and shading (sha, see tr.4, in experiment 1)
Sowing date	:	August 23, 1988	August 24, 1989 (early) September 9, 1989 (late)
Sowing rate	:	10 kg ha^{-1}	6 kg ha^{-1} (low seed rate) 10 kgha^{-1} (high seed rate)
Row distance	:	24 cm	24 cm
Plant density in spring	:	tr. 1: ca. 24 pl m^{-2}	tr. 1: ca. 42 pl m^{-2}
	:	tr. 2: ca. 68 pl m^{-2}	tr. 2: ca. 50 pl m^{-2}
	:	tr. 3: ca. 23 pl m^{-2}	tr. 3: ca. 57 pl m^{-2}
	:	tr. 4: ca. 27 pl m^{-2}	tr. 4: ca. 41 pl m^{-2}
Date of start shading	:	20-4-1989	24-4-1990
Harvest dates: (day-month)	:	13-3, 28-3, 10-4, 24-4, 8-5, 16-5, 22-5, 29-5, 5-6, 12-6, 19-6, 26-6, 3-7, 10-7	22-3, 18-4, 1-5, 14-5, 28-5, 18-6, 9-7
Soil type	:	40 % Clay 1.9 % Humus 0.1 % Lime pH-KCL= 6.8	52 % Clay 2.5 % Humus 0.8 % Lime pH-KCL=7.4
Soil reserves		35 kg N ha^{-1} (0-100 cm)	36 kg N ha^{-1} (0-60 cm)
Fertilizer		13-3-1989: 180 kg N ha^{-1}	28-3-1990: 150 kg N ha^{-1}
Crop protection			
Autumn	:	Weeds (1.3 kg ha^{-1} metazachloor), Stem flea beetle (*Psylliodes chrysocephala*; 500 g ha^{-1} Parathion), Slugs (60 g ha^{-1} Methio-carb)	
Spring	:	Pollen beetle (*Meligethes aeneus*) and Stem weevil (*Ceuthorrhynchus assimilis*; 5 g ha^{-1} Deltamethrin), Sclerotinia (*Sclerotinia sclerotiorum*) and Botrytus (*Botrytis cinerea*; 500 g ha^{-1} Vinchozolin), Altenaria (*Altenaria brassica*; 500g ha^{-1} Iprodion), Cylindrosporium (*Cylindrosporium concentrium*; 450 g ha^{-1} Prochloraz).	
Irrigation	:	25 mm on 27 May and 26 June 1989	

Reserve carbohydrates (starch and water soluble sugars) were measured in the first experiment, in roots, leaves, stems and pod hulls. Sugars were analysed according to Shaffer and Somogyi (1933); starch was analysed similarly, after enzymatic hydrolysis. The contribution of reserve carbohydrates to seed yield was estimated from their decline (g m^{-2} glucose-equivalents) during the seed filling phase corrected for leaf shedding. The conversion factors, representing growth respiration given by Penning de Vries et al. (1989) were used to convert carbohydrates into seed dry matter. Losses due to maintenance respiration were not taken into account, thus contribution of reserve carbohydrates to seed yield may have been overestimated. Loss of carbohydrates due to leaf shedding was derived from the product of decrease in weight of green leaves during the seed filling phase and their carbohydrate content just before shedding (in yellow leaves still attached to the plant).

In experiment 1, the number of pods and seeds per pod were also counted per branch in consecutive groups of 15 peduncles (irrespective of the presence of a pod) and the height of each peduncle group in the canopy was measured (Fig. 2.1). The timing of pod initiation per peduncle group (defined as the period in which over 50 % of the flower buds opened) was also determined. Therefore, three periods were distinguished between consecutive harvests during flowering, and each peduncle group was assigned to the period in which over 50 % of the peduncles were counted. As the peduncles were counted after cessation of flowering of individual flowers, the dates delimiting the periods of pod initiation were derived as the harvest dates minus the duration of flowering of individual flowers (= 64.5 °Cd with a base temperature of 0 °C, data not shown; boundary dates of the periods I:14-4/2-5; II:3-5/10-5; III:11-5/22-5).

Individual seed growth in marked pods was followed in experiment 1. On three dates during the flowering period of the whole crop (21-4, 28-4 and 3-5), on two plants per sub-plot, coloured wire was attached to the main stem and the first two primary branches above the last open flower. Each week two marked plants were harvested and individual seed weights of the first 4 pods above each marker recorded.

Regression analysis, orthogonal polynomial analysis and analyses of variance (ANOVA) were carried out with the GENSTAT statistical program package (GENSTAT 5 committee, Rothamsted, UK). Differences between means of treatments per experiment were compared by the least-significant difference test at the 0.05 level of probability ($LSD_{0.05}$). Differences between the overall means of both experiments were compared by the Student t-test also at the 0.05 level of probability ($t_{0.05}$). The R^2 of the regression analysis is the adjusted R^2 statistic, expressed as a percentage (the percentage variance accounted for):

$$R^2 = 100 \times (1-(\text{Residual mean squares})/(\text{Total mean squares})).$$

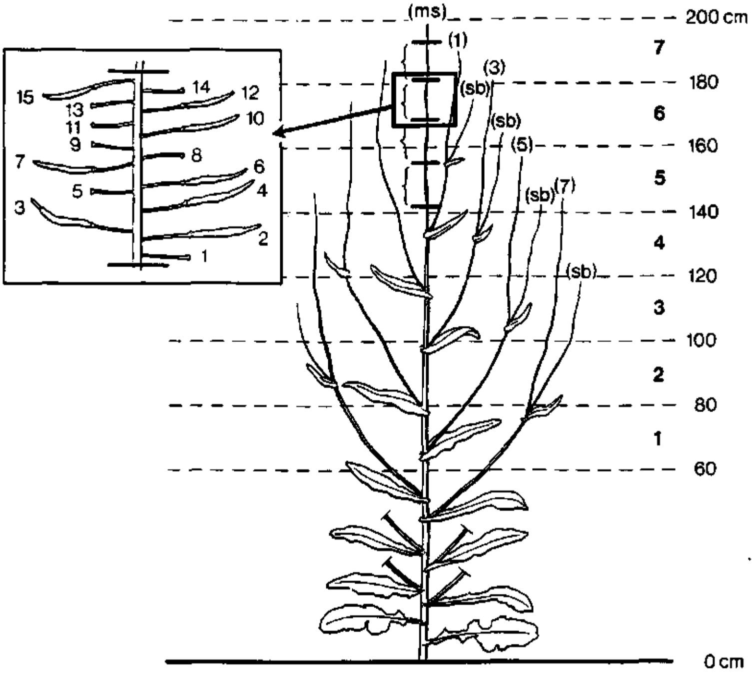

Figure 2.1 Groups of 15 peduncles distinguished on the main stem and odd primary branches (1,3,5,...) for measurements of the potential and actual number of pods and seeds per pod per branch, at different heights (in cm above soil level) in the canopy and on pods initiated at different moments during flowering (ms: mainstem; sb: secondary branches).

RESULTS

Seed yield and yield components

Spring growth started earlier in experiment 2 (1990) than in experiment 1 (1989) and, averaged over the treatments, this resulted in higher total dry matter production at flowering (data not shown) and higher pod density (Table 2.2; $t < 0.05$). Seeds per pod showed an opposite trend: values were higher in experiment 1 (15.8) than in experiment 2 (9.8). This higher seed number per pod more than compensated for the lower pod density, resulting in a considerably higher seed density in experiment 1 (Table 2.2). However, due to the lower mean seed weight (msw), seed yield was only slightly higher in experiment 1. In both seasons different treatments resulted in differences ($P < 0.05$) in pod density, seed

Table 2.2 Yield components and seed yield of winter oilseed rape in two field experiments. (msw: mean seed weight; a: for comparing with lsr; b: for comparing with the other treatments; $t_{0.05}$: for comparing the means of experiment 1 and 2). See Table 2.1 for explanation of treatment codes.

Treatment		Pods (m^{-2})	Seeds/ Pod	Seeds (10^3 m^{-2})	msw (g)	Seed yield (g m^{-2})
Experiment 1						
lpd		5652	16.0	90.4	4.44	397
hpd		6571	15.5	101.6	4.59	462
rsb		3992	17.7	70.8	4.60	325
sha		3702	14.1	52.1	4.53	235
Mean :		4979	15.8	78.7	4.54	355
Experiment 2						
lsr		7262	9.8	71.0	5.13	364
hsr		7603	9.7	73.8	5.02	370
lso		5519	13.0	71.8	5.16	372
sha		4351	6.6	28.4	5.34	152
Mean:		6399	9.8	63.2	5.16	324
$LSD_{0.05}$,	exp 1	789	2.6	16.4	0.55	46
	exp 2a	805	1.3	10.4	0.25	52
	exp 2b	930	1.5	12.0	0.29	59
$t_{0.05}$,	exp 1-2	387	1.0	6.5	0.20	24

density, seed numer per pod and seed yield. Shading (sha) resulted in lower pod and seed density and seed yield compared to the control (lpd and lsr, respectively) in both seasons. Removal of side branches (rsb) in experiment 1 and later sowing (lso) in experiment 2 resulted in reduced pod density, but that was partially compensated through the number of seeds per pod.

In experiment 1, higher plant density (hpd) resulted in higher pod density and higher seed yield. Mean seed weights were not different among treatments, despite considerable differences in total light interception between the shaded and non-shaded treatments during seed filling. In experiment 2, mean seed weight differed slightly between high seed rate (hsr) and shading.

In both seasons pod density remained fairly constant from just after flowering until final harvest (Figs 2.2a and 2.2b). The apparent decline in potential pod density is due to shedding of peduncles without a pod. Seed density reached its final value at the latest two weeks after flowering ($LSD_{0.05}$).

Pod formation

The distribution of the potential number of pods and seed-bearing pods over branch numbers, the height in the canopy and the periods of pod initation in experiment 1 (lpd, hpd and sha) are presented in Fig. 2.3. As differences among treatments were small, mean values are given. Pod set (ratio of actual and potential number of pods) was highest on the main stem (83 %), lowest on the secondary branches (10 %). On the primary branches, it varied between 42 and 60 %. About 28 % (range 23-33) of the total number of pods set per plant were on the main stem and this increases to more than 90 %, if primary branches 1 to 7 are included.

Pod set was about 50 % (range 42-60) between 80 and 160 cm above ground level and negligible outside that region (Fig. 2.3b). More than 90 % of the pods were situated in the 100 - 140 cm height zone. Pod set and pod number decreased with later flowering (Fig. 2.3c). About 75 % (range 69-85) of the seed-bearing pods were initiated before mid-flowering, expressed in degree days.

Both potential and actual pod density in all treatments in both experiments correlated closely with total crop dry matter (including dead leaves) at the end of flowering ($R^2 = 76.9$ % and 79.2 %, respectively; Fig. 2.4). Potential pod density also correlated well with total crop dry matter at the onset of flowering ($R^2 = 76.1$ %), but not actual pod density ($R^2 = 35.7$ %). Overall pod set varied between 43 and 58 %.

Seed set

Seed number per pod varied with primary branch number in experiment 1 (orthogonal polynomial analysis, $P < 0.001$; Fig. 2.5). However, as only a small proportion of the pods (< 10 %) was situated on branches having fewer than average number of seeds seeds per pod (branch number 9, 10, 11......etc.), the overall effect of branch number on mean number of seeds per pod was small. The number of seeds per pod in pods on the main stem, the primary branches and the secondary branches also differed among treatments. No interaction was found between treatment and branch number.

Seed set was analysed for the three crop layers between 100 and 160 cm above groundlevel, as the other layers contained too few pods. The number of seeds per pod varied among treatments, but not among crop layers, neither was there an interaction with treatment (Table 2.3).

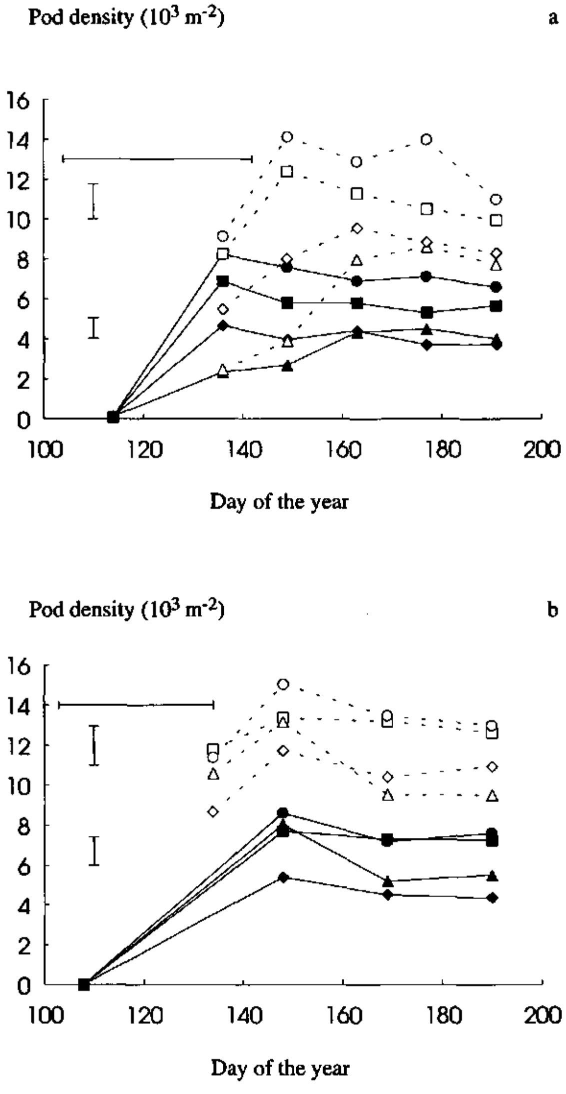

Figure 2.2 Potential (open symbols) and actual pod density (solid symbols) in experiment 1 (a) and in experiment 2 (b) against day of the year. Vertical bars represent the LSD values at the 5 % level for comparing harvest dates and treatments:
□ : lpd (Exp.1) and lsr (Exp.2); ○: hpd (Exp.1) and hsr (Exp.2); Δ : rsb (Exp.1) and lso (Exp.2); ◊ : sha (Exp.1 and Exp.2). ⊢⊣ represents the flowering period.

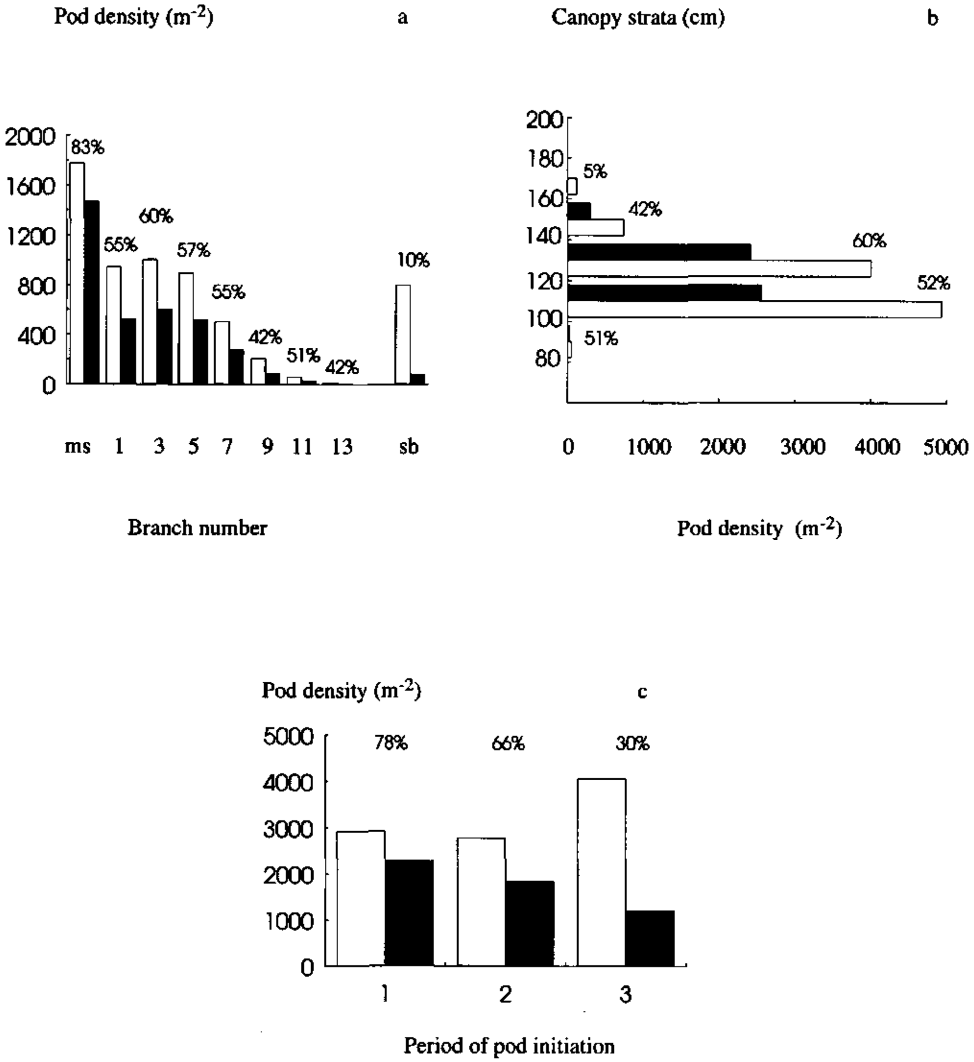

Figure 2.3 Distribution of potential (white columns) and actual pod density (block columns) over the branches (a), over the height in the canopy (b) and over the periods of pod initiation (c): mean numbers of lpd, hpd and sha in experiment 1 and averaged over the last three harvests. The ratio of actual pod density to potential pod density is given in percentages per branch, height and period (ms: main stem; sb: secondary branches).

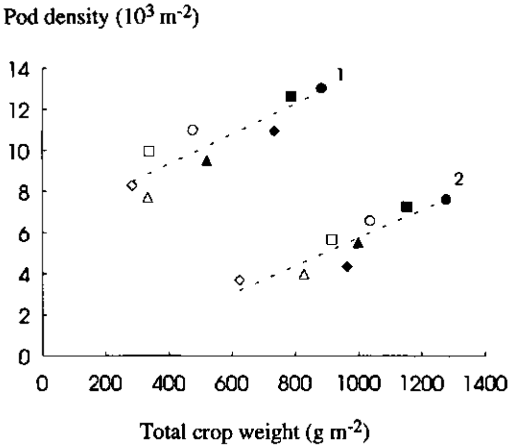

Figure 2.4 Relationship between potential (1) and actual pod density (2) and total crop dry matter (including dead leaves) at the onset of flowering and at the end of flowering, respectively, for both experiments combined:
□ :lpd; ○ :hpd; Δ :rsb; ◊ :sha in experiment 1 and ■ : lsr; ● :hsr; ▲ :lso; ◆ :sha in experiment 2. Linear regressions: Y= 6380 + 7.34X, R^2 = 76.1 % (1) and Y=–1021 + 6.76X, R^2 = 79.2 % (2).

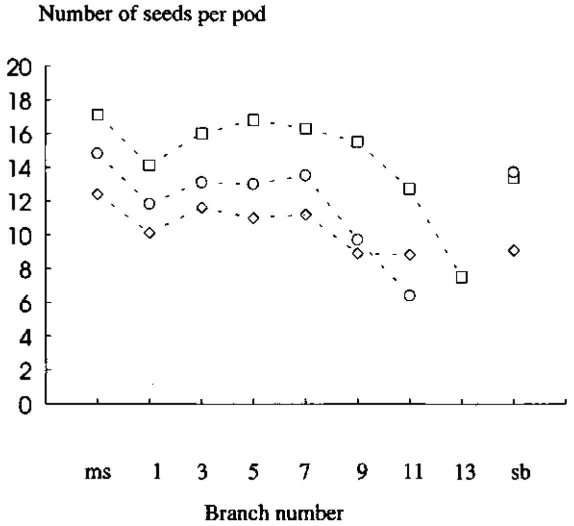

Figure 2.5 *Number of seeds per pod as a function of the position of the pods on different branches,* averaged over the last three harvests in □ :lpd; ○ :hpd and ◊ :sha of experiment 1. (ms: main stem; sb: secondary branches).

Table 2.3 Mean number of seeds per pod at various heights in the canopy in experiment 1.

Treatment	Height (cm)			Mean
	100-120	120-140	140-160	
lpd	15.5	15.4	16.4	15.8
hpd	13.0	13.2	13.4	13.2
sha	10.5	10.9	11.0	10.8
Mean	13.0	13.2	13.6	13.3

$LSD_{0.05}$: 2.0 (All), 1.5 (Treatments), 1.1 (Height)

Table 2.4 Mean number of seeds per pod in relation to period of pod initiation in experiment 1 (boundary dates of the periods of pod initiation: I: 14-4/2-5; II:3-5/10-5; III: 11-5/22-5).

Treatment	Period			Mean
	I	II	III	
lpd	16.6	14.9	13.7	15.5
hpd	13.2	13.8	12.4	13.3
sha	10.7	12.2	9.2	11.2
Mean	13.5	14.0	12.4	13.3

$LSD_{0.05}$: 1.9 (All), 1.7 (Treatments), 0.8 (Period)

When averaged over all treatments pods initiated in the third period (11-22/5) contained fewer seeds (Table 2.4). An interaction was found between period and treatment, with, however a stronger effect of treatment.

Final mean number of seeds per pod in all treatments in both experiments correlated well with total crop dry matter accumulation per pod during flowering ($R^2 = 84.3$ %), and seed density correlated well with total crop dry matter accumulation during flowering ($R^2 = 81.9$ %; Fig. 2.6). No correlation was found between seed density and total crop dry weight at the onset nor at the end of flowering.

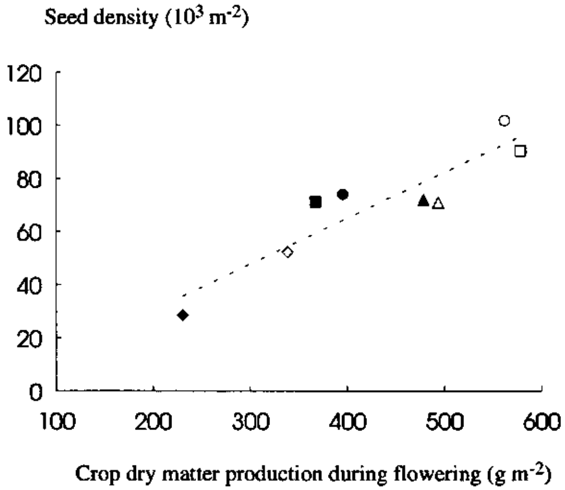

Figure 2.6 Relationship between final seed density and total cumulative dry matter production of the crop during flowering for both experiments combined: □ :lpd; ○ :hpd; Δ :rsb; ◊ :sha in experiment 1 and ■ :lsr; ● :hsr; ▲ :lso; ◆ :sha in experiment 2. Linear regression: Y= –4247 + 173X, R^2 = 81.9 %

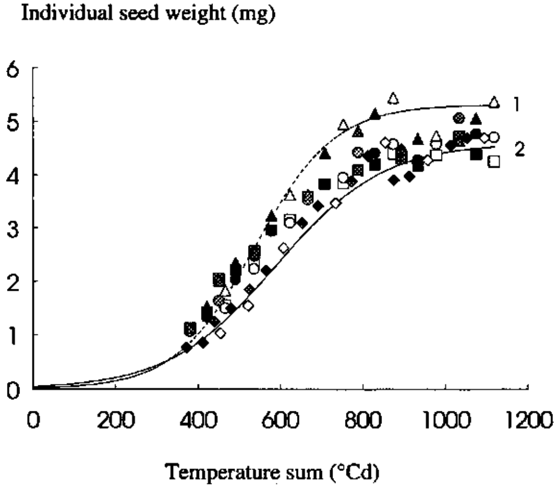

Figure 2.7 Individual seed weight versus temperature sum (ts) from the onset of flowering per flower bud (open symbols: 21-4, solid symbols :28-4 and grey symbols: 3-5) until final harvest in all treatments of experiment 1: □ : lpd; ○ : hpd; Δ :rsb; ◊ :sha.

The curves with the greatest and least final seed weight are Y=5.32/(1+exp(–0.0104(ts–539))), R^2 = 86.9 % (1) and Y = 4.60/(1+exp (–0.00775(ts–590))), R^2 = 93.8 % (2), respectively.

Seed filling

A logistic curve ($y=A + C/(1+\exp(-B(ts-M)))$) was fitted between individual seed weight in pods, initiated (and marked) on three dates during the flowering period and temperature sum (ts, with a base temperature of 0 °C) from initiation until final harvest for all treatments (Fig. 2.7). Parameter A was assumed to be zero because of the very low weight of the ovules at initiation. Parameter B differed among initiation dates and treatments and parameter M differed among initiation dates ($P < 0.05$). Interaction was found between treatment and initiation date for final individual seed weight (i.e. parameter C). The curves with the highest (rsb/21-4: 5.32 mg) and lowest final seed weight (sha/3-5: 4.60 mg) are presented in Fig. 2.7.

Fig. 2.8 shows the weight of stems, flowers and flower buds, pod hulls and seeds from the onset of flowering as a function of temperature sum, for each of the experiments averaged over all treatments. Leaves and roots reached maximum weight around the onset of flowering (OF), flowers and flower buds and stems at the end of flowering (EF) and pod hulls at about 500 °Cd after OF.

Accumulation of dry matter in the seeds started around the end of flowering and, after the pod hulls reached their maximum weight, seed growth accounted for the change in total crop weight. The ratio of seed weight to pod hull weight increased during seed filling and was much higher in experiment 1 than in experiment 2 (1.22 and 0.61 at 800 °Cd and 1.75 and 1.00 at final harvest, respectively).

Reserve carbohydrates continued to accumulate until 400 to 600 °Cd after OF (experiment 1), followed by a decline during the seed filling phase (Fig. 2.9). Leaf shedding after flowering accounted for a decline of between 1 and 3.5 % of the maximum amount of reserve carbohydrates. Remobilization of reserve carbohydrates contributed at most between 7 and 12 % to final seed yield. The lowest maximum level of reserve carbohydrates and the lowest contribution to final seed yield was recorded under shading; the highest maximum level was recorded at high plant density (hpd) and the highest contribution to final seed yield after removal of side branches at flowering (rsb). Shading (sha) resulted in a lower reserve carbohydrates content (7.2 %) than the other treatments (11 %) just before the decline of reserves at the end of flowering.

DISCUSSION

The different treatments in this study resulted in differences in pod density, seed density, number of seeds per pod and final seed yield in both years, showing that yield and yield components can be influenced by crop management. Mean seed weight differed mainly

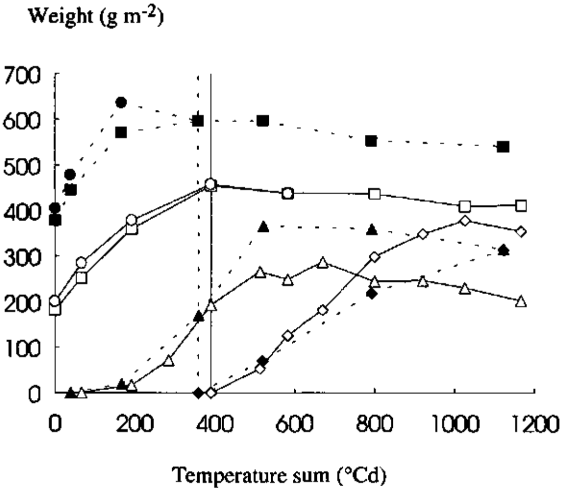

Figure 2.8 Weight of stems (□), flower buds and flowers (O), pod hulls (Δ) and seeds (◊) from the onset of flowering as a function of temperature sum, averaged over four treatments in experiment 1 (open symbols) and experiment 2 (solid symbols). The vertical lines represent the end of flowering in experiment 1 (——) and 2 (-----).

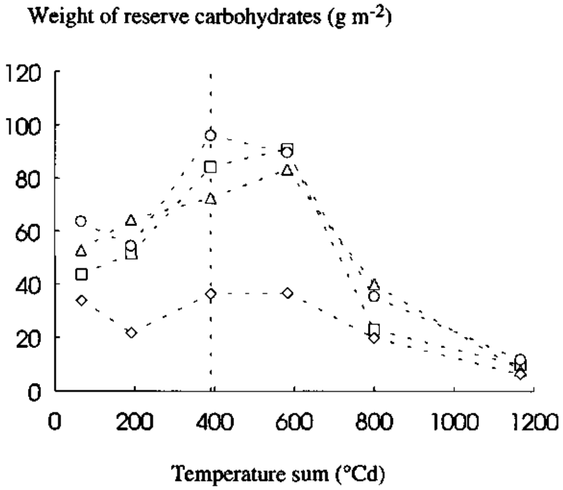

Figure 2.9 Weight of reserve carbohydrates (in glucose equivalents) versus temperature sum from the onset of flowering in experiment 1: □ : lpd; O :hpd; Δ :rsb; ◊ :sha. The vertical line represents the end of flowering.

between years. Pod density and seed density reached their final value shortly after flowering, in contrast to the results of Mendham et al. (1981), who reported continued pod abortion until maturity, especially in dense crops (12-22000 pods m^{-2}). The continued reduction in the number of seed-bearing pods they found, may have been due to low light intensities in the lower part of the canopy and, hence, to insufficient assimilate availability to maintain the lower pods and seeds. Apparently such conditions did not occur in our experiments, not even under shading.

Potential pod number was evidently not limiting, as in all positions in the canopy (branch number and height) and for all periods of pod initiation the potential number far exceeded the actual number. Assimilate availability to the crop during various growth stages before the end of flowering is a major determinant of the number of flowers and seed-bearing pods (Mendham and Scott, 1975; Evans, 1984; Leterme, 1985). This was confirmed in this study by the strong correlations between potential and actual pod density and total dry matter production at the onset and at the end of flowering, respectively, i.e. total assimilate availability over the preceding period. These correlations indicate that whereas potential pod number was largely determined at the onset of flowering, assimilate availability both before and during flowering controlled final pod density. Based on French experiments with cv. Darmor and various doses of nitrogen (0 to 250 kg ha^{-1}) at various sites near Dijon (Palleau, 1989), similar linear relations were derived between pod density (pods m^{-2}) and stem weight (g m^{-2}) two or three weeks before final harvest. Stem weight was used, as total crop dry weight was not recorded. Stem growth stops at the end of flowering and in our experiments stem weight was linearly related to total crop dry weight (including dead leaves) at that moment (data not shown, R^2 = 98.4 %). The regressions between pod density (Y) and stem weight (X) at the end of flowering for the French data (Y=1068+7.16X, R^2 = 83.3 % and Y=131+6.24X, R^2 = 97.6 %) and pooled data from our experiments (Y=−938+6.24X, R^2 = 73.4 %) were not identical, illustrating that stem weight does not fully explain the variation in pod density. Differential responses of assimilate production and partitioning, phenological development rate and organ formation rate to environmental factors and between varieties may be the cause of the different regression parameters presented (Rawson and Bagga, 1979; van Keulen and Seligman, 1987).

The smaller number of seeds per pod on branches of higher order and in pods initiated later may be due to respectively the greater sink strength of the stem relative to the pods on higher order branches (Keiller and Morgan, 1988b) and to growth of the earlier formed pods reducing assimilate availability for seed set in the pods initiated later (Tayo and Morgan, 1979). In our experiment seed number per pod did not vary with height in the canopy, in contrast with the findings of Mendham et al. (1981) and Tayo and Morgan (1979); however, this may be due to the limited number of crop layers distinguished. The effect of both, position in the canopy (branch and height) and time of pod initiation, on the number of seeds per pod had little influence on the mean value for the canopy or on differences among treatments (Figs 2.3 and 2.5 and Tables 2.3 and 2.4). Therefore, these effects in the process of seed set are not discussed further. The statistically highly significant correlation between mean number of seeds per pod and total dry matter production per pod during flowering and that between seed density and total dry matter production during flowering (Fig. 2.6), suggest that seed set is mainly determined by assimilate availability during flowering. That would be expected only when pollination, subsequent fertilization and pod density do not limit seed number. Pollination and fertilization generally do not limit the potential number of seeds per pod under field conditions (Leterme, 1985; Mendham et al., 1981; Williams et al., 1987). This potential number, i.e. the number of ovules per pod, varies between 18 and 35, depending on variety (Mendham et al., 1984; Pechan and Morgan, 1983). For Jet Neuf up to 25 seeds per pod were recorded in the first experiment. Potential seed density for all treatments in both experiments, calculated by multiplying potential seed number per pod and actual pod density, ranged from 92 to 190 thousand per m^2, hence far exceeded the actual densities, and thus appeared not to be limiting. Leterme (1985) derived a linear relation between mean number of seeds per pod and cumulative light interception per flower during flowering (Q) for two growing seasons. However, in one season a better relation was found between mean number of seeds per pod and the ratio of Q to the temperature sum accumulated during flowering (V). This ratio expresses the supply of assimilates (light interception; source) per unit sink demand (mean temperature) and determined initial seed set per pod, whereas Q determined the degree of realization of this initial number (Leterme, 1985). In our study a significant correlation was observed between seed density and total dry matter production during flowering, and as the length of the flowering period (expressed in degree days) was very similar in both experiments (391 and 359 °Cd, respectively), seed density and the ratio of cumulative dry matter production to the length of the flowering period in degree days were also strongly correlated ($R^2 = 83.5$ %). It was not possible to distinguish between initial seed set and the degree of realization as major determinants of final seed density.

Individual seed weight can be plotted against temperature sum from the onset of flowering per pod (Fig. 2.7), to derive a maximum growth rate of individual seeds during different phases of development, provided that assimilate availability is not a limiting factor (Vos et al., 1982; O'Leary et al., 1985). These conditions seem to have been met in experiment 1 for seeds in pods from first pod initiation date after removal of the side branches at flowering (rsb, d1) resulting in the highest final seed weight (i.e. 5.32 mg) of all combinations of treatments and initiation dates.

Pod hulls are the only competing sinks during early seed fill until about 500 °Cd after the onset of flowering. The higher value of the seed weight/pod hull weight ratio in experiment 1 than in experiment 2 could be related to the higher seed density and consequently higher sink capacity (Fig. 2.8). This higher sink capacity allowed more assimilates to be allocated to the seeds in experiment 1, whereas in experiment 2 the surplus of assimilates accumulated in the pod hulls. The higher mean seed weight in experiment 2 (Table 2.2) confirms the suggestion that in this experiment sink capacity was more limiting than in experiment 1.

The maximum levels of reserve carbohydrates recorded in this study varied between 40 and 110 g m^{-2} (glucose equivalents), contributing at most 12 % to final seed yield, with only small differences among treatments (range 7-12). Quilleré and Triboi (1987) recorded a maximum level of 150 g m^{-2} reserve carbohydrates (glucose equivalents) and a contribution of remobilization to final seed yield of at most 17.5 % (variety Jet Neuf). They did not account for the losses due to leaf shedding and maintenance respiration. The carbohydrate contents at the end of flowering were very similar for the French data and the treatments without shading in experiment 1 (about 11 %) and the main cause of the different amounts of reserve carbohydrates and maximum possible contribution to final seed yield seems to be differences in total dry matter production. The lower carbohydrate content under shading (7.2 %) may be the result of a higher ratio of demand for assimilates for growth during flowering to assimilate availability from current assimilation.

The results of this study indicate that assimilate availability during flowering is the determinant for seed set. This suggests that increased assimilate availability during flowering may ultimately lead to higher seed yields, provided sufficient assimilates are available during seed filling to utilize the increased sink capacity to be used. One way of increasing assimilate availability could be to reduce the growth of unproductive side branches during flowering (Keiller and Morgan, 1988a) and concomitantly increase the sink strength of developing pods and seeds in the early stages of development. Alternatively, the light available for assimilate production could be increased by breeding varieties with smaller petals or by developing apetalous lines (Yates and Steven, 1987). Prolonging the flowering period might increase sink size, but would result in a wider range of pod ages at maturity, causing harvesting problems (Keiller and Morgan, 1988b). However, this problem may be solved by genetic improvement of seed retention, so that harvest can be delayed until all seeds are mature. Further options to increase final seed weight include increasing the potential growth rates of the seeds, extending the seed-filling period and improving the utilization of pre-flowering assimilates by enhancing accumulation of reserves before flowering and improving the efficiency of translocation during seed filling. A simulation model would be useful, as that would enable quantitative evaluation of the influence of various eco-physiological factors and crop characteristics on seed yield.

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CHAPTER 3

A MODEL OF THE PHENOLOGICAL DEVELOPMENT OF WINTER OILSEED RAPE (*BRASSICA NAPUS* L.) IN NORTH-WEST EUROPE

ABSTRACT

An empirical model, BRASNAP-PH, was developed to predict emergence, onset and end of flowering and maturity of winter oilseed rape in North-West Europe in relation to temperature and photoperiod. The basic structure of the model and the range of parameter values were derived from literature. Experimental data collected in the Netherlands, Germany and France were used to calibrate the model. Best calibration results for the period from sowing until onset of flowering were obtained when the effects of temperature (on vernalization too) and photoperiod were included. After flowering, only temperature was taken into account. When the simulation results were compared with experimental data used for calibration the mean deviations between simulated and experimental dates were 1.25 d for emergence, 1.9 d for onset of flowering, 1.1 d for end of flowering and 2.9 d for maturity. The latter three were 79 % to 87 % lower than the mean deviations based on time. When the model was validated with independent data, i.e. 31 sowings for ten years in the Netherlands and France, the mean deviations between simulated and experimental dates were 1.7 d for emergence, 3.0 d for onset of flowering, 2.6 d for end of flowering and 5.5 d for maturity. The latter three were 38 % to 75 % lower than the mean deviations based on time. The model appears to be reliable for predicting the onset and end of flowering and the maturity of winter oilseed rape in North-West Europe.

INTRODUCTION

Phenological development of winter oilseed rape is an important aspect of the yield formation process (Mendham et al., 1981; Leterme, 1985; Daniels et al., 1986; Habekotté, 1993; Chapter 2). During the period from sowing until the onset of flowering, yield potential is set by the number of flower buds and leaf area index at onset of flowering (Mendham et al., 1981; Leterme, 1985). Conditions during flowering are particularly important for pod formation and seed set (Daniels et al., 1986; Leterme, 1985; Habekotté, 1993), and the length of the seed filling phase partly determines assimilate availability for seed filling (Mendham et al., 1981). Different sowing dates lead to variation in the length and timing of various developmental phases and may result in different growth patterns and yield levels (Mendham et al., 1981). Therefore, it is important to have more insight into the phenological development of the crop in relation to sowing date and environmental factors and to quantify this, to better understand yield formation.

Field observations in the Netherlands, the United Kingdom, Germany and France have shown that winter oilseed rape starts flowering in the period from early April until late May (Grosse, 1989; Mendham et al., 1981; Leterme, 1985; Tittonel and Palleau, 1991).

The time of flowering depends on a combined effect of photoperiod and temperature (Daniels et al., 1986). The low temperature requirement ensures that flower development of autumn-sown varieties is delayed until the following spring as photoperiods and temperatures increase in spring (Roberts and Summerfield, 1987).

Research in growth chambers has shown that plants of the variety Jet Neuf, grown at 22 °C remain vegetative (Netzer et al., 1986). Flower initiation occurred at temperatures up to 17 °C and was achieved most rapidly at temperatures between 3 and 12 °C (Netzer et al., 1986; Andrew et al., 1991; Hodgson, 1978). Tittonel and Palleau (1991) showed that vernalization not only influenced the development rate until flower initiation but also flower development after initiation.

In the varieties Jet Neuf and Mikado it has been found that long photoperiods enhance the development rate in the period from emergence until flower initiation and flowering (Netzer et al., 1986; Andrew et al., 1991). After flowering, temperature is the main determinant of development rate (Hodgson, 1978).

The objective of the study described in this paper was to develop an empirical model describing phenological development of winter oilseed rape as a function of the most important environmental factors, temperature and photoperiod. The basic structure of the model was based on previous research (Hodgson, 1978; Daniels et al., 1986; van Keulen et al., 1982; Netzer et al., 1986; Reinink et al., 1986; Thornley, 1987; Spitters et al., 1989; Andrew et al., 1991; Tittonel and Palleau, 1991). Experimental data collected in the Netherlands, Germany and France were used for calibration and the model was tested with independent data sets. The resulting model, BRASNAP-PH, will be incorporated in a crop growth model of winter oilseed rape (LINTUL-BRASNAP), developed to explore options for increasing winter oilseed rape production (Habekotté, 1996a, b; Chapters 4 and 5).

MATERIALS AND METHODS

Model description

Development stage is characterized by *DVS*, a state variable that has the value 0 at sowing, 1 at emergence (E), 2 at the onset of flowering (OF), 3 at the end of flowering (EF) and 4 at maturity (M). The development stage is obtained by integrating of the development rate (d*DVS*/d*t*) with time steps of one day, according to van Keulen et al. (1982). Development rate is directly related to temperature (Thornley, 1987) and is assumed to be a linearly related with effective daily temperature (T_{eff}), expressed by the parameter a_T (Thornley, 1987; Spitters et al., 1989).

In the period from emergence until the onset of flowering the development rate is also influenced by the degree of vernalization (F_v) and photoperiod ($\mathrm{F_p}$):

$$DVS(t) = \int_{t_i}^{t_e} \mathrm{d}DVS/\mathrm{d}t$$

with:

t_i, t_e: beginning and end of a particular development phase, respectively

$$\begin{aligned} \mathrm{d}DVS/\mathrm{d}t &= T_{\mathrm{eff}}\, \mathrm{a}_{\mathrm{T,x}} && 0 \leq DVS \leq 1 \\ &= T_{\mathrm{eff}}\, \mathrm{a}_{\mathrm{T,x}}\, F_v\, \mathrm{F_p} && 1 \leq DVS \leq 2\ ;\ F_v \geq 0; \mathrm{F_p} \geq 0 \\ &= T_{\mathrm{eff}}\, \mathrm{a}_{\mathrm{T,x}} && 2 \leq DVS \leq 4 \end{aligned}$$

with:

x: the relevant development phase

Effective daily temperature (T_{eff}) for development is calculated from the average day temperature (T_{day}) and a base temperature (T_b) for development (Thornley, 1987):

$$\begin{aligned} T_{\mathrm{eff}} &= T_{\mathrm{day}} - T_b && T_b < T_{\mathrm{day}} \\ &= 0 && T_b \geq T_{\mathrm{day}} \end{aligned}$$

Average day temperature (T_{day}) is calculated as the mean value of daily minimum and maximum temperatures. Vernalization and the effect of photoperiod and vernalization on development rate were described using the approach Weir et al. (1984) and Reinink et al. (1986) applied to winter wheat. The degree of vernalization is represented by a state variable (F_v), with values between 0 (not vernalized) and 1 (fully vernalized) and is calculated by integrating the vernalization rate ($\mathrm{d}F_v/\mathrm{d}t$) from emergence until the onset of flowering or until full vernalization. The effect of temperature on the vernalization rate is described in a vernalization temperature response curve (Fig. 3.1a).

The multiplication factor for photoperiod ($\mathrm{F_p}$) varies between 0 and 1 and increases linearly between a basal photoperiod (P_b) and a saturating photoperiod (P_{sat}) (Fig. 3.1b).

The variables input into the model are latitude of experimental sites, year of sowing, sowing date and daily minimum and maximum temperatures at 1.5 m above soil level. The model is written in FORTRAN-77 (Meissner and Organick, 1984), using the FSE (FORTRAN Simulation Environment) system (van Kraalingen, 1995) for crop simulation. Photoperiod is calculated from latitude and date (van Keulen et al., 1982).

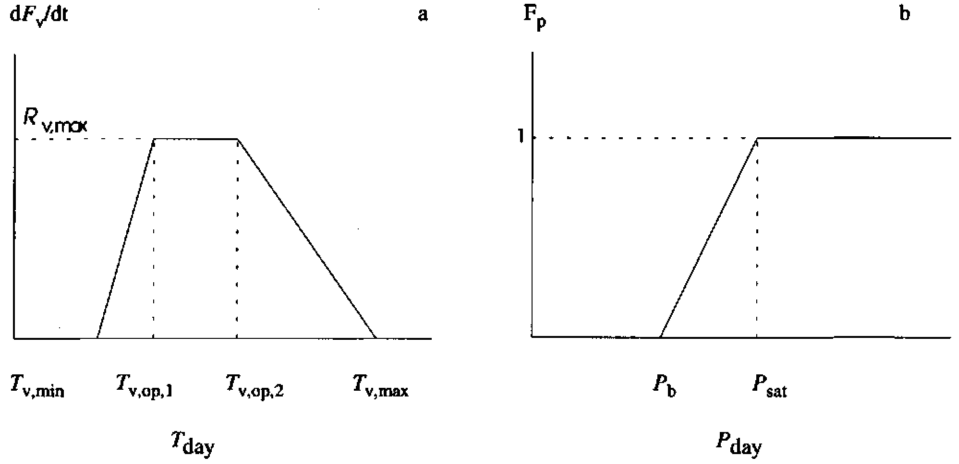

Figure 3.1 The relation between the rate of vernalization (dF_v/dt) and daily temperature (T_{day}, °C) ($T_{v,min}$: minimum temperature for vernalization, $T_{v,op,1}$: the lowest optimum temperature for vernalization, $T_{v,op,2}$: the highest optimum temperature for vernalization, $T_{v,max}$: the maximum temperature for vernalization, $R_{v,max}$: the maximum rate of vernalization) (a). The relation between the multiplication factor for photoperiod effects (F_p) and daily photoperiod (P_{day}, h) (P_b: basic photoperiod, P_{sat}: saturating photoperiod) (b).

Field data

Experimental data on the development of winter oilseed rape variety Jet Neuf, recorded in the Netherlands near Wageningen (Habekotté and Smid, 1992), in Germany near Kiel (Grosse, 1989) and in France near Dijon (Dijon-low) (Table 3.1) were used to estimate parameters and to evaluate the structure of the model (calibration). Experimental data from the locations Lelystad (Habekotté, 1987-89; A.J. Remmelzwaal, IJsselmeerpolder Development Authority Lelystad (RIJP), pers. comm., 1990); van der Meulen, 1990a, 1990b) and a higher site in Dijon (Dijon-high: Leterme, 1985; J.P. Palleau, Département Etudes et Recherches (CETIOM), pers. comm., 1991) were used to test the model with independent data (validation) (Table 3.1).

The two locations near Dijon in France differ in altitude, some of the experimental plots being located between 400 and 600 m above sea level (Dijon-high) and others at about 200 m above sea level (Dijon-low; Leterme, 1985) (Table 3.1). Fertilization, pest and disease control were carried out according to current optimal practice. Crop damage due to pests, diseases, frost and drought was limited and therefore was assumed not to have affected phenological development of the selected experimental data (Habekotté, 1987; A.J. Remmelzwaal, RIJP, pers. comm., 1990; Habekotté and Smid, 1992; Grosse, 1989; J.P. Palleau, CETIOM, pers. comm., 1991). The input variables daily minimum and maximum temperatures, were collected at weather stations located near (< 20 km) the experimental sites (Table 3.1).

The development stages recorded were emergence (E; in the Netherlands only), onset of flowering (OF), end of flowering (EF; not in Germany) and maturity (M). The criteria for these development stages were that half of the plants per plot had: two cotyledons above ground (E), at least one open flower (OF), no open flowers any more (EF) and seeds in all pods had completed seed filling and the crop was ready for swathing (M). In Germany only, OF was identified as the moment that 30 % of the plants had one open flower and in France the dates of M were calculated by subtracting 12 days from the recorded dates of final harvest (when all seeds were dark coloured and hard; Hebinger, CETIOM, pers. comm., 1993). The reported data on development stages are mean values of 3, 4 or 5 plots.

Table 3.1 Details of the experimental sites (E: emergence, OF: onset of flowering, EF: end of flowering, M: maturity).

Detail / Site	Kiel	Wageningen	Dijon-low	Lelystad	Dijon-high
Period	1983-'85	1988-'89	1983-'86,'88	1980-'84, '86-'89	1983,'85-'88
Sowings per year	1	1 or 2	1	2 or 3	1 or 2
Total number of sowings	3	3	5	23	9
Sowing dates	22-8	23-8/9-9	27-8/31-8	31-8/25-9	28-8/5-9
Development stages recorded	OF,M	E,OF,EF,M	OF,EF,M	E,OF,EF,M	OF,EF,M
Soil type	loamy sand	clay	clayey loam	clay	loamy sand
Preceding crop	winter barley	winter barley	winter barley	spring barley	winter barley
Fertilizer	< circa 200 kg N ha^{-1} minus soil reserves >				
Location of exp. site	Hohenlieth	Randwijk	the valley of Dijon	near Swifterbant	the Plateaux du Chatillonnais
Distance between exp. site and weather station	< 10 km	< 10 km	< 15 km	ca. 20 km	< 15 km
Altitude of weather station (is similar for experimental site) (m above sea level)	unknown	7	219	–4	410
Longitude	10° 12'	5° 40'	5° 05'	5° 38'	5° 05'
Latitude	54° 19'	51° 58	47° 16'	52° 34'	47° 16'

Calibration and validation

During calibration on the combined data of Wageningen, Kiel and Dijon-low (Table 3.1), four periods were distinguished to parameterize the model: 1) from sowing until emergence; 2) from emergence until the onset of flowering; 3) from the onset of flowering until the end of flowering; 4) from the end of flowering until maturity. The ranges in the parameter values were derived from literature (Table 3.2) and their optimal values were estimated per period by an optimization method based on Price's algorithm (Price, 1979) as adapted by Klepper and Rouse (1991).

The parameters were estimated for the response of development rate to temperature for the four relevant periods. For the second period (from emergence until the onset of flowering) parameters were also estimated for the influence of vernalization and/or photoperiod on development rate included in the model.

The mean sum of squares (MSS) of the differences in simulated dates (D_{mod}, dates expressed in day of the year) and experimental dates (D_{exp}) of the relevant development period weighted for different numbers of sowings per year and years per location, was used as a criterion for the model's performance. It is calculated with the following equation ($N_{\mathrm{s,y}}$: number of sowings per year; $N_{\mathrm{y,loc}}$: number of years per location; N_{loc}: number of locations per calibration run; i varies between 1 and N_{run}, the first and last number of the sowings per calibration run, respectively):

$$\mathrm{MSS} = \sum_{i=1}^{N_{\mathrm{run}}} \left[\left(D_{\mathrm{mod},i} - D_{\mathrm{exp},i} \right)^2 \left(1/N_{\mathrm{s,y},i} \right) \left(1/N_{\mathrm{y,loc},i} \right) \left(1/N_{\mathrm{loc},i} \right) \right]$$

A weighted MSS was used instead of a weighted mean deviation (MD) between simulated dates and experimental dates, to account for deviating development patterns in years with more extreme temperature conditions (Stol et al., 1992).

Optimal parameter values were obtained by minimizing MSS per development period. In the first step of the procedure, a number of parameter sets were generated, with fifty values selected at random per parameter within the given parameter bounds (Table 3.2). In the second step new parameter sets were generated to replace existing sets if the new set produced output with a lower MSS. The optimization procedure was halted when the range in MSS values was less than 5 % or after 3000 iterations had been carried out. The range in MSS values (RTOL) was calculated as the fractional range from best to worst parameter set with the lowest and highest values of MSS, respectively ($\mathrm{MSS}_{\mathrm{low}}$ and $\mathrm{MSS}_{\mathrm{high}}$):

$$\mathrm{RTOL} = 2 \left(\mathrm{MSS}_{\mathrm{high}} - \mathrm{MSS}_{\mathrm{low}} \right) / \left(\mathrm{MSS}_{\mathrm{high}} + \mathrm{MSS}_{\mathrm{low}} \right)$$

Table 3.2 Description of the parameters and ranges in parameter values (K: Kiel, W: Wageningen, DL: Dijon-low).

Parameter	Description		Bounds	Literature
Temperature:				
$T_{b,x}$	Base temperature for development for development phases 1 to 4 (x) (°C)		0. - 5.	Netzer et al., 1986
$a_{T,x}$	Response of development rate to temperature for the development phases 1 to 4 (x) (10^{-3} d^{-1} $°C^{-1}$)	1: S-E:	6.75 - 22.57	estimated from experimental data near W, K, DL (Table 3.1)
		2: E-OF:	0.40 - 3.33	
		3: OF-EF:	1.50 - 10.00	
		4: EF-M:	0.50 - 5.00	
Vernalization:				
$T_{v,min}$	Minimum temperature for vernalization (°C)		–5.00 - 0.00	after Reinink et al., 1986; Hodgson, 1978
$T_{v,op,1}$	Lowest optimum temperature for vernalization (°C)		0.01 - 5.00	Andrew et al., 1991; Netzer et al., 1986; Hodgson, 1978
$T_{v,op,2}$	Maximum optimum temperature for vernalization (°C)		5.01 - 17.00	Andrew et al., 1991; Netzer et al., 1986; Hodgson, 1978
$T_{v,max}$	Maximum temperature for vernalization (°C)		17.01 - 22.00	Netzer et al., 1986
$R_{v,max}$	Maximum rate of vernalization (d^{-1} $°C^{-1}$)		0.014 - 0.072	Netzer et al., 1986
Photoperiod				
P_b	Basic photoperiod (h)		0.00 - 6.00	Netzer et al., 1986
P_{sat}	Saturating photoperiod (h)		6.01 - 24.00	estimated from experimental data near K, W and DL (Table 3.1)

After calibrating the model per developmental period, the model's performance was tested with simulation from sowing until E, OF, EF and M, respectively, using the same experimental data (11 sowings).

The model was also tested on two independent data sets at the locations Lelystad and Dijon-high (32 sowings) for the development stages E, OF, EF and M (validation).

The results of calibration and testing are expressed as the mean deviation (MD_{mod}) between simulated and experimental dates (dates in day of the year) and these values were compared with the mean deviation between the experimental dates and the dates estimated by the mean length (in number of days) of the relevant development period (MD_{time}). The MD values were weighted for different numbers of sowings per year and years per location and for the number of locations included, respectively, and were calculated similarly to MSS:

$$MD = \sum_{i=1}^{N_{run}} \left[\left(D_{mod,i} - D_{exp,i} \right) \left(1/N_{s,y,i} \right) \left(1/N_{y,loc,i} \right) \left(1/N_{loc,i} \right) \right]$$

RESULTS

Calibration

At the locations Kiel, Wageningen and Dijon-low the crop was sown between 22 August and 8 September (Table 3.6; Fig. 3.2a). Average sowing date was earliest for Kiel (23 August), followed by Wageningen (28 August) and Dijon-low (1 September). Data on crop emergence were only available for Wageningen. The duration of the pre-emergence period varied between 8 and 11 d and was 9 d on average.

The duration of the period from emergence until the onset of flowering varied between 208 and 260 d. The average duration of this period was 220 d for Wageningen, 231 for Dijon-low and 257 d for Kiel.

The duration of the flowering period varied between 18 and 38 d. The average duration of the flowering period was shorter for Dijon-low (29 d) than for Wageningen (35 d).

The duration of the period from the end of flowering until maturity varied between 36 and 51 d for Wageningen and Dijon-low, combined. The average duration was 41 d for Dijon-low and 48 d for Wageningen. Based on an estimated length of the flowering period (expressed in degree days, T_b = 4.9163 °C), the average duration of this period was 54 d for Kiel.

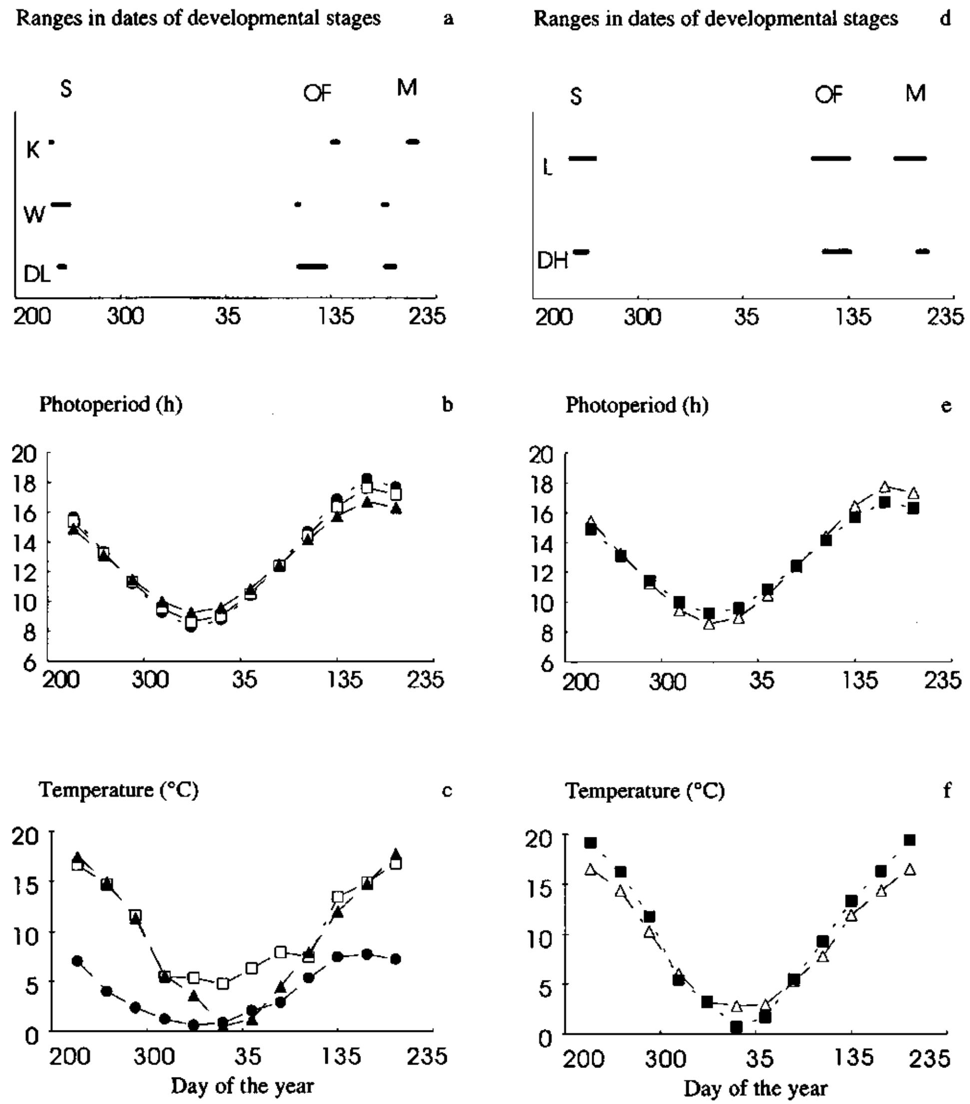

Figure 3.2 Ranges in sowing date, onset of flowering and maturity of winter oilseed rape (variety Jet Neuf) at Kiel (K), Wageningen (W) and Dijon-low (DL) (a) and at Lelystad (L) and Dijon-high (DH) (d).The photoperiod pattern and average monthly day temperatures are given per location for the data used for calibration (b and c, respectively) and for the data used for validation (e and f, respectively) (black circles: Kiel; open squares: Wageningen; black triangles: Dijon-low; open triangles: Lelystad; black squares: Dijon-high).

For the period from sowing until emergence the lowest MSS value was found with a $T_{b,1}$ value of 0.302 °C and an $a_{T,1}$ value of 7.721 10^3 d^{-1} $°C^{-1}$ (Table 3.4). The corresponding MD_{mod} value (1.3 d) was slightly higher than MD_{time} (1.0 d) (Table 3.3).

For the period from emergence until onset of flowering, with development rate identified as a function of temperature, temperature and vernalization, temperature and photoperiod, and the three factors combined, simulated predictions of onset of flowering all improved the predictions based on time (Table 3.3). When only temperature was taken into account, the simulated onset of flowering was reached too early for Wageningen (on average: −17 d) and too late for Dijon-low (on average: +7.2 d) and Kiel (on average: +11 d). These differences were due to temperature differences during this developmental period. Highest average temperatures were recorded in Wageningen, followed by Dijon-low and Kiel (Fig. 3.2c). Including the response of development rate to temperature and vernalization, improved the prediction of onset of flowering (Table 3.3). However, simulated onset of flowering was still reached too early for Wageningen (– 8 d) and too late for Dijon-low (+7 d) and Kiel (+7 d).

Table 3.3 Results of calibration of BRASNAP-PH for the periods: 1) from sowing until emergence (*S-E*), 2) from emergence until the onset of flowering (E-OF), 3) from the onset of flowering until the end of flowering (OF-EF), 4) from the end of flowering until maturity (EF-M), with experimental data from the locations Kiel (K), Wageningen (W) and Dijon-low (DL) combined, as far as available for the different periods (Table 3.1). Mean deviations (MD_{mod}, d) between data obtained with the model and experimental data of the various developmental stages are given, with various factors taken into account (*T*: temperature; *V*: vernalization; *P*: photoperiod). For comparison, the mean duration of the various developmental phases (D_d, d) and the MD values based on time (MD_{time}, d) are also given.

Period	Factor	MD_{mod} (d)	MD_{time} (d)	D_d (d)	Locations
S-E	*T*	1.3	1.0	9.0	W
E-OF	*T*	11.2	15.1	236.8	W, K, DL
	T,V	7.6	,,	,,	
	T,P	3.9	,,	,,	
	T,V,P	1.9	,,	,,	
OF-EF	*T*	1.1	4.8	31.6	W, DL
EF-M	*T*	2.9	5.3	47.7	W, K, DL

The effect of vernalization subdued the positive response of development rate to temperature in autumn and winter until the modelled vernalization requirement was fulfilled: on average on 20 December in Kiel, on 31 December in Wageningen and on 3 January in Dijon-low. Because of the vernalization effect, the differences in the simulated dates of flowering were mainly due to differences in spring temperatures, which were highest for Wageningen, followed by Dijon-low and Kiel (Fig. 3.2c). Including the effect of temperature and photoperiod on development rate strongly reduced the discrepancy between average simulated and experimental dates of the onset of flowering per locations: –0.5 d for Wageningen, −1.7 d for Kiel and +0.2 d for Dijon-low. Deviations for individal sowings were still quite large (−11 up to 13 d). Best results were obtained with the three factors combined. Deviations between the simulated and experimental dates of onset of flowering varied between −5 and +3 d per sowing, and on average were 0 d for Wageningen and Dijon-low and −2.3 d for Kiel.

Table 3.4 Optimal parameter values obtained with calibration (Table 3.3).

Period	Parameter	Value	Dimension
S-E	$T_{b,1}$	0.3024	°C
	$a_{T,1}$	7.7212	10^{-3} d^{-1} °C^{-1}
E-OF	$T_{b,2}$	0.5444	°C
	$a_{T,2}$	2.0083	10^{-3} d^{-1} °C^{-1}
	$T_{v,min}$	−3.7182	°C
	$T_{v,op,1}$	0.7260	°C
	$T_{v,op,2}$	5.3770	°C
	$T_{v,max}$	17.2022	°C
	$R_{v,max}$	0.014553	d^{-1}
	P_b	5.7416	h
	P_{sat}	14.8014	h
OF-EF	$T_{b,3}$	4.9163	°C
	$a_{T,3}$	5.1036	10^{-3} d^{-1} °C^{-1}
EF-M	$T_{b,4}$	0.6870	°C
	$a_{T,4}$	1.4651	10^{-3} d^{-1} °C^{-1}

Calibrating the model for the flowering period improved the predicted dates based on time by 78 % (MD_{mod}= 1.1 d, and MD_{time}= 4.8 d; Table 3.3). Calibrating the model for the period from the end of flowering until maturity improved the predicted dates based on time by 45 % (MD_{mod}= 2.9 d, and MD_{time}= 5.3 d; Table 3.3).

These results indicate that much of the experimental variation in duration of the first, third and fourth developmental periods could be explained by the effects of temperature, and much of the experimental variation in the duration of the second period could be explained by the interactive effects of temperature, vernalization and photoperiod.

Validation

After calibration per development period, the model's performance was tested by simulating from sowing until E, OF, EF and M for the same experimental data. This resulted in values of MD_{mod} of 1.3 d for emergence, 1.9 d for the onset of flowering, 1.1 d for the end of flowering and 2.9 d for maturity. The latter three were 79 to 87 % lower than the MD_{time} values (Table 3.5).

The experimental data used for validation (32 sowings at the Lelystad and Dijon-high locations) also showed variation in the dates of emergence, onset of flowering, end of flowering and maturity (Fig. 3.2d, Table 3.6). These differences might also be due to different sowing dates, different temperature regimes among years and locations and to different photoperiod patterns between the two locations (Figs 3.2e and 3.2f). The differences in temperature regimes between years per location are illustrated in Fig. 3.3 for a relatively cold growing season (1984/85) and a relatively warm growing season (1988/89) near Lelystad.

Validating the model with these independent data resulted in MD_{mod} values of 1.7 d for emergence, 4.5 d for onset of flowering, 2.8 d for end of flowering and 5.9 d for maturity. The latter three were 35 to 73 % lower than the mean deviations based on time.

The large discrepancy of 21 d between D_{exp} and D_{mod} of the sowing in 1984 at Dijon-high (Table 3.6) is striking. Without this sowing the MD_{mod} values for onset of flowering, end of flowering and maturity were lower: 3.0, 2.6 and 5.5 d, respectively, i.e. 38 to 75 % lower than mean deviations based on time (Table 3.5).

For individual sowings, the deviations (in d) between simulated and experimental dates varied between 0 and 4 d for emergence, between 0 and 8 d for onset of flowering without the deviating sowing in 1984 near Dijon-high, and between 0 and 21 d with this sowing included, between 0 and 11 d for end of flowering and between 0 and 12 d for maturity (Table 3.6).

These results confirm that much of the variation in duration of the periods from sowing until the onset of flowering, until the end of flowering and until maturity is attributable to the effects of temperature, vernalization and photoperiod.

Table 3.5 Results of testing BRASNAP-PH for simulation from sowing until emergence (E), until the onset of flowering (OF), until the end of flowering (EF) and until maturity (M), with experimental data already used for calibration: Kiel (K), Wageningen (W) and Dijon-low (DL) and with independent data from the locations: Lelystad (L) and Dijon-high (DH), as far as data are available for the various developmental stages (Table 3.1). Mean deviations between the data obtained with the model and experimental data (MD_{mod}, d) are given per developmental stage. For comparison the MD values based on time are also given (MD_{time}, d). The results in brackets are those obtained without the deviating sowing of Dijon-high in 1984 (see Table 3.6) (- : data not available).

Location	E		OF		EF		M	
	MD_{time}	MD_{mod}	MD_{time}	MD_{mod}	MD_{time}	MD_{mod}	MD_{time}	MD_{mod}
Data used for calibration:								
K	-	-	1.3	2.3	-	-	3.1	5.7
W	1.0	1.3	6.4	1.0	8.8	0.5	6.6	0.8
DL	-	-	6.1	2.4	5.0	1.4	1.5	2.3
K,W, DL	1.0	1.3	15.1	1.9	7.1	1.0	13.8	2.9
Independent data:								
L	1.1	1.7	10.0	3.0	10.2	3.7	9.6	5.2
DH	-	-	7.8	6.0	8.7	1.8	4.2	6.5
			(7.2)	(3.0)	(8.3)	(1.4)	(4.3)	(5.9)
L, DH	1.1	1.7	9.9	4.5	10.2	2.8	9.1	5.9
			(9.3)	(3.0)	(10.4)	(2.6)	(8.9)	(5.5)

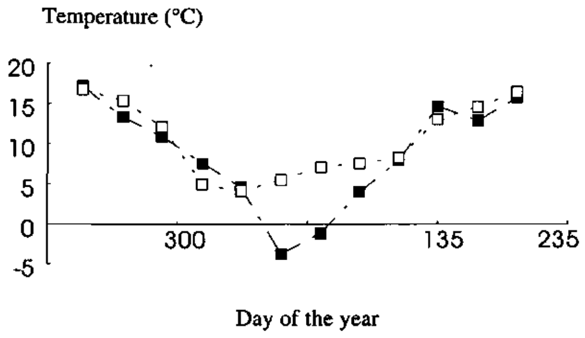

Figure 3.3 Average monthly day temperature during the growing season in 1984/85 (closed squares) and in 1989/90 (open squares) at the Lelystad location.

DISCUSSION

Various models have been proposed to describe the influence of temperature and photoperiod on phenological development of various crops (Weir et al., 1984; Roberts and Summerfield, 1987; Thornley, 1987; Hodges and Ritchie, 1991; Miglietta, 1992). The empirical approach in which the development stage is associated with a single variable and is obtained by integrating the development rate, which is related to the environmental factors considered, has been shown to be successful for making predictions (van Keulen et al., 1982; Thornley, 1987; Roberts and Summerfield, 1987). This approach was followed in this study to describe phenological development of winter oilseed rape. No attempt was made to evaluate the basic assumptions of the various approaches and to test other models. This would have required more experimental data and factorial experiments in controlled environments (Roberts and Summerfield, 1987).

Best calibration results were obtained by including the effects of temperature, photoperiod and vernalization in describing the development rate in the period from sowing until the onset of flowering (Table 3.3). These results indicate that all three factors are important for predicting the phenological development of winter oilseed rape (variety Jet Neuf) from sowing until the onset of flowering at different locations (Table 3.6; Figs 3.2 and 3.3). After flowering, only temperature was taken into account, and this improved the predictions based on time (Table 3.3).

The calibrated model predicted the onset and end of flowering and the maturity of 32 independent sowings in different years (1980-1989), at 2 locations in the Netherlands and France fairly well. The mean deviations between simulated and experimental dates were 3.0, 2.6 and 5.5 d for the development stages OF, EF and M, respectively, for the two locations combined and disregarding one aberrant sowing in 1984 near Dijon-high (Tables 3.5 and 3.6). The simulated predictions of OF, EF and M improved the predictions based on time by 38 to 75 % (Table 3.5). These results confirm the model's suitability for making predictions.

The large deviation between the predicted and experimental date of the onset of flowering for the sowing in 1984 near Dijon-high may have been due to crop damage caused by the environmental conditions frost or drought (Thore, 1986; J.P. Palleau, CETIOM, pers. comm., 1995), which may have retarded the onset of flowering.

Predicting emergence, on the basis of a relation between the development rate and air temperature did not improve the predictions based on time. This suggests that other factors such as soil moisture, sowing depth and soil temperature may be important for the rates of germination and emergence (Leterme, 1988; Daniels et al., 1986; van Keulen and Seligman, 1987). However, the absolute mean differences between experimental and simulated dates of emergence were only 1.3 and 1.7 d for Wageningen and Lelystad, respectively, and for individual sowings varied between 0 and 4 days.

Table 3.6 Experimental data (day of the year, D_{exp}) of the various developmental stages per sowing, year and location. The results of testing BRASNAP-PH (Table 3.5) are given per sowing ($dd = D_{mod} - D_{exp}$) for the data used for calibration (K, W, DL) and for the independent data (L, DH) (S: Sowing, E:emergence, OF: onset of flowering, EF: end of flowering, M: maturity, W: Wageningen, K: Kiel, DL:Dijon-low, L:Lelystad) (- : data not available).

Location	Year of sowing	S	E		OF		EF		M	
		D_{exp}	D_{exp}	dd	D_{exp}	dd	D_{exp}	dd	D_{exp}	dd
Data used for calibration:										
K	1983	234	-	-	139	0	-	-	217	−6
	1984	235	-	-	141	−5	-	-	211	−5
	1985	234	-	-	137	−2	-	-	209	−6
W	1988	236	244	1	104	0	142	0	187	0
	1989	236	245	1	103	−2	134	−2	185	−1
		251	262	−2	103	2	134	0	185	2
DL	1983	243	-	-	120	3	157	−1	193	4
	1984	245	-	-	121	−5	149	−2	191	−1
	1985	242	-	-	130	0	148	0	187	2
	1986	247	-	-	122	−1	148	4	195	−2
	1988	244	-	-	104	3	138	0	-	-
Independent data:										
L	1980	238	246	2	110	8	145	1	187	8
	„	249	256	2	118	2	145	1	188	8
	„	259	266	1	126	−5	151	−4	192	3
	1981	238	245	2	131	0	152	1	191	6
	„	248	256	1	135	−2	153	1	194	2
	1982	236	243	4	122	0	153	2	193	5
	„	249	258	0	126	−3	158	−2	195	3
	1983	237	243	2	129	−1	157	5	205	7
	„	248	257	2	129	4	158	5	206	6
	„	259	267	3	135	0	164	0	211	3

Continuation of Table 3.6.

Location	Year of sowing	S	E		OF		EF		M	
		D_{exp}	D_{exp}	dd	D_{exp}	dd	D_{exp}	dd	D_{exp}	dd
Independent data:										
	1984	236	244	0	132	–5	151	–6	200	–5
	„	248	258	1	134	–6	155	–9	204	–8
	„	257	266	1	134	–5	156	–9	205	–9
	1986	237	245	3	125	–7	157	–2	204	0
	„	247	257	4	125	–3	162	–3	207	1
	„	258	268	3	132	–6	172	–11	214	–4
	1987	243	250	2	116	1	138	3	188	3
	„	251	259	1	117	2	140	2	190	2
	„	259	268	0	117	3	141	1	192	0
	1988	245	251	3	106	3	136	9	177	12
	„	253	263	0	108	4	137	8	180	10
	1989	236	246	1	102	3	135	–2	180	6
	„	248	255	1	107	1	135	–1	181	5
DH	1983	242	-	-	128	1	168	–1	209	–1
	„	252	-	-	127	6	167	0	208	1
	1984	245	-	-	135	–21	155	–4	206	–9
	1985	240	-	-	136	–2	160	0	198	2
	„	246			135	0	156	5	198	3
	1986	240	-	-	127	–4	158	0	208	–7
	„	245			128	–3	159	0	210	–9
	1987	240	-	-	117	–3	138	3	201	–12
	1988	242	-	-	111	–4	143	–1	-	-

Factors other than temperature and photoperiod may be important for the phenological development of winter oilseed rape, as suggested for the period from sowing until emergence. This study did not consider the reported influence of leaf production and dry matter accumulation on vernalization (Hodgson, 1978; Netzer et al., 1986; Tittonel et al., 1988; Andrew et al., 1991) or the effect of the nutrient or hormonal status of the crop on the termination of flowering (Keiller and Morgan, 1988), because the mechanisms underlying the response of development rate to these factors are still poorly understood and not enough experimental data were available to test whether incorporating these factors would improve model predictions.

An extensive range of responses to environmental conditions among varieties of oilseed rape has been reported (Hodgson, 1978; Evans and Ludeke, 1987; Myers et al., 1982). It may be expected that varieties adapted to a specific environment have similar responses to environmental conditions (Reinink et al., 1986). This implies that the model is directly applicable to all varieties with a developmental pattern similar to that of variety Jet Neuf. The calibration and validation procedure might have to be repeated for other varieties.

The model developed and parameterized in this study, proved to be a good instrument for predicting the onset and end of flowering and the maturity of winter oilseed rape at various locations in North-West Europe and may be used for practical purposes or as a module in a crop growth model.

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CHAPTER 4

EVALUATION OF SEED YIELD DETERMINING FACTORS OF WINTER OILSEED RAPE (*BRASSICA NAPUS* L.) BY MEANS OF CROP GROWTH MODELLING

ABSTRACT

An existing model 'LINTUL' was extended to integrate key processes of yield formation of winter oilseed rape and to simulate crop growth and development under optimum growth conditions. The extended model 'LINTUL-BRASNAP' calculates 1) light reflection and absorption by the green canopy and flower layer, 2) total dry matter production based on light absorption and light use efficiency by the green canopy 3) seed density, 4) partitioning of dry matter to the seeds based on whether seed growth is limited by source or sink, 5) accumulation and remobilization of reserve carbohydrates. Its parameterization was partly based on literature. This article describes how the relationship (LUE) between light absorption and crop growth was analysed in two field experiments (experiments 1 and 2) in two growing seasons with varying plant density, sowing date and application of shading. LUE was low in early spring and increased until flowering. LUE gradually declined from the onset of flowering until just before maturation and then declined sharply at the end of the growth period.

Two hypotheses on the duration of a critical period for seed set in a crop, the duration of the flowering period (1) and a period of 350 °Cd since onset of flowering (2), were tested by means of the model. Variations in seed density were better simulated with the second hypothesis.

It was hypothesized that LINTUL-BRASNAP reproduces the yield formation process of winter oilseed rape in sufficient detail to satisfactorily simulate variations in various crop characteristics for different sowing dates and years under optimum growth conditions. When the model was tested with data used for parameterization (variety Jet Neuf) and with other data (variety Victor), highly significant correlations were found between simulated and experimental data of various crop characteristics such as total dry matter production at various stages of crop development, seed density, pod density and seed yield. The differences between sowing dates were simulated better than the differences between years per sowing date.

LINTUL-BRASNAP appears to be a useful tool for identifying the main crop characteristics responsible for variation in winter oilseed rape yield such as leaf area development, density of the flower layer and subsequently light absorption during the critical period of seed set. It can be used to explore options for improving the seed yield of winter oilseed rape.

INTRODUCTION

The seed yield of winter oilseed rape varies with sowing date, years and locations (Mendham et al., 1981a, 1984; Leterme, 1985; Grosse, 1989; Habekotté 1993). Generally, it is highly correlated with seed density (numbers of seeds per m^2) (Mendham et al., 1981a; Mendham et al., 1984; Leterme, 1985; Pouzet et al., 1988; Grosse, 1989; Habekotté 1993). Pod and seed set largely depend on assimilate availability for the crop in growth phases until the end of flowering (Tayo and Morgan, 1979; Mendham et al., 1981a; Evans, 1984; Leterme, 1985; Keiller and Morgan, 1988b; Habekotté, 1993). From emergence until about flowering most of the assimilates are produced in the leaves. Leaf area index peaks around flowering and then declines and stems and pods take over assimilate production (Brar and Thies, 1977; Chapman et al., 1984; Addo-Quaye et al., 1985). The remobilization of reserve carbohydrates that have accumulated up to the onset of seed filling, may contribute upto 17.5 % of seed yield (Rood et al., 1984; Addo-Quay et al., 1985; Quilleré and Triboi, 1987; Habekotté, 1993).

The main objective of the study described here was extension of an existing simple crop growth model (Spitters and Schapendonk, 1990), to integrate the key processes of yield formation of winter oilseed rape and to test the performance of the extended model by simulating crop growth and development under optimal growth conditions with ample supply of water and nutrients in a pest, desease and weed-free environment (Spitters et al., 1989). Model extension and parameterization were mainly based on literature (Habekotté 1996a). In this paper the relationship between radiation absorption and crop growth is analysed using data from field experiments in two growing seasons with varying plant density, sowing date and the application of shading and otherwise near optimal growing conditions (Habekotté and Smid, 1992). The model may be used to analyse the effect of single processes on seed yield formation under optimum growth conditions and its application to explore options for improving the yield of winter oilseed rape is illustrated in Habekotté (1996c; Chapter 5).

To ascertain whether the model simulates satisfactorily variations in various crop characteristics for different sowing dates and years under optimal growth conditions, simulations were first compared with data used for parameterization (variety Jet Neuf; Habekotté and Smid, 1992). Secondly, the model's performance was evaluated by comparing the simulation results with the general trends in yield formation of early and late sown crops, presented by Mendham et al. (1981a). Finally, seed yield variation in both data sets used for testing (Habekotté and Smid, 1992; Mendham et al., 1981a), was analysed quantitatively by means of the model.

MATERIAL AND METHODS

The model

The model, LINTUL-BRASNAP, simulates crop growth and development under optimal growth conditions and is described in detail by (Habekotté, 1996a). It is an extended version of LINTUL, based on Light INTerception and UtiLization for total dry matter production, and harvest index for seed yield (Spitters, 1990). The equations for light absorption, crop growth and partitioning of dry matter to the seeds are presented in Table 4.1 and a schematic representation is given in Fig. 4.1. The symbols used are described in Table 4.2. LINTUL-BRASNAP is written in FORTRAN-77 (Meisner and Organick, 1984), using the FSE system (FORTRAN Simulation Environment, Van Kraalingen (1995)) for growth crop simulation (Habekotté, 1996a).

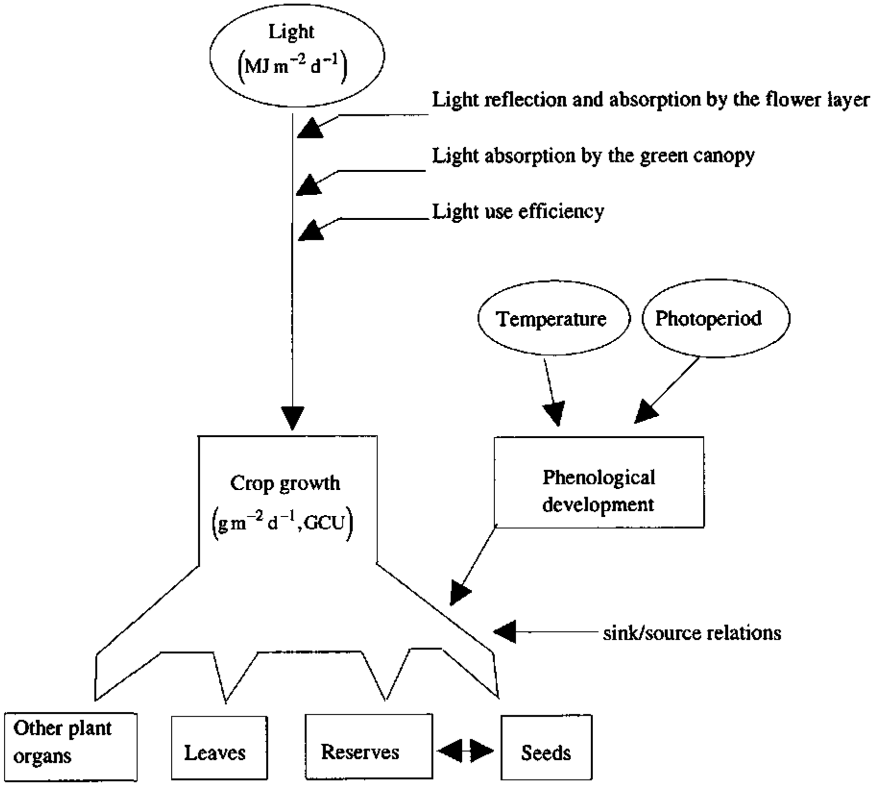


Figure 4.1 Schematic representation of crop growth and partitioning of drymatter of winter oilseed rape as described in LINTUL-BRASNAP.

Extension of LINTUL

It has been shown that the harvest index of the crop (seed yield per unit total aboveground dry matter at final harvest) of winter oilseed rape is variable (Mendham et al., 1981a; Grosse, 1989). Generally, seed yield is highly correlated with seed density (Mendham et al., 1981a; Leterme, 1985; Pouzet et al., 1988; Grosse, 1989) and daily seed growth appears to be determined either by daily assimilate availability (source) or by the maximum growth rate of the seeds (sink) (Mendham et al., 1981a; Habekotté 1993). This is why the partitioning of dry matter to the seeds is not described with a constant harvest index as in LINTUL (Spitters, 1990), but is based on sink or source limited growth of the individual seeds (Spitters et al., 1989).

Reflection and absorption of light by the yellow flowers during the period of seed set have been suggested to be important in determining final seed yield (Yates and Steven, 1987; Rao et al., 1991). Therefore, LINTUL was extended to calculate light reflection and absorption by the green and yellow crop canopy separately, and the total dry matter production is related to light absorption instead of light interception.

LINTUL-BRASNAP also includes accumulation and reallocation of reserve carbohydrates, as they may contribute up to 17.5 % to final seed weight (Rood et al., 1984; Addo-Quay et al., 1985; Quilleré and Triboi, 1987; Habekotté, 1993).

Crop phenology

In LINTUL-BRASNAP, the phenological state of the crop is characterized by *DVS*, a variable that has the value 0 at sowing, 1 at emergence, 2 at the onset of flowering, 3 at the end of flowering and 4 at maturity. The modelling of the phenological development has been described by Habekotté (1996b; Chapter 3).

Light absorption and total dry matter production

LINTUL-BRASNAP relates dry matter production to light (PAR: photosynthetically active radiation) absorption by the green parts of the canopy. Incoming light (I_0) is partly reflected by the green canopy and, during flowering, part of the I_0 is reflected and absorbed by the yellow flowers. Transmission (TR) of light by the flower layer is influenced by total flower area (*FAI*), calculated from the density of open flowers (N_f; Eq. 4.3), the surface area per open flower (A_{if}) and the ratio (D_{if}/D_{fp}) of the duration of flowering per flower and the duration of the flowering period, both expressed in degree days (Eq. 4.6). To calculate light transmission through the flower layer, the total spectrum of PAR is separated into two parts i.e. 400-525 nm (a: violet, blue and green light) and 525-700 nm (b: yellow, orange and red light) (Yates and Steven, 1987) and light reflection

Table 4.1 Equations of light absorption, crop growth and partitioning of dry matter to the seeds in LINTUL-BRASNAP (Habekotté, 1996a). Symbols used are described in Table 4.2 and in the text.

Leaf area

$$LAI = LAI_s \exp(\mathrm{RGR_{LAI}}\ tt) \qquad 0 < LAI \le 0.75 \tag{4.1}$$

$$LAI = \int (\mathrm{d}W_{tot}/\mathrm{d}t)\, \mathrm{P_{l,DVS}}\ \mathrm{SLA}\ \mathrm{d}t \qquad LAI > 0.75 \tag{4.2}$$

Flower density, pod density and seed density

$$N_f = \mathrm{f_1} + \mathrm{f_2}\ W_{tot,OF} \tag{4.3}$$

$$N_p = \mathrm{p_1} + \mathrm{p_2}\ W_{tot,EF} \tag{4.4}$$

$$N_s = \mathrm{s_1} + \mathrm{s_2}\ \Delta W_{tot,cp} \qquad N_s \le \mathrm{SPP_{pot}}\ N_p \tag{4.5}$$

Flower area

$$FAI = N_f\ \mathrm{A_{if}}\ (\mathrm{D_{if}}/\mathrm{D_{fp}}) \tag{4.6}$$

Reflection of light by the flower layer per spectral part a (400-525 nm) or b (525-700 nm) (x)

$$\mathrm{REF_{f,x}} = \left(1 - \sqrt{1 - (\mathrm{tr_x} + \mathrm{ref_x})}\right) \Big/ \left(1 + \sqrt{1 - (\mathrm{tr_x} + \mathrm{ref_x})}\right) \left(1 - \exp(-\mathrm{K_{FAI,x}}\ FAI)\right) \tag{4.7}$$

with:

$$\mathrm{K_{FAI,\,x}} = 0.8 \sqrt{(1 - (\mathrm{tr_x} + \mathrm{ref_x}))} \tag{4.8}$$

Transmission of light through the flower area

$$\mathrm{TR} = \mathrm{P_a}(1 - \mathrm{REF_{f,a}}) \exp(-\mathrm{K_{FAI,a}}\ FAI) + \mathrm{P_b}(1 - \mathrm{REF_{f,b}}) \exp(-\mathrm{K_{FAI,b}}\ FAI) \tag{4.9}$$

Residual light at the bottom of the canopy

$$I_r = I_0\ \mathrm{TR}\ (1 - \mathrm{REF_g}) \exp(-\mathrm{K_{LAI}}\ LAI) \qquad 1 < DVS \le 3.5 \tag{4.10a}$$

$$I_r = I_0\ (\mathrm{F_{I,r}} + \mathrm{RF_{I,r,DVS}}\ (DVS - 3.5)) \qquad DVS > 3.5 \tag{4.10b}$$

Continuation of Table 4.1.

Light absorption

$$I_a = I_0 \ \mathrm{TR} \left(1 - \mathrm{REF_g}\right) - I_r \qquad 4.11$$

Total crop growth

$$\mathrm{d}W_{tot} \,/\, \mathrm{d}t = \mathrm{LUE_{DVS}} \ I_a \qquad 4.12$$

Seed growth

$$\mathrm{d}\,W_s/\mathrm{d}t = \mathrm{P_{s,DVS}} \ \mathrm{d}W_{tot}/\mathrm{d}t - \mathrm{d}\,W_{res}/\mathrm{d}t \qquad 4.13$$

with: $\mathrm{d}\,W_s/\mathrm{d}t \le R_{\mathrm{is,pot,DVS}} \left(T_{\mathrm{day}} - T_{\mathrm{b,4}}\right) N_s$

Accumulation or remobilization of reserve-carbohydrates

$$\mathrm{d}\,W_{res}/\mathrm{d}t = -\left[R_{\mathrm{is,pot,DVS}} \left(T_{\mathrm{day}} - T_{\mathrm{b,4}}\right) N_s - \mathrm{P_{s,DVS}}\left(\mathrm{d}W_{tot}/\mathrm{d}t\right)\right] \quad DVS > 3.3 \qquad 4.14$$

with: $\mathrm{d}W_{res} \,/\, \mathrm{d}t \le W_{res} \ \mathrm{RGR_{res,max}}$

Crop biomass

$$W_{tot} = \int_{t_s}^{t} \left(\mathrm{d}W_{tot}/\mathrm{d}t\right) \mathrm{d}t \qquad 4.15$$

$$W_s = \int_{t_{DVS=3}}^{t} \left(\mathrm{d}W_s/\mathrm{d}t\right) \mathrm{d}t \qquad \text{with: } W_s = W_{\mathrm{is,s}} \ N_s \qquad DVS = 3 \qquad 4.16$$

$$W_{res} = \int_{t_{DVS=3.3}}^{t} \left(\mathrm{d}W_{res}/\mathrm{d}t\right) \mathrm{d}t \qquad \text{with: } W_{res} = F_{res} \ W_{tot} \qquad DVS = 3.3 \qquad 4.17$$

Green crop units

$$\mathrm{GRQ_g} = \mathrm{F_r} \ \mathrm{GRQ_r} + \mathrm{F_{st}} \ \mathrm{GRQ_{st}} + \mathrm{F_l} \ \mathrm{GRQ_l} \qquad 4.18$$

$$\mathrm{GRQ_{s,tt}} = \mathrm{RF_{oil,tt}} \mathrm{F_{oil,M}} \mathrm{GRQ_{oil}} + \mathrm{F_{pro,tt}} \mathrm{GRQ_{pro}} + \left(1 - \mathrm{R_{oil,tt}} \mathrm{F_{oil,M}} - \mathrm{F_{pro,tt}}\right) \mathrm{GRQ_{car}} \qquad 4.19$$

Table 4.2 Description of symbols in LINTUL-BRASNAP.

Symbol	Unit	Description
A_{if}	m^2	Area per individual flower
D_{fp}	°Cd	Average duration of the flowering period
D_{if}	°Cd	Duration of flowering per flower
D_{sow}	d	Sowing day (day of the year)
DVS		Phenological development stage of the crop
F_r	$g\ g^{-1}$	Average fraction of root dry matter to total dry matter excluding seeds
F_{st}	$g\ g^{-1}$	Average fraction of stem dry matter to total dry matter excluding seeds
F_l	$g\ g^{-1}$	Average fraction of leaf and pod hull dry matter to total dry matter excluding seeds
f_1 ; f_2	m^{-2}; -	Parameters for calculating flower density
FAI	$m^2\ m^{-2}$	Flower area index
$F_{l,r}$	$MJ\ MJ^{-1}$	Fraction of incoming PAR at the bottom of the canopy
$F_{oil,M}$	$g\ g^{-1}$	Maximum oil content of the seeds at maturity
$F_{pro,\ tt}$	$g\ g^{-1}$	Protein content of the seeds as a function of thermal time since pod initiation
$F_{res,DVS=3.3}$	$g\ g^{-1}$	Initial fraction of reserve carbohydrates (as fraction of total crop dry matter)
GRQ_{car}	$g\ g^{-1}$	Glucose units required for formation of carbohydrates
GRQ_g	$g\ g^{-1}$	Glucose units required for green crop units dry matter
GRQ_l	$g\ g^{-1}$	Glucose units required for leaf and pod dry matter
GRQ_{oil}	$g\ g^{-1}$	Glucose units required for formation of oil
GRQ_{pro}	$g\ g^{-1}$	Glucose units required for formation of protein
$GRQ_{s,tt}$	$g\ g^{-1}$	Glucose units required for formation of seed dry matter
GRQ_{st}	$g\ g^{-1}$	Glucose units required for stem dry matter
GRQ_r	$g\ g^{-1}$	Glucose units required for root dry matter
I_0	$MJ\ d^{-1}$	Daily incoming PAR
I_a	$MJ\ d^{-1}$	PAR absorbed daily by the green crop canopy
I_r	$MJ\ d^{-1}$	Daily residual PAR at the bottom of the canopy
K_{LAI}		Extinction coefficient of leaves
$K_{LAI,a;...b}$	$J\ J^{-1}$	Extinction coefficient for the flower layer for two parts of the total spectrum of PAR: a (400-525 nm) and b (525-700 nm)
LAI	$m^2\ m^{-2}$	Leaf area index
LAI_s	$m^2\ m^{-2}$	Initial leaf area index at the start of regrowth in spring

Continuation of Table 4.2.

Symbol	Unit	Description
$\mathrm{LUE}_{\mathrm{DVS}}$	g MJ^{-1}	Light use efficiency related to the phenological development of the crop
N_f	m^{-2}	Flower density
N_p	m^{-2}	Pod density
N_s	m^{-2}	Seed density
PAR	MJ m^{-2}	Photosynthetic active radiation (400-700 nm)
$\mathrm{P_a}$; $\mathrm{P_b}$	J J^{-1}	Parts of PAR found in two parts of the total spectrum of PAR: a (400-525 nm) and b (525-700 nm)
p_1 ; p_2	m^{-2} ; -	Parameters for calculating pod density
$\mathrm{P}_{\mathrm{l,DVS}}$	g g^{-1}	Partitioning of daily crop growth to the leaves
$\mathrm{P}_{\mathrm{s,DVS}}$	g g^{-1}	Partitioning of daily crop growth to the seeds
$\mathrm{ref}_{\mathrm{a;...b}}$	MJ MJ^{-1}	Reflection coefficient for individual petals for two spectral parts of PAR (a: 400-525 nm and 525-700 nm)
$\mathrm{REF}_{\mathrm{f,b}}$	MJ MJ^{-1}	Reflection coefficient of incoming PAR in the flower layer (spectral part b: 525-700 nm)
$\mathrm{REF}_{\mathrm{f,a}}$	MJ MJ^{-1}	Reflection coefficient for incoming PAR in the flower layer (spectral part a: 400-525 nm)
$\mathrm{REF}_{\mathrm{f,b}}$	MJ MJ^{-1}	Reflection coefficient of incoming PAR in the flower layer (spectral part b: 525-700 nm)
$\mathrm{REF}_{\mathrm{g}}$	MJ MJ^{-1}	Reflection coefficient for incoming PAR in the green canopy
$\mathrm{RF}_{\mathrm{l,r,DVS}}$		Increase of the fraction of PAR at the bottom of the canopy
$\mathrm{RF}_{\mathrm{oil,tt}}$		Relative oil content of the seeds as a function of thermal time since pod initiation
$\mathrm{RGR}_{\mathrm{LAI}}$	$°\mathrm{Cd}^{-1}$	Relative increase rate of LAI
$\mathrm{RGR}_{\mathrm{res,max}}$	g g^{-1} d^{-1}	Maximum depletion rate of reserve carbohydrates (GCU)
$R_{\mathrm{is,pot,DVS}}$	g °Cd	Potential growth rate of the seeds (per 1000 seeds (GCU))
S	MJ m^{-2}	Daily incoming global radiation (300-3000 nm)
s_1 ; s_2	m^{-2} ; -	Parameters for calculating seed density
SLA	m^2 g^{-1}	Specific leaf area of young leaves
$\mathrm{SPP}_{\mathrm{pot}}$		Potential number of seeds per pod
T_4	°C	Base temperature for calculation of the development rate from the end of flowering until maturity
$T_{\mathrm{b,is}}$	°C	Base temperature for calculation of thermal time since pod initiation, for protein, oil and carbohydrate content of individual seeds
T_{min}	°C	Daily minimum temperature

Continuation of Table 4.2.

Symbol	Unit	Description
T_{max}	°C	Daily maximum temperature
T_{day}	°C	Average daily temperature
TR	MJ MJ^{-1}	Transmission coefficient of PAR through the flower layer
$tr_{a;...b}$	MJ MJ^{-1}	Transmission coefficient for individual petals for two spectral parts of PAR (a: 400-525 nm and 525-700 nm)
t	d	Time
t_s	d	Time of start of regrowth of the crop in spring (day of the year)
tt	°Cd	Thermal time
$W_{is,s}$	g	Initial mean seed weight (GCU per 1000 seeds)
W_{res}	g m^{-2}	Weight of reserve carbohydrates (GCU)
W_s	g m^{-2}	Seed weight (GCU)
$W_{tot,s}$	g m^{-2}	Initial total crop dry weight at t_s GCU)
$W_{tot,OF}$	g m^{-2}	Total crop dry weight (including dead leaves and roots (GCU) at onset of flowering
$W_{tot,EF}$	g m^{-2}	Total crop dry weight (including dead leaves and roots (GCU) at the end of flowering
$\Delta W_{tot,cp}$	g m^{-2}	Total crop growth during the critical period of seed set dry (GCU)
W_{tot}	g m^{-2}	Total crop dry weight (including dead leaves and roots (GCU)

by the flower layer is calculated separately for both components (Eqs 4.7 and 4.8) according to Goudriaan (1977) (J. Goudriaan, Wageningen, Agricultural University (WAU), pers. comm., 1993). Light transmitted through the flower layer (Eq. 4.9, J. Goudriaan, WAU, pers. comm., 1993) is partly reflected by the green canopy and partly absorbed (Eqs 4.10 and 4.11, Spitters et al., 1989).

Leaf area is calculated since the start of regrowth of the crop in spring at t_s. At early stages of crop regrowth, temperatures rather than assimilate availability determine leaf area growth (Eq. 4.1). When leaf area index exceeds 0.75, the increase in leaf area is calculated as the product of the increase in leaf dry weight and specific leaf area of young leaves (Eq. 4.2, Spitters et al., 1989).

It is assumed that the minimum residual fraction of I_0 at the bottom of the canopy attained at the moment of maximum LAI around flowering remains constant for the remainder of the growing period until just before maturation (Eq. 4.10a) (Mendham et al., 1981a; Habekotté and Smid, 1992). This residual fraction ($F_{l,r}$) increases at the end of the growing period with increasing development stage of the crop (Eq. 4.10b) (Habekotté and Smid, 1992).

Daily crop growth rate ($\mathrm{d}W_{\mathrm{tot}}/\mathrm{d}t$) is calculated from the start of regrowth in spring at t_s as the product of daily light absorption (I_a) and the light use efficiency ($\mathrm{LUE}_{\mathrm{DVS}}$) (Eq. 4.12). $\mathrm{LUE}_{\mathrm{DVS}}$ expresses the ratio of dry matter production and light absorption, defined as a function of the developmental stage of the crop. Total crop weight is calculated by integration of daily crop growth rate (Eq. 4.15).

Organ formation

In LINTUL-BRASNAP flower density (N_f) and pod density (N_p) are derived from total dry matter at the onset ($W_{\mathrm{tot,OF}}$) and the end of flowering ($W_{\mathrm{tot,EF}}$), respectively (Eqs 4.3 and 4.4, Habekotté, 1993). Seed density (N_s) is derived from total dry matter production during the critical period of seed set (ΔW_{cp}) with a maximum defined as the product of potential number of seeds per pod ($\mathrm{SPP}_{\mathrm{pot}}$) and actual pod density (Eq. 4.5).

The duration of the critical period of seed set at crop level was estimated previously as the duration of the flowering period for reasons explained by Leterme (1985) and Habekotté (1993), i.e. 196 °Cd with a base temperature of 4.9 °C (Habekotté, 1996b; Chapter 3). Thus, the duration (in days) of the flowering period strongly depends on temperature regime. Formulated in this way, dry matter production during the flowering period and thus seed set (Habekotté, 1993; Chapter 2) are also strongly influenced by temperature regime.

An alternative hypothesis for the critical period of seed set in a crop is defined in this paper. This hypothesis is based on three known facts: a) the critical period of seed set per pod is 300 °Cd (T_b=0 °C) since pod initiation (Leterme, 1985), b) from about the end of the critical period of seed set, pod growth becomes increasingly dependent on its own photosynthesis (Leterme, 1985) and c) the influence of temperature is less pronounced on pod initiation than on flower production (own unpublished data). Pod initiation is defined as the moment flowers open (Habekotté, 1993; Chapter 2). The duration of the flowering period varies between 250 and 475 °Cd (T_b=0 °C); Leterme, 1985). The difference in temperature response between pod set and flower formation may result in similar durations of the period of pod set (expressed in °Cd) for a range of durations of the flowering period (expressed in °Cd), as illustrated schematically in Figs 4.3a and 4.3b. In earlier research (Habekotté and Smid, 1992) it was found that in flowering periods in the middle of this range, pod initiation was about 50 % at one-third of the flowering period and 75 % at mid-flowering (Fig. 4.3c). The critical period for individual pods (300 °Cd since pod initiation) of 75 % of the initiated pods is indicated by the dashed bold line in Fig. 4.3c. The mean critical period of seed set at crop level was defined based on two

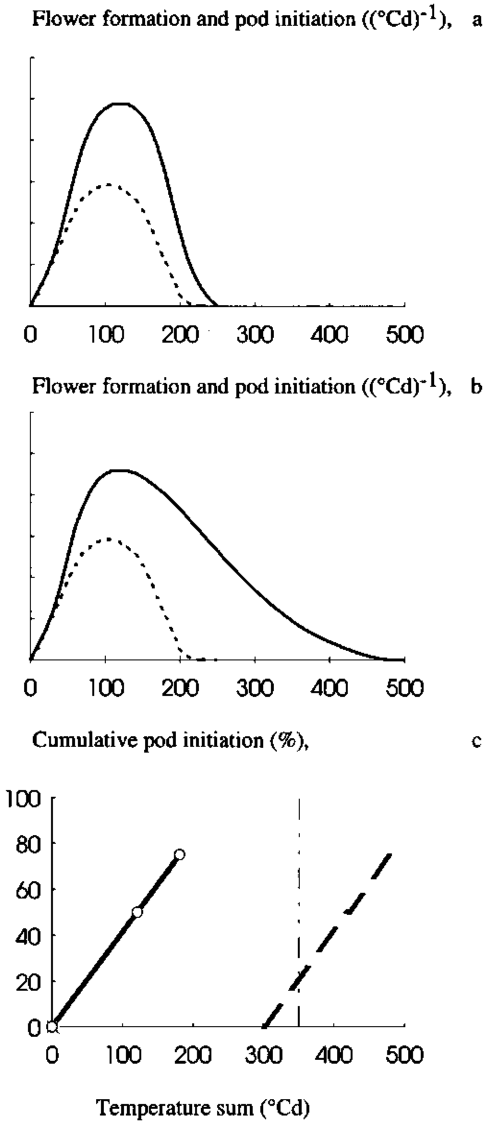


Figure 4.2 Schematic representation of flower formation rate (solid line) and pod initiation rate (dashed line) as a function of temperature sum since the onset of flowering for relatively short (a, 250 °Cd, T_b=0 °C) and long (b, 475 °Cd, T_b=0 °C) flowering periods. Average percentages of cumulative pod initiation versus temperature sum (after Habekotté and Smid, 1992) are given for a moderate length of the flowering period (362.5 °Cd, T_b=0 °C) with a solid bold line (c). The parallel dashed solid line represents the critical period for seed set per initiated pod (solid line plus 300 °Cd). The estimated end of the critical period of seed set at crop level is given by the vertical dashed line at 350 °Cd after onset of flowering (c).

conditions: 1) At least 50 % of the critical period of 75 % of all pods initiated is included in the critical period at crop level; 2) The individual critical period of less than 25 % of all pods initiated ends during the critical period at crop level, to minimize interference with independent crop growth. Thus, the critical period at crop level must be between 331 and 361 °Cd. The alternative hypothesis for the duration of the critical period for seed set in a crop is set at 350 °Cd since onset of flowering, for crops with flowering periods of variable length.

Both the original hypothesis (the flowering period) and the alternative hypothesis (350 °Cd since onset of flowering) for the duration of the critical period of seed set in a crop were used in the simulations described below.

Seed growth

LINTUL-BRASNAP calculates daily seed growth ($\mathrm{d}W_s/\mathrm{d}t$) from available carbohydrates for the seeds with a maximum of the potential growth rate per individual seed multiplied by seed density (Eq. 4.13; Spitters et al., 1989; Habekotté, 1996a). When current assimilates cannot cover the daily growth capacity of the seeds, additional assimilates may be drawn from the reserves up to a maximum depletion rate of the reserve pool ($\mathrm{RGR}_{\mathrm{res,\ max}}$) (Habekotté and Smid, 1992). A possible surplus of current assimilates is added to the pool of reserves (Eqs 4.14 and 4.19).

Total seed weight and the amount of reserves are calculated by integration of daily rates of change (Eqs 4.16-4.17).

Green crop units (GCU)

Seed weight and reserve carbohydrates are both expressed in weight units similar to those of the green canopy (GCU, g m^{-2}: green crop units), to allow for differences in chemical composition. The glucose requirement per unit green crop production ($\mathrm{GRQ_g}$ in g glucose g^{-1} dry matter) is derived from average fractions of spring and summer production of roots (F_r), stems (F_{st}) and leaves plus pod hulls (F_l) of total dry matter production of the green canopy and from the conversion factors given by Penning de Vries et al., (1989) (Eq. 4.18), based on the chemical composition of roots, stems and leaves. Glucose requirements for seed production ($\mathrm{GRQ_{s,tt}}$) change with the carbohydrate, protein and oil content of the seeds, defined as a function of thermal time (*tt*, with $T_b=T_{b,is}$) since pod initiation (Eq. 4.19). The conversion of seed weight into green crop units is calculated as the ratio $\mathrm{GRQ_{s,tt}/GRQ_g}$. The conversion of reserve carbohydrates into green crop units is calculated as $1/\mathrm{GRQ_g}$.

Parameterization, initial conditions and input data

The parameterization of LINTUL-BRASNAP, as described in detail by Habekotté (1996a), was mainly based on literature data (Appendix 4.1). The relationship between light absorption and crop growth is analysed in this paper on the basis of data from two field experiments (Habekotté and Smid, 1992). The initial conditions required for modelling crop development and crop growth are: sowing date in autumn (D_{sow}), initial total crop dry weight ($W_{tot,s}$) and initial leaf area index (LAI_s) at the start of crop growth in spring at t_s.

LINTUL-BRASNAP requires data on daily incoming global radiation (S, MJ m^{-2} d^{-1}) and daily minimum and maximum temperatures (T_{min} and T_{max}, respectively). PAR (MJ m^{-2} d^{-1}) is calculated as S/2 and thermal time is calculated by integration of daily effective temperature ($T_{eff}= ((T_{min} + T_{max})/2) - T_b$).

Experiments 1 and 2

The two field experiments used to parameterize and evaluate LINTUL-BRASNAP were carried out in 1988/89 (experiment 1) and 1989/90 (experiment 2) (Habekotté and Smid, 1992) with variety Jet Neuf on a heavy clay soil near Wageningen, the Netherlands (5 ° 40' E, 51° 58' N). Treatments were applied to establish variation in total dry matter production and pod density, by varying seed rate, plant density, sowing date, removing of side branches and application of shading.

Crop development according to the phenological scale of Habekotté (1978) was recorded weekly from early spring until final harvest. Total aboveground dry weight, plant density and the dry weight of roots, green leaves, yellow leaves, main stems, side branches, flower buds, flowers, pod hulls and seeds were recorded at intervals of two or three weeks. Area and weight of green leaves were recorded to determine the specific area (SLA) of the leaves and the area of 5 samples of 50 flowers each were measured to determine mean surface per open flower. The areas were measured with a Licor 3100 area meter (Li-Cor Inc., Lincoln, Nebraska, USA). Light interception of the crop was determined at one to two-weekly intervals at noon, by measuring PAR intensity at 5 cm above the soil surface with a portable tube solarimeter. For further details about the experiments see Habekotté and Smid (1992) and Habekotté (1993; Chapter 2).

For analysing LUE, total crop dry weight was expressed in GCU (g m^{-2}). Regression analysis and analysis of variance (ANOVA) were carried out with the GENSTAT statistical program package (GENSTAT 5 committee, Rothamsted, UK). Differences between means of treatments per experiment were compared by the least-significant difference test at the 0.05 level of probability ($LSD_{0.05}$). Differences between the overall means or between treatments in the two experiments were compared by the Student *t*-test at the 0.05 level of probability ($t_{0.05}$). The R^2 of the regression analysis is the adjusted R^2 statistic, expressed as a percentage (the percentage variance accounted for):

$$R^2 = 100\left(1-(\text{Residual mean squares})/(\text{Total mean squares})\right)$$

Model testing

Model parameterization was mainly based on data of the variety Jet Neuf. It may be expected that varieties adapted to a specific geografical region respond similarly to sowing date and environmental conditions (Mendham et al., 1981a). Therefore, it is reasonable to infer that the general trends in seed yield formation, simulated by the model may be tested with data of other winter oilseed rape varieties grown in North-West Europe. In this study, the model was tested with data of the varieties Jet Neuf and Victor.

Model performance, including the two hypotheses for seed set, was first tested with experimental data from experiments 1 and 2 (variety Jet Neuf). Data on seed weight, total dry matter at final harvest and mean seed weight were transformed into GCU. Initial values of total crop weight ($W_{\mathrm{tot,s}}$), leaf area index (LAI_{s}) and initial day of crop growth simulation (t_{s}) were derived from the first harvest in spring (Habekotté and Smid, 1992). Weather records were from the meteorological station at Wageningen, the Netherlands (5° 40'E, 51°58'N).

A second test referred to the general trends in yield formation of early and late sown crops of variety Victor near Sutton Bonington (Mendham et al., 1981a), UK, as summarized in Table 4.3 and Figs 4.4a and 4.4b. Sowing winter oilseed rape cv. Victor late in autumn (late September until early Novemer) in seven seasons from 1970 to 1977 resulted in seed yields varying from 120 to 450 g m^{-2} (Mendham et al., 1981a). All late sown crops made little growth before winter and seed yield was related to total dry matter (g m^{-2}) of the crop at full flowering. Early sown crops produced more consistent seed yields, 280-360 g m^{-2}, regardless of total dry matter of the crop at flowering (Mendham et al., 1981a).

As drought influenced crop growth and yield formation in 1973/74 and in 1975/76 and because LINTUL-BRASNAP simulates yield formation under optimum growth conditions, data from these years were excluded from the test.

Weather data from the meteorological station at Rothamsted, Harpenden, UK (0°22'E, 51°49'W) were used in the simulations. Dates of start of regrowth of the crop in spring were estimated with the method used by Mendham et al. (1981a): 'the date when mean temperatures rose and were maintained above 5 °C. Initial values of total crop weight ($W_{\mathrm{tot,s}}$) at the onset of crop regrowth in spring were based on Mendham et al. (1981a), Mendham et al. (1981b) and Mendham and Scott (1975). Initial values of leaf

Table 4.3 Experimental data of sowings in the UK (Mendham et al., 1981). Seed yield (W_s) and mean seed weight (msw) are given in GCU. Total dry matter is measured at full flowering (onset of flowering plus seven days)(W_{ff}). Start conditions for growth in spring are total dry matter ($W_{tot,s}$), leaf area index (LAI_s) and start date of regrowth (t_s) (after Mendham et al., 1981a, b; Mendham and Scott, 1975) (N_s: seed density; N_p: pod density).

Sowing									
Year	Date	W_s	msw	N_s	N_p	W_{ff}	$W_{tot,s}$	LAI_s	t_s
		g m^{-2}	g	10^3 m^{-2}	m^{-2}	g m^{-2}	g m^{-2}	m^2 m^{-2}	d
1969	22 - 8	405	6.66	60.8	9000	836	308.	1.87	103
	11 - 9	429	6.54	65.5	11100	649	172.	1.04	„
	2 -10	163	5.88	27.6	3900	220	13.4	0.081	„
1971	20 - 8	464	6.81	68.0	7400	770	343.	2.08	73
	4 - 9	422	6.60	64.0	8300	770	234.	1.42	„
	17 - 9	342	6.58	51.7	6200	583	20.2	0.122	„
	1 -10	442	6.96	63.5	5500	539	13.4	0.0813	„
1972	12 - 8	480	7.67	62.5	12200	1320	457.	2.77	78
	14 - 9	478	7.40	64.7	8700	968	200.	1.21	„
	28 - 9	344	6.94	49.6	5000	572	20.2	0.122	„
	13 -10	310	6.78	45.7	4500	528	13.4	0.0813	„
1974	23 - 8	395	5.85	67.4	6800	814	354.	2.14	101
	8 - 9	381	5.67	67.3	5900	715	210.	1.27	„
	24 - 9	388	5.38	72.1	4800	484	20.2	0.122	„
	9 -10	288	5.33	54.1	3600	341	13.4	0.0813	„
1976	21 - 8	409	6.00	68.2	8400	759	342.	2.07	62
	8 - 9	433	6.53	66.3	8470	891	122.	0.762	„
	13 -10	549	5.86	93.6	3100	693	13.4	0.0813	„
	3 -11	609	6.08	100.2	4300	847	13.4	0.0813	„

area index (*LAI*$_s$) were calculated as the product of $W_{tot,s}$, the ratio of aboveground dry matter and total dry matter at the start of regrowth (0.833 g g^{-1}, Mendham et al., 1981a), the ratio of leaf weight and total aboveground crop dry weight (0.74 g g^{-1}, Habekotté and Smid, 1992) and SLA of winter grown leaves in spring (0.00981 m^2 g^{-1}; Habekotté and Smid, 1992).

RESULTS

Experiments 1 and 2

In both seasons different treatments resulted in differences ($P < 0.05$, Table 4.4) in total dry matter production. Shading (sha) in experiments 1 and 2, the removal of side branches (rsb) in experiment 1 and later sowing in experiment 2 (lso) resulted in reduced total dry matter production compared to the control. High plant density in experiment 1 (hpd) resulted in higher total dry matter production compared to the control.

Mean total dry matter production was higher in experiment 2 (1701 g m^{-2}, GCU) than in experiment 1 (1346 g m^{-2}, GCU) (Table 4.4; $t < 0.05$). Seed yield showed an opposite trend: higher mean values in experiment 1 than in experiment 2 (527 g m^{-2} compared to 482 g m^{-2}, GCU). This higher mean seed yield was mainly due to the higher seed density (78.7 m^{-2} compared to 63.2 m^{-2}), resulting in a higher harvest index (0.389 compared to 0.278 g g^{-1}, GCU; $t < 0.05$; Table 4.4).

Light use efficiency

In both experiments 1 and 2 the mean values of the light use efficiency for the periods between successive harvests were related to development stage of the crop (Fig. 4.3). Between DVS=2 and 3.5, LUE showed a slightly decreasing trend with increasing developmental stage of the crop ($P < 0.05$, based on both experiments), but did not differ between the treatments per experiment ($P < 0.05$) or between treatments of both experiments ($t < 0.05$) except for a slightly higher value under shading in experiment 1. The mean value of LUE during this growth period was slightly higher in experiment 1 than in experiment 2 (2.466 g MJ^{-1} compared to 2.173 g MJ^{-1}, respectively, $t < 0.05$). LUE values were low at the beginning of spring and at the end of the crop growth period.

Table 4.4 Total dry matter production at final harvest (W_m; including dead leaf weight and removed side branches in experiment 1 (rsb), seed yield (W_s), harvest index (HI), seed density (N_S) and mean seed weight (msw) in two field experiments in 1988/89 and 1989/90, respectively. W_m, W_s, msw are expressed in green crop units of dry matter (GCU). The HI is the ratio of W_s and W_m (a: for comparing with lsr; b: for comparing with the other treatments; $t_{0.05}$ for comparing the means of experiment 1 and 2). See text for explanation of treatment codes.

Treatment	W_m $g\ m^2$	W_s $g\ m^2$	HI $g\ g^{-1}$	msw g	N_S $10^3\ m^{-2}$
Experiment 1					
lpd	1485	590	0.398	6.59	90.4
hpd	1669	686	0.411	6.81	101.6
rsb	1323	483	0.364	6.84	70.8
sha	906	349	0.385	6.72	52.1
Mean	1346	527	0.389	6.74	78.7
Experiment 2					
lsr	1877	541	0.287	7.62	71.0
hsr	1919	549	0.286	7.46	73.8
lso	1587	552	0.346	7.66	71.8
sha	1244	226	0.181	7.92	28.4
Mean	1701	482	0.278	7.66	63.2
$LSD_{0.05}$					
exp1	134	69	0.032	0.82	16.4
exp2a	243	88	0.021	0.37	10.4
exp2b	211	76	0.019	0.43	12.0
$t_{0.05}$	87	35	0.012	0.30	6.5

Model testing

Experiments 1 and 2

Two steps were distinguished in testing the model with experimental data from experiments 1 and 2. First the model was tested for simulation of seed density based on the two hypotheses for the duration of the critical period of seed set. Secondly, the model was tested for simulation of total dry matter at the onset and the end of flowering and at maturity, and for simulation of pod density, mean seed weight and seed yield.

Simulation of seed densities based on the alternative hypotheses for the critical period of seed set resulted in similar values for the correlation coefficients between simulated and observed values ($r = 0.905$ and $r = 0.909$, respectively; Table 4.5). Because of the slightly higher value for the second hypothesis, other correlation coefficients are given for simulations based on that hypothesis only (Table 4.5).

Highly significant relationships were found between simulated and observed data for experiments 1 and 2 for total dry matter at the onset of flowering, at the end of flowering and at maturity, seed density and pod density ($P < 0.005$; Table 4.5). Variations in observed mean seed weight did not correlate with variations in simulated mean seed weight (Table 4.5).

Variation in mean seed weight (coefficient of variation (cv) of simulated data: 2.5 %, of experimental data: 7.2 %) was low compared to variation in seed density (cv of simulated data: 31.4 %, of experimental data: 32.2 %) and seed yield appeared to be mainly determined by seed density for both experimental and simulated data ($R^2 \geq 92.1$ %).

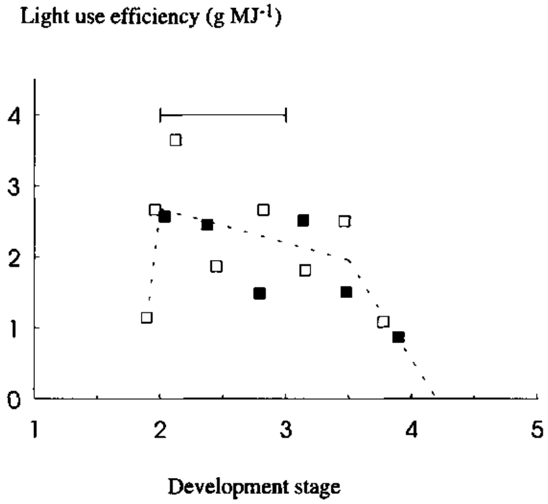


Figure 4.3 Average radiation use efficiency (LUE, g MJ^{-1}) in experiment 1 (open symbols) and experiment 2 (solid symbols) as a function of development stage of the crop (*DVS*). The horizontal bar represents the flowering period.

Table 4.5 Results of testing LINTUL - BRASNAP with data from experiments 1 and 2 (variety Jet Neuf) and with experimental data from Mendham et al., 1981a (variety Victor). The results are presented as correlation coefficients between simulated and experimental data of total dry matter at various development stages ($W_{tot,OF}$: at the onset of flowering; $W_{tot,ff}$: at full flowering; $W_{tot,EF}$: at the end of flowering; $W_{tot,m}$: at maturity), seed yield (W_s), mean seed weight (msw), seed density (N_s) and pod density (N_p), respectively (n: not significant, s: significant ($P < 0.005$), s': significant ($P < 0.05$)) (h1: the flowering period as critical period for seed set; h2: with 350 °Cd since onset of flowering as critical period for seed set). For the first hypothesis of the duration of the critical period, the results are only given for seed density. For the data of the UK, the model was tested with all sowings together (all) and for the early (early) and late sowings (late), separately.

Hypothesis	$W_{tot,OF}$	$W_{tot,ff}$	$W_{tot,EF}$	$W_{tot,m}$	W_s	msw	N_s	N_p
Experiments 1 and 2								
h1							0.905s	
h2	0.991s	-	0.977s	0.964s	0.914s	0.416n	0.909s	0.892s
Experimental data from the UK								
h1 (all)							0.663s	
h2 (all)	-	0.829s	-	-	0.727s	– 0.088n	0.693s	0.687s
h2 (early)	-	0.445s'	-	-	– 0.089n	– 0.288n	0.445n	0.233n
h2 (late)	-	0.865s	-	-	0.895s	– 0.268n	0.803s	0.008n

Data from the UK

In testing the model with experimental data from Mendham et al. (1981a), three steps were distinguished. First the model was tested for simulation of seed density based on the two hypotheses for the duration of the critical period of seed set. Secondly, the model was tested for simulation of total dry matter production at full flowering, pod density, mean seed weight and seed yield for all sowings combined, and for early and late sowings separately. Finally, the model was tested for the general trends in yield formation of early and late sowings (Fig. 4.4).

Simulations based on the second hypothesis for the critical period of seed set resulted in a slightly higher value for the correlation coefficient between experimental (variety Victor) and simulated data (variety Jet Neuf), than those based on the first hypothesis (r = 0.693

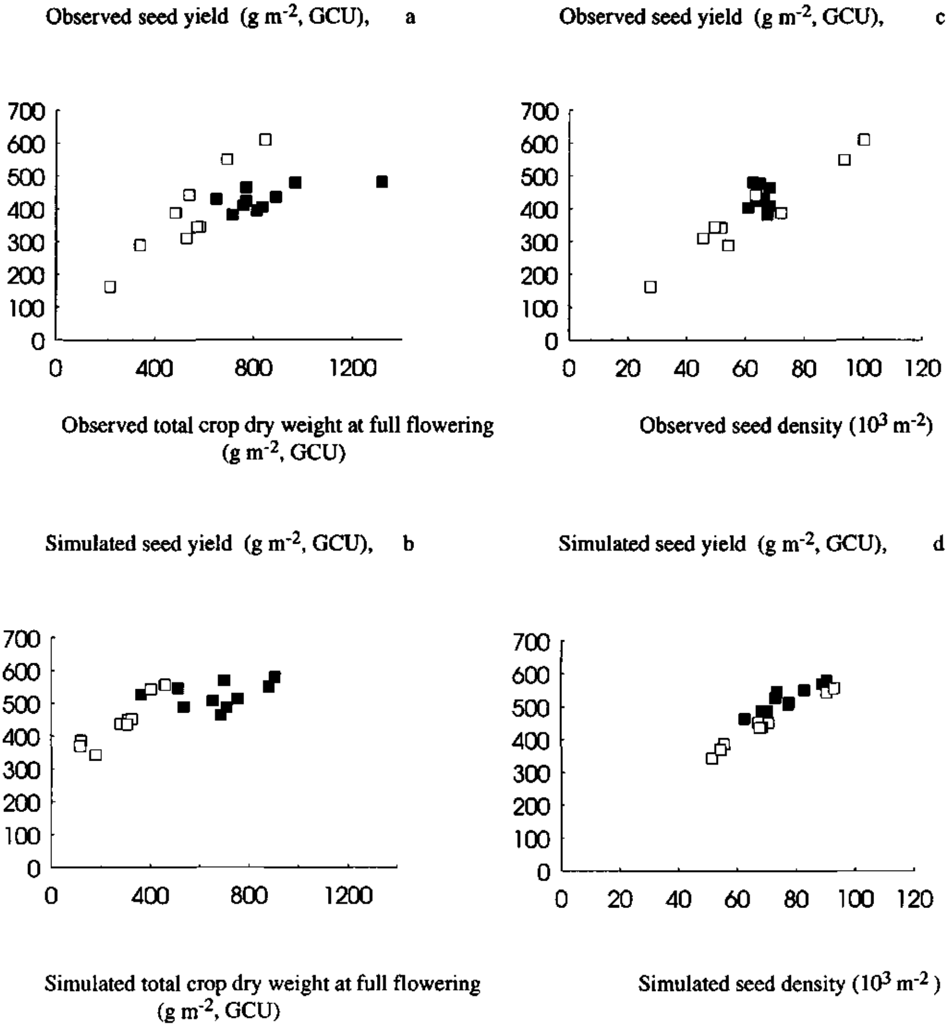


Figure 4.4 Seed yield versus total dry weight at full flowering (a and b) and seed yield versus seed density (c and d) of early (before mid September; solid symbols) and late (after mid September; open symbols) sowings in 1969, 1971, 1972, 1974 and 1976 in the UK. Full flowering is defined as onset of flowering plus seven days. Observed data refer to the variety Victor (a and c) (Mendham et al., 1981a), modelled data to the variety Jet Neuf (b and d).

Table 4.6 Results of the test of LINTUL-BRASNAP on the general trends of yield formation as found by Mendham et al. (1981a). Mean values (Mv), ranges (Rg) and standard deviation (Sd) of observed and simulated data of seed yield (W_s, in GCU, g m^{-2}) and seed density (N_s; 10^3 m^{-2}) of early and late sowings in 1969, 1971, 1972, 1974 and 1976 in the UK (early: before mid september; late:after mid September). Observed data refer to the variety Victor, simulated data to the variety Jet Neuf. The simulated data on seed density are given for simulations with the first (h1) and second (h2) hypothesis for the duration of the critical period of seed set (see text).

Data	Sowing	W_s			N_s		
		Mv	Sd	Rg	Mv	Sd	Rg
Experimental	early	429.	34.5	381.-480.	65.5	2.47	61.- 68.
	late	381.	136.	162.-609.	62.	23.3	28.-100.
Simulated, h1	early				79.2	13.3	57. - 97.
	late				69.7	14.8	45. - 91.
h2	early	523.	37.7	464.-579.	76.3	8.97	62.-89.
	late	441.	72.1	343.-556.	68.6	14.8	51.- 93.

Table 4.7 Mean values of observed and simulated mean seed weight (g per 1000 seeds, GCU) in experiments 1 and 2 and for the early and late sowings in the UK (after Mendham et al., 1981a).

Data	Experimental	Simulated
Experiment 1	6.75	6.80
Experiment 2	7.58	6.99
Early sowings UK	6.57	6.89
Late sowings UK	6.20	6.49

and 0.663, respectively; $P < 0.005$; Table 4.5). Variation in experimental seed densities is clearly less for the early sowings than for the late sowings (standard deviations: 2.47 and 23.3, respectively and ranges: 61 - 68 compared to 28 - 100 10^3 m^{-2}, respectively, Table 4.6). These trends were also best simulated with the second hypothesis for the critical period for seed set (Table 4.6). Therefore, further calculations were based on this hypothesis.

For all sowings combined, highly significant correlations were found between simulated and observed data for total crop weight at full flowering, seed yield, seed density and pod density (Table 4.5). Simulated variations in mean seed weight did not correlate with observed variations (Table 4.5). However, both observed and simulated mean seed weight were lower for the late sowings than for the early sowings (Table 4.7, $t < 0.05$).

For the early sowings, a significant correlation between simulated and observed data was only found for total crop weight at full flowering (Table 4.5). For the late sowings, the correlations between simulated and observed data were highly significant for total crop weight at full flowering, seed yield and seed density. Simulated data on pod density and mean seed weight did not correlate with the observed data (Table 4.5). Hence, differences in various characteristics between sowing dates were simulated more accurately than differences between years per sowing date.

For both the simulated and observed data, the seed yields of late sowings were correlated with total dry matter production at full flowering; this was not true for the seed yields of the early sowings. Simulated variations in seed density and seed yield were smaller for late sowings (standard deviations of 14.8 % and 72.1 %, respectively) and greater for early sowings (standard deviations of 8.97 % and 37.7 %, respectively) than in the observed data (standard deviations: late sowings: 23.3 % and 136 %, respectively; early sowings: 2.47 % and 34.5 %, respectively; Table 4.6).

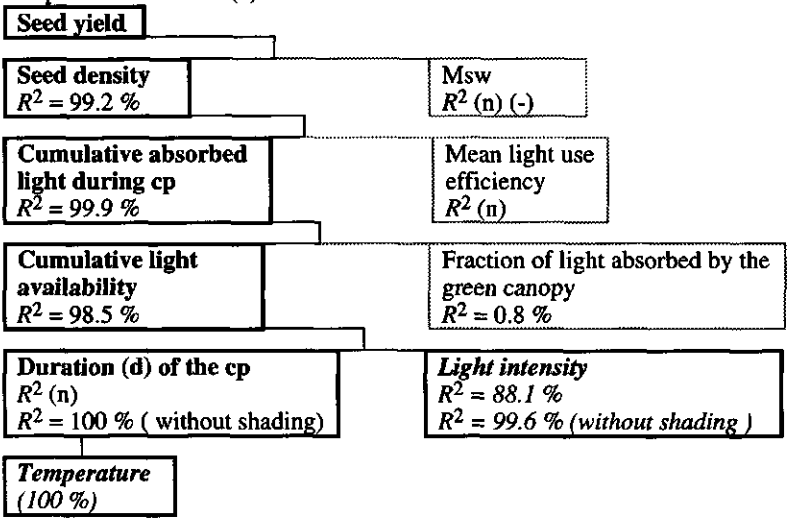
Both the observed and simulated data showed a significant linear relationship between seed yield and seed density (Fig. 4.4; R^2 = 82.1 % (observed) and 84.5 % (simulated), respectively) (Fig. 4.4). The highest observed seed densities and seed yields were obtained with the late sowings in 1976/77. The highest simulated seed density was also obtained with late sowing in 1976/77, however, this late sowing did not result in the highest seed yield, because of insufficient seed filling (Fig. 4.4d and Table 4.6).

Analysis of seed yield variation

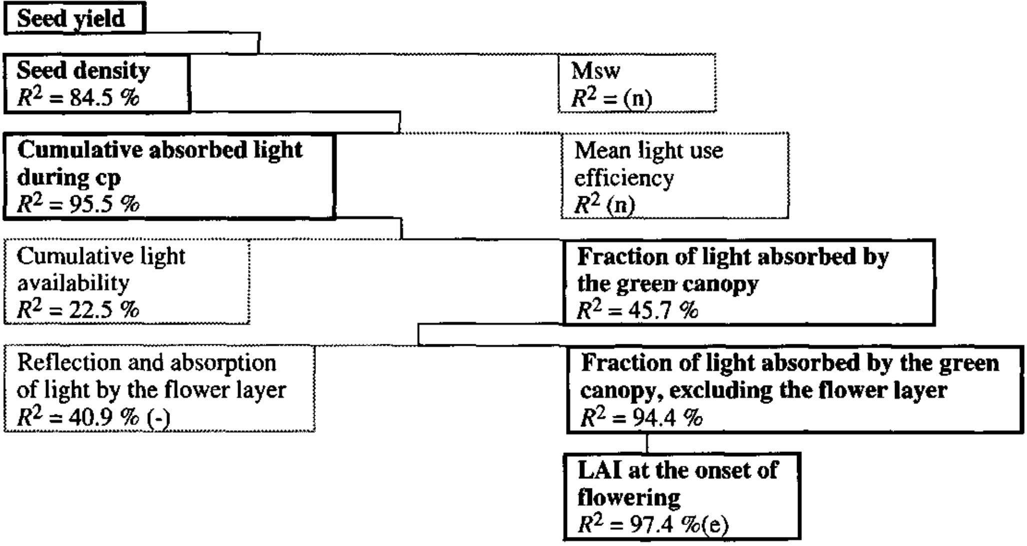
Experiments 1 and 2

Seed yield variation in experiments 1 and 2 was highly correlated with seed density (Fig. 4.5a). In LINTUL-BRASNAP seed density is determined by total crop dry matter

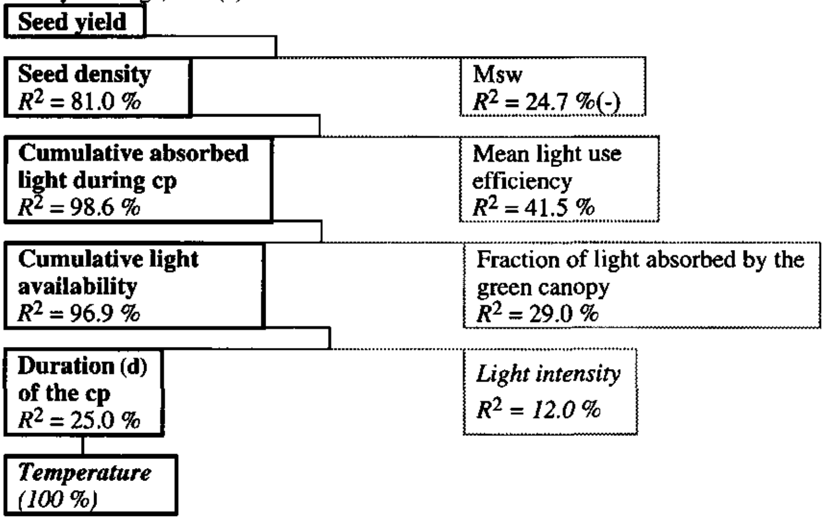
Experiments 1 and 2 (a)



All sowings, UK (b)



Early sowings, UK (c)



Late sowings, UK (d)

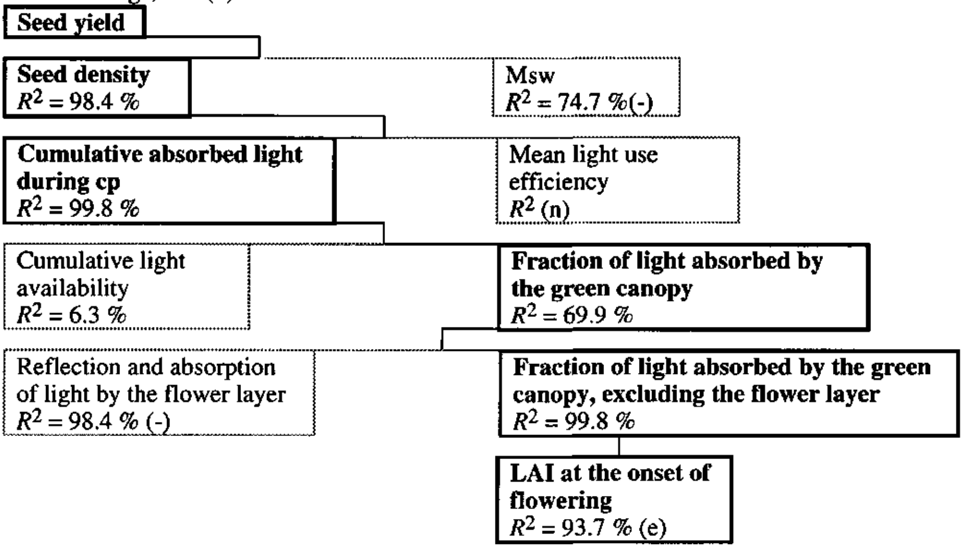


Figure 4.5 Analysis of yield formation of experiments 1 and 2 (a), of all (b), early (c) and late (d) sowings in the UK by means of LINTUL-BRASNAP. At each level of analysis, the most important crop characteristic or environmental factor to explain the variation in a crop characteristic at a preceding level, is given bold. The regression analysis was based on straight lines (Y= a + b X), except for (e): an exponential curve ($Y = a + b\, r^X$). If there was only one explanatory factor, R^2 was not calculated (100%) (n: Residual variance exceeded variance of Y variate; (-): indicates a negative correlation).

production during the critical period of seed set, calculated by integration of the product of daily light (=PAR) absorption and LUE. Mean light use efficiency during the critical period of seed set was similar for all treatments in both experiments (range: 2.48-2.54 g MJ^{-1}) and thus variation in seed density was the result of variation in cumulative light absorption (Fig. 4.5a). Growth before flowering was sufficient to attain high and similar levels of fractional light absorption during this period (range: 66-71 %) and variation in cumulative light absorption resulted from variation in cumulative light availability (Fig. 4.5a). The shading treatments in both experiments provided variation in available light intensity (range: 40-100 % of incoming PAR; Habekotté, 1993) and light intensity appeared the most important factor to explain variation in cumulative light availability (Fig. 4.5a). Without the shading treatments, the duration of the critical period of seed set was the most important factor explaining variation in cumulative light availability (Fig. 4.5a). This analysis shows that variations in seed yield in experiments 1 and 2 were indirectly determined by variations in light intensity during the critical period of seed set.

Data from the UK

Variations in seed yield of early and late sowings combined could be explained by seed density, seed density by cumulative light absorption during the critical period of seed set and cumulative light absorption by fraction of light absorbed (I_a/I_0) during the critical period (Fig. 4.5b). In LINTUL-BRASNAP, the fraction of light absorbed is influenced by transmission (TR) of light by the flower layer and by the fraction of light absorbed by the green canopy ($F_g = (1-REF_g) \exp(-K_{LAI}\, LAI)$ Eqs 4.6-4.11, Table 4.1) separate from the effect of the flower layer. The fraction of light absorbed correlated more strongly with F_g than with TR (Fig. 4.5b). Variations in F_g during the critical period of seed set could be explained by leaf area index at the onset of flowering (LAI_{OF}) (Fig. 4.5b). LAI_{OF} was highly correlated with initial LAI at the start of regrowth in spring (LAI_s) (R^2 = 70.3 %). LAI_s was highly negatively correlated with date of sowing (R^2 = 79.2 %). This analysis shows that sowing date indirectly determines seed yield and that LAI_{OF} is an important characteristic for seed yield formation (Fig. 4.7).

Simulated early sowings all achieved an LAI_{OF} of at least 1.7 $m^2\, m^{-2}$, resulting in high and similar fractions of absorption of PAR by the green canopy of 69.8 % on average (range: 67.4-72.6), similar to experiments 1 and 2. For these sowings, simulated variation in seed density could be explained by the same crop characteristics and environmental factors as in experiments 1 and 2, excluding the shading treatments (Figs 4.5a and 4.5c).

Late sowing resulted in low average values of LAI at the onset of regrowth in spring (LAI_s, Table 4.2) and spring growth was generally insufficient to reach a minimum value of LAI at the onset of flowering to attain sufficient light absorption during the critical period of seed set (Fig. 4.7). For the late sowings, the fraction of light absorbed was on 61.1 % on average

(range: 44.9-71.9). Variation in seed yield was indirectly determined by the fraction of light absorbed during the critical period of seed set, mainly governed by LAI_{OF} (Fig. 4.5d).
Transmission of light by the flower layer was on average slightly higher for the late sowings than for the early sowings (84 compared to 79 %), but this did not compensate for the relatively low values of LAI_{OF}.

DISCUSSION

Light use efficiency

The cumulative dry matter production of crops adequately supplied with moisture and nutrients has been shown to be linearly related to absorbed or intercepted solar radiation (Monteith, 1977; Gosse et al., 1986; Kiniry et al., 1989). The slope of this relation represents the average light use efficiency (LUE). Analysis of this relation in experiments 1 and 2 showed lower values at the beginning of spring and at the end of the growing season. Mendham et al. (1981a) also found a lower LUE in early spring, and suggested a relation with low temperatures. In experiments 1 and 2 no relation was found with temperature. The lower value in the beginning of spring may be due to the lower photosynthetic activity of winter grown leaves and a lower *LAI* at the onset of regrowth (Spitters, 1990; Habekotté and Smid, 1992). At low *LAI* values the leaves are more exposed to saturating light intensities than at higher *LAI*s, resulting in lower light use efficiency in the crop (Habekotté, 1996c; Chapter 5).
At the onset of crop growth, the crop's light absorption and dry matter production are governed by leaf area. *LAI* peaks around flowering and subsequently declines with increasing development stage of the crop and as light absorption and dry matter production are taken over by stems and pods. Some measurements of gross photosynthetic capacities of leaves, stems and pods show that the gross photosynthetic capacities of stems and pods are lower than that of leaves: about 69 % and 38 %, respectively (Rode et al., 1983; de Boer and Langenhuysen, 1985). This may partly explain the gradual reduction in LUE after the onset of flowering in experiments 1 and 2 (Fig. 4.2) (Habekotté, 1996c; Chapter 5). The sharp decline at the end of the growing season (*DVS* > 3.5) may be due to a decline in the photosynthetic capacity of the green canopy with increasing age (Rode et al., 1983; de Boer and Langenhuysen, 1985; Spitters, 1990).
Despite statistically significant differences in total dry matter production between experiments 1 and 2 and between the treatments per experiment (Table 4.4), the relation between LUE and *DVS* was similar in both experiments. At least 95.3 % (range 95.3-97.2) of the differences in total dry matter production at the onset of flowering, the end of

flowering and at maturity were explained by LUE_{DVS}. Hence, differences in total dry matter production were largely attributable to cumulative light absorption.

Model testing

Testing the model with data from experiments 1 and 2 and with the experimental data from the UK (Mendham et al., 1981a) showed that variations in seed density were better explained with the second hypothesis for the duration of the critical period of seed set (350 °Cd since onset of flowering, T_b=0.0 °C) than with the first hypothesis, the flowering period (196 °Cd, T_b=4.9 °C) (Tables 4.5 and 4.6). The duration (d) of the critical period of seed set based on the second hypothesis is influenced less by fluctuations in temperature than the duration of the flowering period, because of a lower base temperature.

Simulated variation in seed density was greater for the early sowings in the UK than in the observed data, but smaller for the late sowings (Table 4.6). For the early sowings, simulated variation in seed density is indirectly determined by the duration of the critical period for seed set (Fig. 4.5c). The greater simulated variation in seed density of the early sowings may be due to the fact that the influence of temperature on the length of the critical period of seed set is still too strong in LINTUL-BRASNAP. This would also explain the low values of the correlation coefficient between simulated and observed values of seed density and seed yield for these sowings (Table 4.5). The duration (d) of the critical period might be partly governed by temperature and partly by other factors. Keiller and Morgan (1988a) found that in oilseed rape the end of pod and flower production coincides with a sudden cessation of apical growth and sink strength. In a companion paper they conclude that the pods nearer the base of the plant inhibited the growth and development of the apical regions, possibly becaus of competition for assimilates or a build-up of inhibitory substances at the apices or a combination of these (Keiller and Morgan, 1988b). Seed set may be regulated by a mechanism similar to pod set. A more explanatory description of the factors that regulate pod and seed set would improve the accuracy of simulation seed density and final seed yield.

The smaller variation in simulated seed density in the late sowings in the UK compared to the observed densities (Table 4.6) can be largely attributed to the higher seed densities observed in 1976/77 and the lower seed density observed in 1969/70. The high seed densities in 1976/77, both observed (Mendham et al., 1981a) and simulated, were partly due to the long period of growth during spring until the onset of flowering, which resulted in an *LAI* high enough to allow sufficient light absorption during the critical period of seed set (Fig. 4.7) (simulated maximum *LAI*: 2.52-2.82 m^2 m^{-2}). A more detailed analysis of the experimental data also showed lower pod densities (50 % lower) for the late sowings in 1976/77 than expected on the basis of total crop dry weight at flowering (Fig. 4.6).

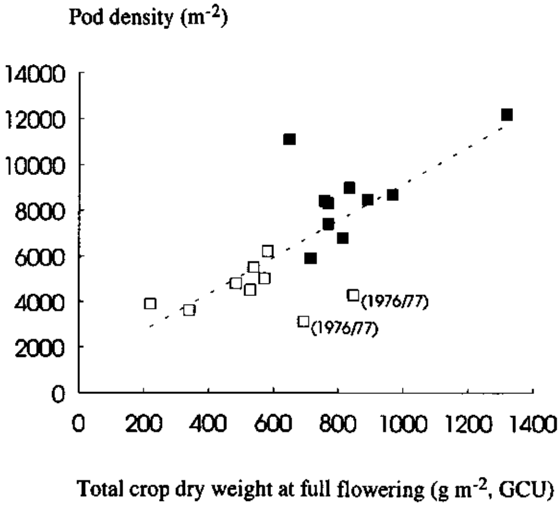


Figure 4.6 Experimental pod density (m^{-2}) of early (before mid September; solid symbols) and late (after mid-september; open symbols) sowings versus total crop dry weight at full flowering Mendham et al. (1981a)(Y=1110.+8.041 X, $R^2 = 85.8$ %, without the deviating densities of 1969/70 and 1976/77)

Simulation with a reduced flower density (50 %) similar to that found for the observed pod densities in 1976/77 (Fig. 4.6), increased the transmission of light through the flower layer and resulted in at most 12 % higher seed densities for the late sowings (101 and 105 x10^3 m^{-2}, respectively) and largely explained the observed high seed densities in 1976/77. This resulted in the simulated variation in seed density of the late sowings increasing by 30 %, i.e. much closer to the observed variation in seed density (simulated data: sd=19.2; observed data: sd=23.3 %).

In addition to the effects of a high *LAI* at the onset of flowering and the low density of the flower layer, Mendham et al. (1981a) suggested that the high seed yields in 1976/77 may have been due to a better utilization of absorbed light for seed set. The latter may be associated either with 1) greater light use efficiency due to improved light distribution through the canopy or 2) a stronger response of seed set to available assimilates, due to a less dense canopy (branches, flowers and pods) with less competition for assimilates. These effects will be discussed futher in Habekotté (1996c; Chapter 5).

Because of a late spring in 1969/70, the late simulated and observed sowing in this growing season reached a limited crop weight at full flowering (180 and 220 g m^{-2}, respectively). Observed seed set was lower than expected from the estimated cumulative light intercep-

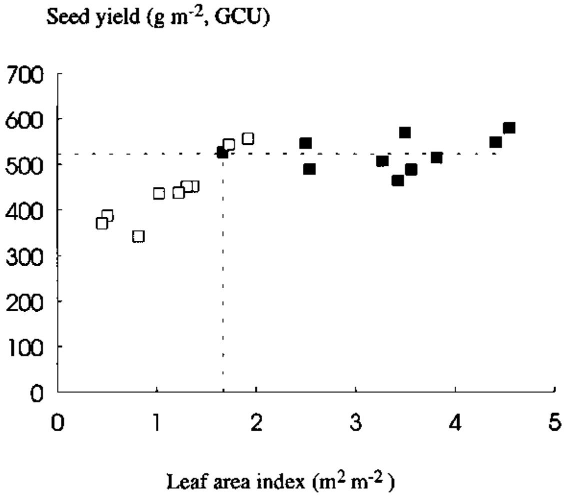


Figure 4.7 The relation between seed yield and LAI at the onset of flowering (LAI_{OF}) of the simulated (variety Jet Neuf) early (solid symbols) and late (open symbols) sowings in the UK (Mendham et al., 1981a).

tion during the critical period of seed set (Mendham et al., 1981a). For this sowing, peak *LAI* was limited (1.5-1.8 m^2 m^{-2}, Scott et al., 1973; Mendham et al., 1981a) and was reached at the onset of flowering (Scott et al., 1973). *LAI* declined rapidly after onset of flowering. Pod density was limited and pod area formation increased slowly after *LAI* began to the decline (Scott et al., 1973). Thus, light interception during the critical period of seed set, based on light interception just before onset of flowering (Mendham et al., 1981a) may have been overestimated.

Simulated maximum *LAI* was also limited for this late sowing in 1969/70 (1.14 m^2 m^{-2}). In accordance with Mendham et al. (1981a), the model assumes that minimum residual fraction of I_0 at the bottom of the canopy attained at the moment of maximum *LAI* around flowering remains constant during the remainder of the growing period until just before maturation. At very low crop weights at flowering with limited *LAI*s and pod formation, this assumption might lead to an overestimation of light absorption during the period of seed set and thus to an overestimation of seed set and final seed weight.

Further testing of the model with the same data sets showed highly significant correlations between simulated and observed data for various crop characteristics, i.e. total dry matter production, seed density, pod density and seed yield (Table 4.5). Simulated variation in mean seed weight of individual sowings did not correlate with the observed variation, although average mean seed weight was lower in experiment 1 than in experiment 2 (not significant for simulated data, significant for experimental data, $t < 0.05$) and was also

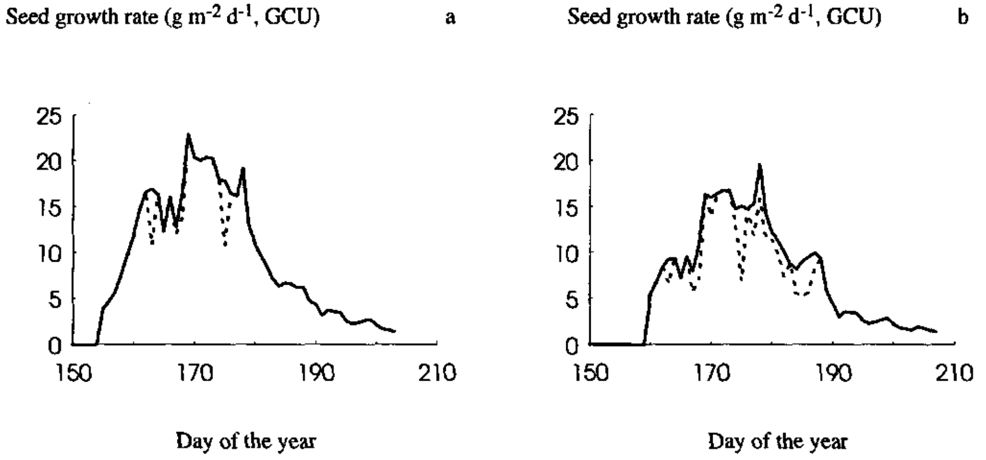


Figure 4.8 Simulated potential (solid line) and actual (dashed line) seed growth rate ($g\ m^{-2}\ d^{-1}$) for an early (a, before mid September) and late (b, after mid September) sowing in 1969 in the UK (Table 4.3; Mendham et al., 1981a).

lower in the late sowings than in the early sowings in the UK (significant, $t < 0.05$), for both observed and simulated data (Table 4.7). This indicates that source limitation of daily seed growth occurred more frequently in experiment 1 than in experiment 2 and in the late sowings than in the early sowings. However, simulation with unlimited potential seed growth rates led to values of mean seed weight being 6 to 36 % higher for all sowings in experiments 1 and 2 and in the UK. This shows that averaged over the seed filling period, seed filling was sink-limited for all crops, as illustrated in Fig. 4.8. Therefore, variations in mean seed weight were relatively small compared to variations in seed density, and for both the observed and the simulated data the seed yield was highly correlated with seed density ($R^2 \geq 82.1$ %).

Analysis of seed yield variation

Mendham et al. (1981a) showed that seed yield of the late sowings was related to total crop dry matter at full flowering and that seed yield of the early sowings was less variable. A similar trend was found for the simulated data, and analysis of seed yield formation by means of the model showed that these trends corresponded with leaf area index at the onset of flowering (Fig. 4.7). All late sowings start with a low leaf area index at the beginning of crop regrowth in spring (Table 4.3) and in most years the period for spring growth was too short for sufficient leaf area to be developed before the onset of the critical period for seed set (Mendham et al., 1981a). This explains the lower seed yield of the late sowings compared to the early sowings.

As shown for the UK data, the density of the flower layer has a direct effect on light absorption during the critical period of seed set and an indirect effect on seed yield. The calculations in this study have shown that high seed yields may be obtained with vigorously growing crops that develop sufficient leaf area at flowering for maximum light interception and that have limited flower density so that light reflection and absorption by petals are limited during the critical period of seed set.

CONCLUSIONS

LINTUL-BRASNAP integrates key processes of growth and development of winter oilseed rape under optimal growth conditions and recognizably reproduced the observed variation in various crop characteristics, such as total dry matter production, pod density, seed density and seed yield resulting from different sowing dates and years with different growth patterns. The model appears to be a useful tool for identifying the main crop characteristics causing variation in winter oilseed rape yield, such as leaf area development, the density of the flower layer and subsequent light absorption during the critical period of seed set.

Habekotté (1996c; Chapter 5) describes the use of the model for exploration of options for increasing the seed yield of winter oilseed rape (Habekotté, 1996c).

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Appendix 4.1 Parameter values in LINTUL-BRASNAP (Habekotté, 1996a).

Parameter	Value	Unit	Source
Light absorption and crop growth			
LUE_{DVS}	0.000, 0.000, 0.999, 0.000, (at t_s), 1.145, 2.000, 2.682, 3.500, 1.957, 4.200, 0.000	g MJ^{-1}	Habekotté and Smid, 1992; this chapter
K_{LAI}	0.986		Habekotté and Smid, 1992; Habekotté, 1996a
$RF_{l,r,DVS}$	0.184		„
SLA	0.0177	cm^2 g^{-1}	„
RGR_{LAI}	0.00732	$°Cd^{-1}$	de Boer and Langenhuysen, 1985; Habekotté, 1996a
$P_{l,DVS}$	0.000, 0.000, 1.000, 0.752, 1.125, 0.752, 1.425, 0.363, 1.580, 0.330, 1.780, 0.298, 2.010, 0.265, 2.321, 0.160, 2.32101, 0.0, 6.000, 0.000		Habekotté and Smid, 1992; de Boer and Langenhuysen, 1985; Habekotté, 1996a
REF_g	0.046 before OF 0.072 after EF		Yates and Steven, 1987; Leach et al., 1989;
A_{if}	2.13	cm^2	Habekotté, 1996a
D_{if}	30.5 (T_b=4.9163 °C)	°Cd	Habekotté, 1996a
D_{fp}	195.94 (T_b=4.9163 °C)	°Cd	Habekotté, 1996b; Chapter 3
ref_a; ref_b	0.035; 0.450		Yates and Steven, 1987
tr_a; tr_b	0.035; 0.150		„
P_a; P_b	0.400; 0.600		„
Flower, pod and seed density			
f_1; f_2	6380; 7.34.	m^{-2};	Habekotté, 1993
p_1; p_2	−1021.; 6.76	m^{-2};	„
s_1; s_2	−7663.; 184.1	m^{-2};	Habekotté, 1993; this Chapter
SPP_{pot}	35		Mendham et al., 1984

Continuation of Appendix 4.1.

Parameter	Value	Unit	Source
Seed growth			
$P_{s,DVS}$	0.00, 0.000, 2.41, 0.000, 2.81, 0.115, 3.30, 1.000, 5.00, 1.000	$g\ g^{-1}$	Habekotté and Smid, 1992; Habekotté, 1996a
$W_{is,s}$	0.254×10^{-3}	g	„
$R_{is,pot,DVS}$	0.000, 0.000, 2.999, 0.000, 3.000, 2.838, 3.110, 6.346, 3.256, 15.386, 3.330, 20.086, 3.505, 20.086, 3.549, 17.917, 3.769, 4.841, 4.355, 0.045, 6.000, 0.000	10^{-3} $g\ °Cd^{-1}$	„
Reserve carbohydrates			
$F_{res,DVS=3.5}$	0.049	$g\ g^{-1}$	„
$RGR_{res,max}$	– 0.0524	$g\ g^{-1}\ d^{-1}$	„
Green crop units (GCU) :			
F_r ; F_{st} ; F_l	0.026; 0.557; 0.417	$g\ g^{-1}$	„
$RF_{oil,tt}$	0.0, 0.00, 275., 0.051, 373., 0.41, 438., 0.69, 490., 0.82, 539., 0.94, 588., 0.98, 641., 1.00, 1200., 1.00	$g\ g^{-1}$	Triboi-Blondel and Ribaillier, 1988; Habekotté, 1993, 1996a
$F_{oil,M}$	0.42 (1988/89, 1989/90)	$g\ g^{-1}$	van der Meulen, 1990a,b
$F_{pro,tt}$	0.00, 0.22, 1200., 0.22	$g\ g^{-1}$	Triboi-Blondel and Ribaillier, 1988
$GRQ_{r;...st;....l}$	1.444; 1.513; 1.463	$g\ g^{-1}$	Penning de Vries et al., 1989
$GRQ_{o;...p;...c}$	3.189; 1.887; 1.275		
$T_{b,is}$	0.0	°C	Habekotté, 1993; 1996a

CHAPTER 5

OPTIONS FOR INCREASING SEED YIELD OF WINTER OILSEED RAPE (*BRASSICA NAPUS* L.): A SIMULATION STUDY

ABSTRACT

The yield formation of winter oilseed rape was compared with that of winter wheat in terms of light absorption, light use efficiency and harvest index. Options for increasing seed yield in winter oilseed rape, related to these three yield determining components were evaluated quantitatively by means of sensitivity analyses with a crop growth model. Finally, crop ideotypes were designed for high-yielding winter oilseed rape under optimal growth conditions, and their relative effects on seed yield for six different locations in North-West Europe were simulated.

The proportion of incoming light absorbed by winter oilseed rape compared favourably with that of winter wheat, whereas cumulative light availability, cumulative light absorption, light use efficiency and harvest index were lower. Exploration of options indicated that higher seed yields may be obtained through (in descending order of importance): a) delayed maturity; b) improved seed set: c) smaller petals or apetalous flowers; d) increased potential growth rate of individual seeds; e) earlier flowering with retention of the duration of total growth period and f) erect clustered pods. The results also showed that increased average seed yields can best be obtained by simultaneously increasing the average sink and source capacity for seed filling.

The most promising crop type for high seed yields matures late, combines early flowering with a maximum *LAI* of about 3 for almost maximum light absorption and has erect clustered pods for source improvement. To take full advantage of the source, the sink has to be increased through a high rate of seed set, a large sink capacity of individual seeds, apetalous flowers or a combination of these characteristics. This crop type showed increased cumulative light absorption, light use efficiency, harvest index and potential seed yield at different locations in North-West Europe. Without a delay in maturity, the potential increases in seed yield were smaller.

INTRODUCTION

Seed yields of winter oilseed rape have been increased by breeding and improved agronomic practices; however, the yields are still moderate compared to winter wheat, a seed crop widely grown in North-West Europe (Leterme, 1985; Daniels et al., 1986; Habekotté 1989). As winter oilseed rape uses the same photosynthetic pathway (C3) and its growth duration is similar to that of winter wheat, similar production levels should be attainable (Daniels et al., 1986; Gosse et al., 1986). Current varieties of winter wheat in the Netherlands yield about 9 t ha^{-1} seed dry matter under near optimum growing conditions (Van der Meulen, 1990a, b, 1991, 1993, 1994). Taking into account the difference in chemical composition of the seeds of both crops (Penning de Vries et al., 1989; Habekotté 1996b), winter oilseed rape should yield about 5.8 t ha^{-1}, i.e. about 2.5 t ha^{-1} more than the currently attainable mean seed yield (Habekotté, 1989).

Increased seed yield of winter oilseed rape is one of a wide range of breeding objectives, which include seed quality, cold tolerance in winter and early spring, resistance to diseases and lodging and seed retention (Thompson and Hughes, 1986; M.J.J. Pustjens, Van der Have, pers. comm., 1989). Since the development of the ideotype concept (Donald, 1968; Thompson, 1983; Sedgley; 1991, Rasmusson, 1991) plant physiologists have become interested in identifying of crop characters that influence the physiological processes determining final seed yield (Thurling, 1974, 1991; Thompson, 1983; Daniels et al., 1986). Smaller petals or apetalous flowers may improve light absorption by the green canopy (Mendham et al., 1981a; Yates and Steven, 1987; Rao et al., 1991); erect leaves and pods may improve light distribution within the canopy, thus improving its photosynthetic capacity (Rasmusson, 1991; Mendham et al., 1984; Thompson and Hughes, 1986; Thurling, 1991); an increase in yield components, pods m^{-2} or seeds per pod, may increase sink capacity and partitioning of assimilates to the seeds (Mendham et al., 1981a; Sedgley, 1991; Thurling, 1991; Grosse et al., 1992b; Habekotté, 1993). In addition to the agronomic benefit, the usefulness of the characters identified as selection criteria depends on other aspects, such as genetic variability, genetic control and measurability of the characters in large-scale trials (Mahon, 1983). Suitable characters may improve the choice of parental lines in breeding programmes and later the selection of superior genotypes (Thurling, 1974, 1991; Thompson, 1983; Rasmusson, 1991; Grosse et al., 1992a; Diepenbrock and Becker, 1992; Engqvist and Becker, 1993).

However, so far the application of knowledge of the crop's physiology in breeding programmes has been limited, because the proposed strategies are not always unambiguous, quantitative effects of various crop traits on seed yield and their mutual interactions have often not been clearly identified. Moreover, studies are frequently based on a limited number of existing varieties which do not represent the possible biologically strategies of yield formation (Link et al., 1992) and recording of proposed characters in breeding programmes were considered as too laborious and expensive (Diepenbrock and Becker, 1992). To meet part of these constraints in the present study, a crop growth model that simulates the yield formation processes in sufficient detail, was used to quantify the effect of hypothetical changes in crop characters on the seed yield of winter oilseed rape in different environments. Various authors (Loomis et al., 1979; Spitters and Schapendonk, 1990; Lawn and Imrie, 1991; van Oijen, 1991; Hunt, 1993; Kropff et al., 1994; Aggarwal, 1995; Kooman, 1995) have recommended using such models for this purpose in other crops.

This article descibes how the yield formation of winter oilseed rape and winter wheat growing under optimum conditions in the Netherlands was compared in terms of light absorption during the growing period from early spring to harvest, light use efficiency and harvest index, to identify strong and weak components in the yield formation process of winter oilseed rape. The resulting frame of references could be used to order and assess options for yield improvement. A simple crop growth model (Habekotté, 1996c) was then used for quantitative evaluation and synthesis of options for improving the seed yield of winter oilseed rape under optimum growing conditions in North-West Europe. These options were based on crop characters that show genetic variability (or seem likely to do so) and most of them can easily be recorded in breeding programmes. The model used, bases total dry matter production on cumulative light absorption and light use efficiency. Therefore, the evaluation of the effect of improved light distribution within the canopy on canopy photosynthesis and light use efficiency, was analysed with a detailed model of daily canopy photosynthesis (Goudriaan, 1988; Spitters et al., 1989).

MATERIALS AND METHODS

Comparison of yield formation of winter oilseed rape and winter wheat

Average potential seed yield was calculated for winter oilseed rape and winter wheat for a location in the centre of the Netherlands, using climatic data from the meteorological station in Swifterbant (5° 05' E 52 34' N) for a 15-year period (1974/75-1988/89). Potential seed yield is defined as the yield under optimum growing conditions, hence determined by genetic characteristics and the climatic factors, radiation, temperature and daylength. The calculations for winter oilseed rape were performed with LINTUL-BRASNAP, with parameters mainly derived from the variety Jet Neuf (Habekotté, 1996c). The calculations for winter wheat were performed with the model SUCROS-WHEAT 4.0, parameterized and tested for high-yielding winter wheat varieties (Bouman et al., 1995; Stol, 1995).

The simulated potential seed yields were compared with average actual seed yields of the five highest yielding varieties of both crops in 5 recent years (1988/89-1992/93), near Swifterbant (van der Meulen, 1990a, 1990b, 1991, 1993, 1994) and with average seed yields of the Netherlands over the same time period (Agricultural Economics Research Institute, 1994).

In addition to potential seed yields, the average values for the cumulative light (PAR: Photosynthetically active radiation) availability, cumulative light absorption from April 15 until maturity, the light use efficiency during that period, the light use efficiency during the period of linear growth, the total aboveground dry matter on April 15, the total above ground dry matter at maturity and the harvest index were calculated.

Options for increasing seed yield

The options for increasing the seed yield of winter oilseed rape were derived from the literature and classified into three groups, i.e. I) light absorption (options 1-4), II) light distribution in the green canopy and canopy photosynthesis (option 5) and III) partitioning of assimilates to the seeds (options 6-8) (Table 5.1). As the absolute ranges of genetic variability of most crop characters are not known, relative changes in crop characters and their effect on seed yield are analysed. This indicates which crop traits offer the best opportunities for yield improvement based on physiological knowledge. The relative changes in the values of most relevant model parameters were 10, 20 and 30 %, except for smaller petals (option 3), in which an absolute range of 0-100 % was introduced to simulate the possible effect of apetalous flowers. The physiologically based potential increase in canopy photosynthesis resulting from improved light distribution in the canopy (option 5) was derived using a detailed model of daily canopy photosynthesis (this paper). The effects of relative changes in model parameters on seed yield and on other crop characters, were calculated with LINTUL-BRASNAP (Table 5.1). LINTUL-BRASNAP was applied to the same location and time period used when calculating the potential seed yields of winter oilseed rape (1974/75-1988/89, Swifterbant). The repercussions of following changes were evaluated:

1) Accelerated leaf area development before full flowering to attain maximum light absorption during reproductive growth (Mendham et al., 1981a, b; Thompson, 1983; Grosse et al., 1992a; Léon, 1993). This was implemented in LINTUL-BRASNAP by increasing the partitioning of assimilates to the leaves (Table 5.1).
2) Delayed onset of flowering, so as to attain sufficient leaf area at flowering for maximum light absorption during reproductive growth (Thurling, 1974; Mendham et al., 1981a, Habekotté 1996b). This was simulated both with (a) and without (b) retention of the duration of the total growth period (Table 5.1). For both simulation sets, the duration of the critical period of seed set (CP) and of the flowering period (FP) were maintained. Delayed onset of flowering was implemented by decreasing the temperature-induced response of development rate before flowering by 10 %, 20 % and 30 %. This led to onset of flowering being delayed (options 2a and 2b) by 4, 7 and 11 d, respectively, and to maturity being delayed (option 2b) by 6, 11 and 18 d, respectively. The average duration (d) of the total growth period in option 2a was kept constant by increasing the temperature-induced response of development rate after flowering.
3) Increased transmission of light through the flower layer brought about by smaller petals or apetalous flowers (Mendham et al., 1981a; Yates and Steven, 1987; Rao et al., 1991). This was achieved by reducing the area per flower (Table 5.1).

Table 5.1 Options for increasing seed yield in winter oilseed rape, related parameters in LINTUL-BRASNAP (Habekotté 1996c) and their values relative to the standard values. Symbols used are described in Table 5.3 (OF: onset of flowering; EF: end of flowering; M: maturity; FP: flowering period; CP:critical period for seed set; SFP: seed filling period; TGP: total growth period).

Option	Related parameter	Relative value (%)
Standard	all parameters	100
Light absorption		
1. Accelerated leaf area development before OF	$P_{l,\,DVS}$	a: 110 b: 120 c: 130
2a. Delay in OF with retention of the duration (d) of TGP	$a_{T,2}$; $a_{T,4}$	a: 90; 110 b: 80; 127 c: 70; 160
2b. Delay in OF	$a_{T,2}$	a: 90 b: 80 c: 70
3. Smaller petals	A_{if}	a: 90 b: 80 c: 0
4. Delay in maturity	$a_{T,4}$	a: 90 b: 80 c: 70
Light distribution and canopy photosynthesis		
5. Improved canopy photosynthesis through improved light distribution	LUE_{DVS}	a: 102.5 - 105 b: 105 - 110
Partitioning of assimilates to the seeds		
6. Increased response of seed set to crop growth during CP	s_2	a: 110 b: 120 c: 130
7. Increased daily potential growth rate of the seeds	$R_{is,pot\,DVS}$	a: 110 b: 120 c: 130
8a. Extended SFP resulting from earlier OF with retention of the duration (d) of TGP	$a_{T,2}$; $a_{T,4}$	a: 110; 90 b: 120; 82 c: 130; 78
8b Extended SFP resulting from earlier OF	$a_{T,2}$	a: 110 b: 120 c: 130

4) Delayed maturity to optimize the use of available light during the growing season (Richards, 1991; Marshall, 1991). In the model, this was accompanied by prolonging the seed filling period, while retaining the duration (d) of the preceding stages, i.e. the vegetative growth period (VGP) until onset of flowering, the flowering period and the critical period for seed set. Maturity was delayed by reducing the response temperature-induced response of development rate after flowering by 10 %, 20 % and 30 %. This delayed maturity by 5, 11 and 18 d, respectively.
5) Higher canopy photosynthesis rates associated with improved light distribution in the canopy induced by leaves and pods more erect (Mendham et al., 1984; Thompson and Hughes, 1986; Rasmusson, 1991) and a change in the clustering of leaves and pods.
6) Increased seed set for given assimilate production during the critical period of seed set, e.g. through reduced branching (Keiller and Morgan, 1988; Habekotté, 1993). This was implemented in the model by increasing the response of seed set to crop growth during the critical period of seed set (Table 5.1) (Habekotté, 1996c).
7) Increased potential daily growth rate of the seeds (Habekotté, 1993).
8) Prolonging the seed filling period (SFP) through earlier flowering of the crop (Thurling, 1991). In these simulations the duration of FP and CP was kept constant and the duration of the total growth period was either kept constant (8a) or modified (8b) (Table 5.1). Flowering was advanced by increasing the temperature-induced response of development rate before by 10 %, 20 % and 30 %. This advanced the onset of flowering by 6, 12 and 17 d, respectively, and maturity (option 8b) by 5, 10 and 13 d, respectively. The average duration (d) of the total growth period (option 8a) was retained by reducing the temperature-induced response of development rate after flowering.

Location, weather data and initial conditions

A location in the centre of the Netherlands near Swifterbant was selected for the comparison of yield formation of winter oilseed rape and winter wheat and for the analysis of options for yield improvement. The selection criteria were: at least 15 years of climatic data and recent experimental data on seed yields of winter wheat and winter oilseed rape were available.

The sowing date was set at August 25, an average date for the central part of the Netherlands (Habekotté, 1989). The initial values for simulating crop growth, initial total crop dry weight ($W_{tot,s}$; 170 g m^{-2}) and leaf area index (LAI_s; 0.80 m^2 m^{-2}) at the onset of crop regrowth in spring were derived from the literature (de Boer and Langenhuysen, 1985; Habekotté and Smid, 1992). The onset of regrowth in spring (t_s) was estimated annually by the method used by Mendham et al., (1981a): 'the date when mean temperatures rose and were maintained above 5 °C. In years, in which temperatures remained above 5 °C for more than 5 days before this estimated onset of regrowth, t_s was advanced according the duration (d) of this period.

To evaluate of the relative effect of a hypothetical improved crop type on potential seed yield and components of yield, six locations in North-West Europe were selected, on the basis of variation in climatic conditions and on availability of long-term mean monthly weather data (Stol, 1994). The optimal sowing date choosen per location was based on literature (Habekotté 1989; Grosse, 1989; Mendham et al., 1981a) and on expert knowledge (M.J.J. Pustjens, Van der Have, pers.comm., 1995). Initial crop conditions were similar to those for the calculations in the Netherlands, except for t_s for south France (Toulouse). At this location, mean daily temperatures in winter were continuously above 5 °C, so t_s was estimated from the duration of crop growth in spring necessary to attain an LAI_{max} within the range of the other locations (range: 3.0-3.3).

LINTUL-BRASNAP

LINTUL-BRASNAP (Habekotté, 1996a; Habekotté, 1996c) is an extended version of LINTUL: a simple crop growth model based on Light INTerception and UtiLization of light for total dry matter production and partitioning of dry matter to the seeds (Spitters, 1990). LINTUL-BRASNAP calculates: 1) light reflection and absorption by the green canopy and flower layer, 2) total dry matter production based on light absorption and light use efficiency (LUE) by the green canopy, 3) seed density, 4) partitioning of dry matter to the seeds based on either source or sink limitation (Mendham et al., 1981a; Spitters et al., 1989; Habekotté, 1996c), 5) accumulation and remobilization of reserve carbohydrates.

LUE is related to the development stage of the crop (Habekotté, 1996c). Seed density is related to cumulative crop growth during the critical period of seed set, 350 °Cd since the onset of flowering (Habekotté, 1993; 1996c). Seed yield and reserve carbohydrates are both expressed in weight units similar to the green canopy (GCU, g m^{-2}: green crop units) to account for differences in protein, oil and carbohydrate content (Habekotté, 1996c). GCU is equivalent to 95 % of the seed dry matter of winter wheat (Habekotté 1996c, Penning de Vries et al., 1989). The model describes the phenological development of the crop from sowing until maturity as a function of mean daily temperature (including vernalization) and photoperiod (Habekotté, 1996b).

It may be expected that varieties adapted to a specific geografical region, such as North-West Europe, respond similarly to sowing date, environmental conditions (Mendham et al., 1981a) and changes in crop characters. For example, delaying sowing generally results in lower seed yields, low temperatures in spring or summer will delay phenological development, and apetalous flowers will improve light distribution through the canopy. The model was developed to simulate these general trends in yield formation and the variety Jet Neuf was used as a reference when quantifying most parameter values (Habekotté, 1996c).

LINTUL-BRASNAP requires data on daily incoming global radiation (S, MJ m^{-2} d^{-1}) and daily minimum and maximum temperatures (T_{min} and T_{max}, respectively). The model has been written in FORTRAN-77 (Meisner and Organick, 1984), using the FSE system (FORTRAN Simulation Environment, van Kraalingen (1995)) for crop growth simulation (Habekotté, 1996a).

Light distribution and canopy photosynthesis

To analyse the effect of spatial distribution and clustering of leaves on light absorption, LUE and canopy photosynthesis, the standard routines for calculating daily gross assimilation in SUCROS on the basis of a spherical leaf angle distribution (Spitters et al., 1989) were used. These routines were extended according to Goudriaan (1988) to be able to calculate canopy photosynthesis on the basis of erectophyl or erect leaf angle distributions. The routines, which will henceforth be referred to as routines DAYASS, calculate canopy assimilation for a given day, using data on incident photosynthetically active radiation (PAR) above the canopy, the proportion of diffuse light, solar elevation, spatial arrangement and clustering of leaves and optical and photosynthetic properties of individual leaves. The latter include the transmission and reflection of PAR, maximum rate of gross photosynthesis ($P_{g,\,max}$) and light use efficiency at low light intensities (ε) of individual leaves. The three types of leaf angle distribution of the canopy are characterized by different fractions (F) of the leaves in three leaf angle classes, 0-30°, 30-60° and 60-90° (spherical: F1=0.134, F2=0.366, F3=0.5; erectophyl: F1=0.076, F2=0.303, F3=0.621; erect: F1=0, F2=0, F3=1). Leaf clustering is taken into account through a cluster factor: the ratio of measured to theoretical values of the extinction coefficient of diffuse radiation in the canopy: $K_{dif} = 0.8\sqrt{(1-SCV)}$ (SCV: scattering coefficient of individual leaves; Goudriaan, 1988; Spitters et al., 1989). The cluster factor not only refers to a clustered distribution of leaves which increases mutual shading, with values of the cluster factor lower than 1, but also to the preference for forming leaves in gaps within the canopy, resulting in high values for K_{dif} and a cluster factor with values greater than 1. For details see the original papers.

DAYASS also calculates canopy photosynthesis, light use efficiency and fractional light absorption for two canopy layers combined, an upper layer in which pods are found and a lower layer consisting of with leaves, with possible differences in angle distribution and clustering of pods and leaves and in the values of $P_{g,max}$ and ε of individual leaves and pods (Table 5.2).

When calculating of light absorption, DAYASS assumpes that individual leaves transmit

Table 5.2 Standard parameter values used for calculating daily canopy photosynthesis, light use efficiency and fractional light absorption with DAYASS. The calculations were carried out for a single leaf layer (I), a pod layer above a leaf layer just after flowering (II) and near maturity (III).

Parameter	Value	Unit	Description and source
I: Leaf layer			
ε	0.0125	mg CO_2 J^{-1}	Light use efficiency of individual leaves, at low light intensities (de Boer and Langenhuysen, 1985)
F1	0.134		Fractions of leaves in leaf angle classes between 0-30°, 30-60° and 60-90°, respectively, for spherical leaf angle distribution (Goudriaan, 1988)
F2	0.366		
F3	0.5		
K_{dif}	0.903		Light extinction coefficient for diffuse light, corrected for light interception by stems near onset of flowering (Habekotté and Smid, 1992)
LAI	1 - 5	m^2 m^{-2}	Leaf area index
$P_{g,max}$	1.1111	mg CO_2 m^{-2} s^{-1}	Maximum photosynthesic rate of individual leaves (Backx and Duivenvoorden, 1984; de Boer and Langenhuysen, 1985; Rode et al., 1983)
SCV	0.2		Scattering coefficient for single leaves for photosynthetic active light (PAR) (Goudriaan, 1988)
$S_{0,\ April\ 1}$	12	MJ m^{-2} d^{-1}	Incomming global radiation at April 1
$S_{0,\ June\ 15}$	19	MJ m^{-2} d^{-1}	Incomming global radiation at June 15
II: pod layer above leaf layer just after flowering			
Leaves			
LAI	3	m^2 m^{-2}	
other parameters as in I, except S_0			
Pods			
ε	0.0125	mg CO_2 J^{-1}	Light use efficiency of individual pods, at low light intensity (de Boer and Langenhuysen, 1985)
F1	0.134		Fractions of leaves in leaf angle classes between 0-30°, 30-60° and 60-90°, respectively, for spherical leaf angle distribution (Goudriaan, 1988)
F2	0.366		
F3	0.5		
K_{dif}	0.716		No clustering of pods
PAI	1, 2	m^2 m^{-2}	Pod area index (based on projected area; Habekotté and Smid, 1992)
$P_{g,max}$	0.4222	mg CO_2 m^{-2} s^{-1}	Maximum photosynthetic rate of individual pods (de Boer and Langenhuysen, 1985; Rode et al., 1983)

variety Jet Neuf was used as a reference when quantifying most parameter values (Habekotté, 1996c).

LINTUL-BRASNAP requires data on daily incoming global radiation (S, MJ m^{-2} d^{-1}) and daily minimum and maximum temperatures (T_{min} and T_{max}, respectively). The model has been written in FORTRAN-77 (Meisner and Organick, 1984), using the FSE system (FORTRAN Simulation Environment, van Kraalingen (1995)) for crop growth simulation (Habekotté, 1996a).

Light distribution and canopy photosynthesis

To analyse the effect of spatial distribution and clustering of leaves on light absorption, LUE and canopy photosynthesis, the standard routines for calculating daily gross assimilation in SUCROS on the basis of a spherical leaf angle distribution (Spitters et al., 1989) were used. These routines were extended according to Goudriaan (1988) to be able to calculate canopy photosynthesis on the basis of erectophyl or erect leaf angle distributions. The routines, which will henceforth be referred to as routines DAYASS, calculate canopy assimilation for a given day, using data on incident photosynthetically active radiation (PAR) above the canopy, the proportion of diffuse light, solar elevation, spatial arrangement and clustering of leaves and optical and photosynthetic properties of individual leaves. The latter include the transmission and reflection of PAR, maximum rate of gross photosynthesis ($P_{g,\ max}$) and light use efficiency at low light intensities (ε) of individual leaves. The three types of leaf angle distribution of the canopy are characterized by different fractions (F) of the leaves in three leaf angle classes, 0-30°, 30-60° and 60-90° (spherical: F1=0.134, F2=0.366, F3=0.5; erectophyl: F1=0.076, F2=0.303, F3=0.621; erect: F1=0, F2=0, F3=1). Leaf clustering is taken into account through a cluster factor: the ratio of measured to theoretical values of the extinction coefficient of diffuse radiation in the canopy: $K_{dif} = 0.8\sqrt{(1-SCV)}$ (SCV: scattering coefficient of individual leaves; Goudriaan, 1988; Spitters et al., 1989). The cluster factor not only refers to a clustered distribution of leaves which increases mutual shading, with values of the cluster factor lower than 1, but also to the preference for forming leaves in gaps within the canopy, resulting in high values for K_{dif} and a cluster factor with values greater than 1. For details see the original papers.

DAYASS also calculates canopy photosynthesis, light use efficiency and fractional light absorption for two canopy layers combined, an upper layer in which pods are found and a lower layer consisting of with leaves, with possible differences in angle distribution and clustering of pods and leaves and in the values of $P_{g,max}$ and ε of individual leaves and pods (Table 5.2).

When calculating of light absorption, DAYASS assumpes that individual leaves transmit

Table 5.2 Standard parameter values used for calculating daily canopy photosynthesis, light use efficiency and fractional light absorption with DAYASS. The calculations were carried out for a single leaf layer (I), a pod layer above a leaf layer just after flowering (II) and near maturity (III).

Parameter	Value	Unit	Description and source
I: Leaf layer			
ε	0.0125	mg CO_2 J^{-1}	Light use efficiency of individual leaves, at low light intensities (de Boer and Langenhuysen, 1985)
F1	0.134		Fractions of leaves in leaf angle classes between 0-30°, 30-60° and 60-90°, respectively, for spherical leaf angle distribution (Goudriaan, 1988)
F2	0.366		
F3	0.5		
K_{dif}	0.903		Light extinction coefficient for diffuse light, corrected for light interception by stems near onset of flowering (Habekotté and Smid, 1992)
LAI	1 - 5	m^2 m^{-2}	Leaf area index
$P_{g,max}$	1.1111	mg CO_2 m^{-2} s^{-1}	Maximum photosynthesic rate of individual leaves (Backx and Duivenvoorden, 1984; de Boer and Langenhuysen, 1985; Rode et al., 1983)
SCV	0.2		Scattering coefficient for single leaves for photosynthetic active light (PAR) (Goudriaan, 1988)
S_0, April 1	12	MJ m^{-2} d^{-1}	Incomming global radiation at April 1
S_0, June 15	19	MJ m^{-2} d^{-1}	Incomming global radiation at June 15
II: pod layer above leaf layer just after flowering			
Leaves			
LAI	3	m^2 m^{-2}	
other parameters as in I, except S_0			
Pods			
ε	0.0125	mg CO_2 J^{-1}	Light use efficiency of individual pods, at low light intensity (de Boer and Langenhuysen, 1985)
F1	0.134		Fractions of leaves in leaf angle classes between 0-30°, 30-60° and 60-90°, respectively, for spherical leaf angle distribution (Goudriaan, 1988)
F2	0.366		
F3	0.5		
K_{dif}	0.716		No clustering of pods
PAI	1, 2	m^2 m^{-2}	Pod area index (based on projected area; Habekotté and Smid, 1992)
$P_{g,max}$	0.4222	mg CO_2 m^{-2} s^{-1}	Maximum photosynthetic rate of individual pods (de Boer and Langenhuysen, 1985; Rode et al., 1983)

Continuation of Table 5.2

Parameter	Value	Unit	Description and source
SCV	0.2		Scattering coefficient for single leaves, also used for pods, for photosynthetic active light (PAR) (Goudriaan, 1977; J. Goudriaan, pers. comm., 1995; see text)
S_0, June 15	19	MJ m^{-2} d^{-1}	Incomming global radiation at June 15
III: Pod layer above leaf layer near maturity			
Leaves			
LAI	1	m^2 m^{-2}	Habekotté and Smid, 1992
$P_{g,max}$	0.3944	mg CO_2 m^{-2} s^{-1}	Maximum photosynthetic rate of old individual leaves (Backx and Duivenvoorden, 1984; de Boer and Langenhuysen, 1985; Rode et al., 1983)
other parameters as in I, except S_0			
Pods			
as in II			

and reflect PAR equally (Goudriaan and Van Laar, 1994). A shift to reflection solely from pods had a negligible effect on the relative change in light absorption caused by a change from spherical to erectophyl or erect pod angle distributions (own data not shown; Goudriaan, 1977; J. Goudriaan, Wageningen Agricultural University (WAU), pers. comm., 1995). The effect on relative changes in light use efficiency and canopy photosynthesis was also assumed to be negligible. Therefore, calculations for the pod layer were carried out with the same value of the scattering coefficient as was used for the leaf layer, calculated as the sum of transmission and reflection of light by individual leaves.

Maintenance respiration was set to 20 % of daily gross photosynthesis (in glucose weight units) (Spitters et al., 1989). The conversion of the remaining assimilates into structural plant material was based on the multiplication factor derived for green crop units (1/1.49= 0.67) (Habekotté, 1996c).

First, calculations were carried out for three standard situations: I) a single leaf layer, before flowering, II) a pod layer above a leaf layer just after flowering with a relatively high *LAI* value (3 m^2 m^{-2}) and III) later during the growth cycle, with a reduced *LAI* (1 m^2 m^{-2}) (Table 5.2). The standard situations were characterized by (Table 5.2) Julian day number, incoming global radiation, $P_{g,max}$, ε, leaf and pod angle distribution, K_{dif} (indicating the degree of clustering of leaves and pods) and area index of leaves (*LAI*) and pods (*PAI*). The calculations for a single leaf layer (I) were carried out for a day in early

Table 5.3 Description of symbols used in Tables 5.1, 5.8 and 5.11.

Symbol	Unit	Description
$a_{T,2}$; $a_{T,4}$	10^{-3} d^{-1} °C^{-1}	Response of development rate to temperature for the period from emergence until flowering (x=2) and for the period from the end of flowering until maturity (x=4)
A_{if}	m^2	Area per individual flower
$F_{res,DVS=3.3}$	g g^{-1}	Initial fraction of reserve carbohydrates (as fraction of total crop dry matter)
HI		Harvest index (W_s/ $W_{top,M}$)
$I_{0,cum}$	MJ m^{-2} d^{-1}	Cumulative daily incoming PAR from 15 April until maturity
$I_{a,\ cum}$	MJ m^{-2} d^{-1}	Cumulative PAR absorbed daily by the green crop canopy from 15 April until maturity
I_r	MJ m^{-2} d^{-1}	Par transmitted daily at the bottom of the canopy
K_{LAI}		Extinction coefficient of leaves for PAR
LAI	m^2 m^{-2}	Leaf area index
LAI_{max}	m^2 m^{-2}	Maximum leaf area index
LUE_{DVS}	g MJ^{-1}	Light use efficiency: total dry matter production (g GCU m^{-2} d^{-1}) per unit absorbed PAR (MJ m^{-2} d^{-1}), related to the development stage (DVS) of the crop
LUE_{tot}	g MJ^{-1}	Average light use efficiency from April 15 until maturity
msw	mg	Mean seed weight
N_p	m^{-2}	Pod density
N_s	m^{-2}	Seed density
$N_{s/p}$	m^{-2}	Number of seeds per pod
PAR	MJ m^{-2}	Photosynthetically active radiation (400-700 nm)
$P_{l,DVS}$	g g^{-1}	Partitioning coefficient of daily crop growth to the leaves
$R_{is,pot,DVS}$	g °Cd	Potential growth rate of the seeds (per 1000. seeds (GCU))
s_1 ; s_2	m^{-2} ; -	Parameters for calculating seed density
TR	MJ MJ^{-1}	Transmission coefficient of PAR through the flower layer
W_s	g m^{-2}	Seed weight (GCU) per unit ground area
$W_{top,M}$	g m^{-2}	Total aboveground crop dry weight at maturity (including dead leaves and roots (GCU))

spring (April 1) and later during the growth period (June 15), as solar elevation, partly defined by Julian day, influences light distribution within the canopy (Goudriaan, 1977). For a pod layer above a leaf layer (II and III) calculations were performed for June 15 only. The values of incoming solar radiation on April 1 (daynumber 91, 12 MJ m^{-2}, Table 5.2) and June 15 (daynumber 166, 19 MJ m^{-2}, Table 5.2) correspond to the average value for the proportion of incoming diffuse light for the growth period of winter oilseed rape from April until maturity, for the years 1974/75-88/89, near Swifterbant, i.e. 0.67.

Subsequently, light absorption, LUE and canopy photosynthesis were calculated for erectophyl or erect leaf and pod angle distributions and for values of K_{dif} lower than those found in reality, and these results were compared with the standard situations.

Table 5.4 Average simulated potential seed yield (t ha^{-1}) of winter oilseed rape and winter wheat near Swifterbant (period 1974/75-1988/89), actual average seed yields at Lelystad near Swifterbant (period 1988/89-1992/93; van der Meulen, 1990a, 1990b, 1991, 1993, 1994) and for the Netherlands (1988/89-192/93; Agricultural Economics Research Institute, 1994). Seed yields of winter oilseed rape were given in normal dry matter (dm) and in green crop units (GCU).

	Potential		Actual			
			Lelystad		Netherlands	
	dm	GCU	dm	GCU	dm	GCU
Winter oilseed rape	3.12	4.66	3.32	4.92	2.90	4.38
Winter wheat	9.89		8.89		6.66	

Table 5.5 Simulated average values for components of potential yields (Table 5.4) of winter oilseed rape and winter wheat: cumulative availability of incoming PAR ($I_{0,cum}$) and absorbed PAR (I_a,cum) from April 15 until maturity, light use efficiency during the same period (LUE_{tot}, g MJ^{-1}), light use efficiency during the period of linear growth (LUE_{lin}, g MJ^{-1}), total aboveground dry matter on April 15 ($W_{top,15}$, t ha^{-1}), total aboveground dry matter at maturity ($W_{top,M}$, t ha^{-1}), seed yield (W_s, t ha^{-1}) and harvest index (HI).

Crop	$I_{0,cum}$	$I_{a,\ cum}$	LUE_{tot}	LUE_{lin}	$W_{top,15}$	$W_{top,M}$	W_s	HI
Winter oilseed rape	829	657	1.86	2.19	2.39	14.6	4.66	0.319
Winter wheat	1034	771	2.98	3.10	0.61	23.5	9.89	0.422

RESULTS

Comparison with winter wheat

The simulated average potential seed yield (1974/75-1988/89) of winter oilseed rape (4.66 t ha^{-1}, GCU) was similar to average actual seed yield for the central part of the Netherlands (4.92 t ha^{-1}, GCU) and in the Netherlands as a whole (4.38 t ha^{-1}, GCU) (Table 5.4, $t > 0.05$). These values correspond to respectively 3.12, 3.32 and 2.90 t ha^{-1} seed dry matter.

The simulated potential seed yield of winter wheat (on average 9.89 t ha^{-1}) was higher than actual seed yields, which averaged 8.89 t ha^{-1} and 6.66 t ha^{-1} (Table 5.4, $t < 0.05$).

The results show a yield gap of 3.8 up to 4.7 t ha^{-1} (GCU, Table 5.4) for winter oilseed rape compared to actual and simulated potential seed yield of winter wheat, corresponding with 2.5 up to 3.1 t ha^{-1} seed dry matter.

The simulated light available for winter oilseed rape was substantially less than that for winter wheat (829 versus 1034 MJ m^{-2}; $t < 0.05$), because it matures four weeks earlier (Fig. 5.1, Habekotté, 1989). A larger fraction of light seems to be absorbed ($I_{a,cum}$ / $I_{0,cum}$) by winter oilseed rape than by winter wheat (0.8 versus 0.75), but this did not fully compensate for less cumulative light being available, and therefore so that cumulative light absorption was less (657 versus 771 MJ m^{-2}, respectively; $t < 0.05$, Table 5.5). The mean light use efficiency for the whole period from 15 April until maturity (LUE_{tot}) was significantly lower for winter oilseed rape (1.86 versus 2.98 g MJ^{-1} for winter wheat, $t < 0.05$, Table 5.5). The same holds for light use efficiency during the period of linear growth (LUE_{lin}) (2.19 versus 3.10 g MJ^{-1}, $t < 0.05$, Table 5.5).

The lower values of cumulative light absorption and light use efficiency resulted in the total dry matter production of winter oilseed rape being less than that of winter wheat and ultimately in a smaller final crop biomass (14.6 (GCU) and 23.5 t ha^{-1}; respectively, $t < 0.05$, Table 5.5). The larger initial crop biomass of winter oilseed rape on 15 April (2.39 versus 0.61 t ha^{-1}, $t < 0.05$, Table 5.5) did not compensate for the lower total dry matter production after April 15. As the harvest index was lower in winter oilseed rape too, the seed yield was substantially below that of winter wheat (4.66 (GCU) versus 9.89 g m^{-2}; respectively, $t < 0.05$, Table 5.5). This analysis indicates that the proportion of light absorbed is favourable but that the availability of cumulative light, the absorption of cumulative light, the light use efficiency and the harvest index are weak points in the yield formation process of winter oilseed rape (Table 5.5).

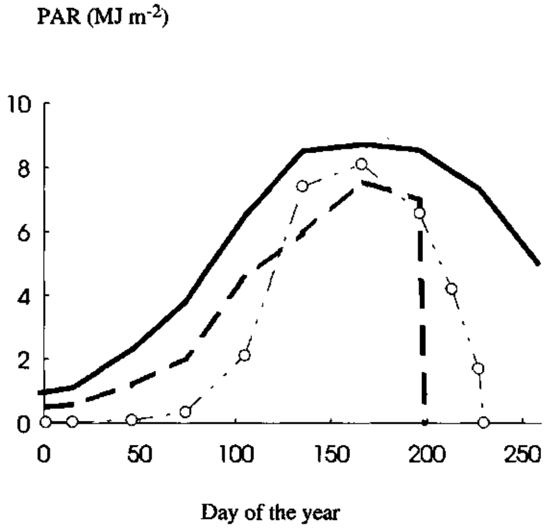


Figure 5.1 Incoming PAR (MJ m^{-2} d^{-1}, bold line) between January 1 and September 15, based on average mean monthly incoming PAR for the period 1974/75-1988/89 for Swifterbant. Average mean monthly absorption of incoming PAR is given for winter oilseed rape (simulated with LINTUL-BRASNAP, dotted bold line) and for winter wheat (simulated with SUCROSW 4.0, open circles).

Light distribution and canopy photosynhesis

The results of the analysis of the effects of leaf angle distribution and clustering of leaves for the period before flowering are shown for Julian day 91 only as those for Julian day 166 were similar. The effect of more upright leaves is shown for erect leaves only as erectophyl angle distributions showed the same trends, albeit less pronounced. Erect clustered leaves (I) did not result in increased canopy photosynthesis up to an *LAI* of about 4 m^2 m^{-2} (Table 5.6), as fractional absorption of light decreases, which offsets the more efficient light use for an *LAI* below about 4 m^2 m^{-2}.

The effects of more erect pods and clustering of pods in a pod layer above a leaf layer are, as for leaves, only shown for their spherical and erect angle distribution. For pod areas of 1 and 2 m^2 m^{-2}, canopy photosynthesis increased by 10 % on average and light use efficiency by 11 % on average for erect and clustered pods compared to the standard situation II, characterizing the canopy just after flowering. The fraction of light absorbed decreased very slightly (on average by 1.2 %). Later during the growth cycle (situation III), canopy photosynthesis increased by 5 % on average 5 % a *PAI* of 1 and 2 m^2 m^{-2}

Table 5.6 Daily canopy photosynthesis (mg CO_2 m^{-2} d^{-1}), light use efficiency (LUE g MJ^{-1}) and fractional light absorption calculated with DAYASS (Table 5.2) with spherical and erect leaf angle distribution and with or without clustering of leaves indicated for different values of K_{dif} (with K_{dif} = 0.716: no clustering). The results are given for daynumber 91 (April 1) for various *LAI* values.

Leaf angle distribution	K_{dif}	*LAI*				
		1	2	3	4	5
Canopy photosynthesis						
Spherical	0.903	25.8	37.7	43.2	45.8	47.1
Erect	,,	25.0	36.2	41.8	44.8	46.4
Spherical	0.716	24.1	36.5	43.0	46.6	48.6
Erect	,,	23.4	35.0 *3*	41.3	45.1	47.3
Spherical	0.6	22.6	35.1	42.3	46.5	49.0
Erect	,,	22.0	33.6	40.4	44.7	47.4
Light use efficiency						
Spherical	0.903	2.69	2.93	3.04	3.12	3.19
Erect	,,	2.72	2.96	3.09	3.19	3.27
Spherical	0.716	2.86	3.07	3.19	3.26	3.31
Erect	,,	2.89	3.10	3.22	3.30	3.37
Spherical	0.6	2.99	3.18	3.29	3.35	3.40
Erect	,,	3.01	3.20	3.31	3.39	3.45
Fractional light absorption						
Spherical	0.903	0.586	0.785	0.865	0.896	0.902
Erect	,,	0.561	0.746	0.825	0.857	0.866
Spherical	0.716	0.514	0.724	0.824	0.873	0.895
Erect	,,	0.495	0.688	0.784	0.833	0.857
Spherical	0.6	0.460	0.673	0.784	0.846	0.879
Erect	,,	0.445	0.641	0.745	0.805	0.839

Table 5.7 Daily canopy photosynthesis (mg CO_2 m^{-2} d^{-1}), light use efficiency (LUE g MJ^{-1}) and fractional light absorption calculated with DAYASS (Table 5.2) for a canopy with a pod layer above a leaf layer just after flowering (II) and near maturity (III) with differences in pod angle distribution and clustering of the pods, indicated by different values for K_{dif} (K_{dif} = 0.716: no clustering). The results are given for daynumber 166 (June 15) for different values of *LAI* and *PAI*.

Pod angle distribution	K_{dif}	*LAI*			
		3 (II)		*1 (III)*	
		PAI		*PAI*	
		1	2	1	2
Canopy photosynthesis					
Spherical	0.716	56.5	54.1	40.5	44.8
Erect	„	58.4	57.2	40.9	45.8
Spherical	0.60	59.5	57.9	41.9	46.7
Erect	„	60.9	60.4	42.1	47.4
Light use efficiency					
Spherical	0.716	2.43	2.28	2.12	2.08
Erect	„	2.53	2.43	2.20	2.21
Spherical	0.60	2.57	2.45	2.26	2.24
Erect	„	2.65	2.58	2.33	2.35
Fractional light absorption					
Spherical	0.716	0.895	0.916	0.737	0.828
Erect	„	0.890	0.908	0.715	0.799
Spherical	0.60	0.890	0.911	0.716	0.805
Erect	„	0.886	0.903	0.697	0.777

(Table 5.7). The decrease in fraction of light absorbed, 6 % on average, partly offsets the improvement in light use efficiency, which was 11 % on average.

These results indicate that canopy photosynthesis could increase by maximally 10 % and 5 % just after flowering and near maturity, respectively, if light distribution through the pod layer were improved. These options were used for further analysis of yield improvement with LINTUL-BRASNAP.

Options for increasing seed yield

Sink and source capacity for seed filling

The effect of hypothetical changes in sink and source capacity for seed filling on seed yield were analysed to form a basis for further evaluation of options for increasing seed yield. Fig. 5.2a gives the simulated response of seed yield to a hypothetical change in sink capacity, in this example obtained through changes in seed density (m^{-2}), averaged for all sowings (1974/75-1988/89, Swifterbant). The average seed yield and seed density for the standard parameter set are indicated by the solid symbol in Fig. 5.2a. At seed densities below the 'standard', about 69 10^3 m^{-2}, seed yield decreases almost linearly with a decrease in seed density. Hence, on average for all sowings, seed yield is almost completely sink-limited at these seed densities. With increased seed density, seed yield increases up to a maximum of 29 %, indicating a source surplus. However, with increasing seed density the source becomes increasingly limiting for seed filling, as illustrated by the decreasing response of seed yield (=msw). These hypothetical increases in seed density were calculated without possible limitation by pod density. When pod numbers are taken into account, simulated pod densities will not limit seed set up to an average seed density of 150 10^3 m^{-2}, as the maximum number of 35 seeds per pod (Habekotté 1996c) is not reached. To attain higher average seed densities without limitation of seed set, pod numbers have to increase.

If only the source capacity during seed filling is increased, by making hypothetical changes to dry matter production after flowering, a surplus in sink capacity (in terms of seeds m^{-2}) is shown of 12 % on average. Reducing the source capacity leads to an almost linear decline in average seed yield (Fig. 5.2b), indicating that at these hypothetically lower values of source capacity, seed yield is almost fully determined by the source.

The compensatory effect of seed density and mean seed weight is illustrated in Fig. 5.2c by the simulated response of mean seed weight to seed density. The effect of increased seed density (sink) without a simultaneous increase in source capacity is largely offset by a decrease in mean seed yield. The dotted line in Fig. 5.2c represents the complete compensation between mean seed weight and seed density (msw=c/nseed; with c=466 g m^{-2}). As source capacity is slightly in excess, the decrease in mean seed weight is slightly less than the dotted line shows. These results suggest that to increase the seed yield of winter oilseed rape, both source and sink capacity for seed filling should be increased simultaneously. Simulations assuming a combined increase in sink and source capacity for seed filling, through a hypothetical simultaneous increase in seed density (by 10-100 %) and in dry matter production (by 10-100 %) after flowering, resulted in a positive interaction effect on seed yield (of 0.8-55 %). The effect was most pronounced at larger

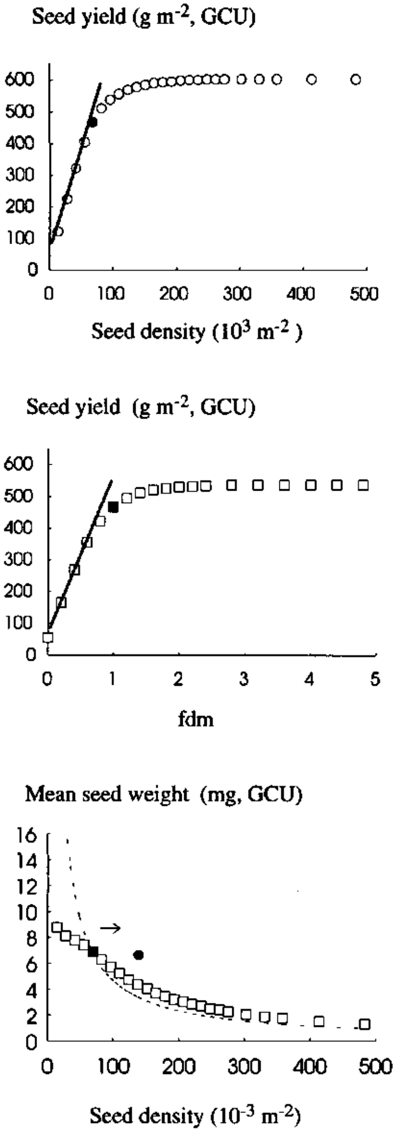


Figure 5.2 Simulated response of a) average seed yield (g m^{-2}) to hypothetical changes in seed density of winter oilseed rape (m^{-2}), b) average seed yield to source availability, obtained through hypothetical relative changes in dry matter production (fdm) after flowering and c) average mean seed weight (mg) to seed density. The dotted line in (b) represents the situation of complete compensation of the increase in seed density with a decrease in mean seed weight (msw=466/seed density). The calculations were carried out for sowings in the period 1974/75-1988/89 using climatic data from Swifterbant. The solid symbols represent the average values obtained with the standard parameter set in LINTUL-BRASNAP (Habekotté, 1996c).

increases in sink and source. This also results in deviations from the line that represents the compensatory effect between seed density and mean seed weight as illustrated in Fig. 5.2c by the black circle, for 100 % increase in sink and source. An increase in sink capacity only, brought about by an increase in seed density (by 10-100 %) combined with a higher daily potential seed growth rate (plus 10-100 %) resulted in negative interaction effects on seed yield (of 0.6-19 %). A negative interaction effect (of 0.01-3.8 %) was also found when only the source capacity was increased by increasing both the dry matter production after flowering (by 10-100 %) and also the availability of reserve carbohydrates for seed fill (by 10-100 %).

Single crop traits

Options for seed yield increase, founded on single crop traits, were ranked according to their effect on cumulative light absorption, light use efficiency and harvest index, and their effect on sink and source capacity for seed filling (Fig. 5.3; Tables 5.8 and 5.9). Promising options were distinguished from options whose effects on seed yield where slightly positive, neutral or negative, based on the arbitrary limit of 3 % increase in seed yield.

Higher ($\geq$ 3 %) average seed yields attributable to greater sink capacity were obtained directly through increases (of 10-30 %) in the response of seed set to cumulative crop growth during the critical period of seed set (option 6) , increases (also of 10-30 %) in the potential growth rate of individual seeds (option 7) and indirectly through increased transmission of light through the flower layer through reduced (by 20-100 %) petal size (option 3), a delay in maturity (5-18 d) and concomittant increase in the ratio of the durations of the seed filling period (SFP) and total growth period (TGP) (option 4) and increased duration of SFP (by 6-17 d) (option 8a).

Higher ($\geq$ 3 %) average seed yields as a result of a greater source capacity were obtained either through a higher dry matter production rate (of 5-10 %) during the seed filling period caused by the introduction of erect clustered pods (option 5) or through an increase in the duration of this period in options 4 (by 5-18 d) and 8a (by 6-17 d). Except for option 5, both groups of options with positive effects on sink or source for seed filling resulted in higher average harvest indices (Table 5.9).

Cumulative light absorption was distinctly increased ($\geq$ 3 %) through a delay (4-11 d) in onset of flowering (option 2b), delayed maturity (5-18 d) (option 4) and apetalous flowers (option 3), although only the latter two resulted in higher seed yields ($\geq$ 3 %).

Light use efficiency was increased (> 3 %) through delayed onset of flowering (11 d) with retention of the duration of the total growth period (TGP) (option 2a) as this extended the relative duration of the vegetative growth period (VGP) compared to TGP and the relative contribution of more productive leaves in the VGP compared to the pods in the seed filling period to total assimilate production. Light use efficiency also increased through improved light distribution in the canopy as a result of erect clustered pods (option 5). Only the latter option resulted in distinctly higher seed yields (Table 5.8).

Increase in leaf area formed up to the onset of flowering hardly increased light absorption and total dry matter production, as shown in options 1 and 2a (range 1-3 %, Table 5.8). The relative decrease in the duration of the seed filling period in option 2a (SFP/TGP, a reduction of 10-40 %) reduced the availability of assimilates for seed filling and hence lowered the harvest index (HI, by 8-37 %) and seed yield (W_s, by 7-35 %).

In option 2b, the delay in onset of flowering also delayed maturity and this increased cumulative light absorption (by 6-18 %). The sink capacity of the seeds increased, because of enhanced seed set, however, the relative availability of assimilates for seed fill decreased as a result of the lower SFP/TGP ratio, which resulted in a lower HI (down by 3-12 %). The higher total crop dry matter at final harvest (up by 5-16 %) compensated for the lower HI, with consequently a slightly higher seed yield (up by 2 %).

Earlier onset of flowering (6-17 d) with associated modification of the duration of the total growth period (option 8b) reduced the duration of the total growth period (by 5-13 d) and hence reduced the cumulative light availability ($I_{0,\mathrm{cum}}$, by 5-14 %) and absorption of light ($I_{a,\mathrm{cum}}$, by 7-20 %). The increase in the relative duration of the seed filling period (by 5-16 %) hardly affected the partitioning of dry matter to the seeds (HI, up by 1-2 %) and did not compensate for the lower total dry matter production and thus resulted in lower seed yield (down by 5-16 %).

The simulated affects of relative changes in crop traits all resulted in moderate numbers of seeds per pod (range in values per year: 8-23, range in average values: 10.2-18.0, Table 5.8). Thus, simulated seed densities were not limited by simulated pod densities.

Combined crop traits

The crop traits described above were combined on a basis of simultaneous increase in sink and source for seed filling and their combined effect on average seed yield (1975/76-1988/89) was calculated (Table 5.10). A seed yield increase of 3-18 % was attained without a change in the developmental pattern of winter oilseed rape. When flowering was advanced (by 6-17 d), the average seed yield rose by 7-25 %, and when maturity was delayed (by 5-18 d), the average seed yield rose by 11-55 %.

A negative interaction effect (> 1 %) occurred only for the combination of earlier flowering (option 8a) and delayed maturity (option 4) (Table 5.10). This was the result of a lower $LAI_{\max}$ at earlier flowering (Table 5.8), which partly offset the increase in source availability through delayed maturity (option 4). Fig. 5.4 shows that at average values higher than about 3, $LAI_{\max}$ does not limit average seed yield.

Table 5.8 Options for increasing seed yield of winter oilseed rape under optimal growth conditions (Table 5.1 and text) and their effect on various crop characteristics calculated with LINTUL-BRASNAP. Results are given in percentages of the standard values, calculated with the standard parameter set. Symbols used are described in Table 5.3.

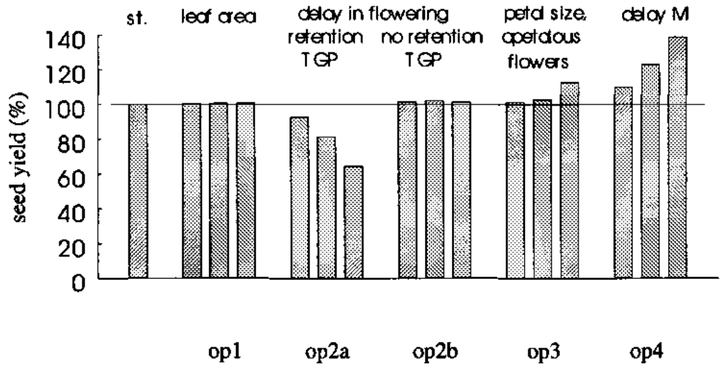
Option			Crop Characteristic												
			W_s	$W_{top, M}$	HI	N_s x10^3	msw	LAI_{max}	SFP/ TGP	TR	$I_{0,cum}$	$I_{a,cum}$	LUE$_{tot}$	N_p	$N_{s/p}$
			g m^{-2}	g m^{-2}	g g^{-1}	m^{-2}	mg	m^2 m^{-2}	d d^{-1}	MJ MJ^{-1}	MJ m^{-2}	MJ m^{-2}	g MJ^{-1}	m^{-2}	
Standard			466	1461	0.319	69.0	6.86	3.23	0.24	0.796	829	657	1.86	5164	13.5
Light absorption															
1	Accelerated leaf area development before OF	a	100	101	100	100	100	109	100	100	100	101	100	101	99
		b	101	101	99	101	100	117	100	100	100	101	100	102	99
		c	101	102	99	101	100	126	100	100	100	101	100	102	98
2a	Delay in OF with retention of the duration (d) of TGP	a	93	102	91	105	89	109	90	99	101	102	101	112	93
		b	82	102	80	107	76	126	77	97	101	101	102	124	86
		c	64	103	63	107	61	148	60	96	100	101	104	139	76
2b	Delay in OF	a	102	105	97	105	98	109	97	99	105	106	101	112	93
		b	102	110	93	107	95	126	92	97	110	111	101	124	86
		c	102	116	88	107	96	148	87	96	117	118	101	139	76
3	Smaller petals	a	101	101	101	103	99	100	100	102	100	101	100	101	101
		b	103	101	102	105	98	100	100	105	100	101	100	103	102
		c	113	107	105	129	89	100	100	126	100	107	102	114	112
4	Delay in M	a	110	104	106	100	110	100	108	100	105	105	100	100	100
		b	123	108	113	100	123	100	116	100	111	112	99	100	100
		c	139	114	122	100	139	100	127	100	119	120	98	100	100

[1] The increase in canopy photosynthesis was implemented from about halfway through the flowering period (*DVS*=2.6, Habekotté, 1996c) with increasing pod area index of the canopy (Habekotté and Smid, 1992).

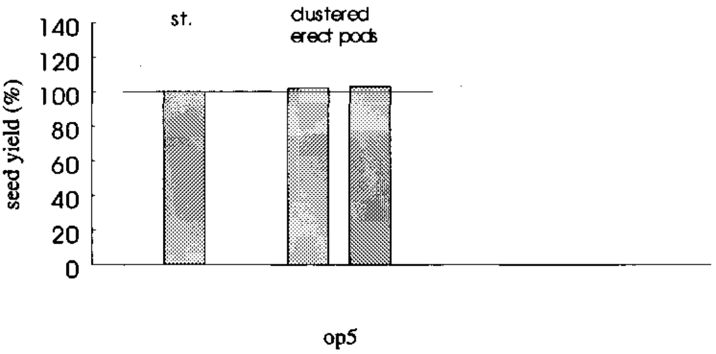
Continuation of Table 5.8

Option			Crop Characteristic												
			W_s	$W_{top, M}$	HI	N_s x10^3	msw	LAI_{max}	SFP/ TGP	TR	$I_{0,cum}$	$I_{a,cum}$	LUE_{tot}	N_p	$N_{s/p}$
			g m^{-2}	g m^{-2}	g g^{-1}	m^{-2}	mg	m^2 m^{-2}	d d^{-1}	MJ MJ^{-1}	MJ m^{-2}	MJ m^{-2}	g MJ^{-1}	m^{-2}	
Standard			466	1461	0.319	69.0	6.86	3.23	0.24	0.796	829	657	1.86	5164	13.5
Light distribution and canopy photosynthesis															
5	Increase in canopy	a	102	102	100	101	101	100	100	100	100	100	102	100	100
	photosynthesis[1]	b	103	103	100	102	102	100	100	100	100	100	104	101	101
Partitioning of assimilates to the seeds															
6	Increased response	a	106	100	106	111	95	100	100	100	100	100	100	100	111
	of seed set to crop	b	110	100	110	122	91	100	100	100	100	100	100	100	122
	growth during CP	c	114	100	114	133	86	100	100	100	100	100	100	100	133
7	Increased potential	a	105	100	105	100	105	100	100	100	100	100	100	100	100
	growth rate of the	b	109	100	109	100	110	100	100	100	100	100	100	100	100
	seeds	c	112	100	113	100	114	100	100	100	100	100	100	100	100
8a	Extended SFP	a	105	98	108	93	114	83	113	101	100	99	98	88	105
	resulting from	b	107	94	112	86	125	72	125	102	100	95	96	76	111
	earlier OF and retention of TGP	c	108	91	116	80	136	63	135	103	101	95	94	67	116
8b	Extended SFP	a	96	94	102	93	103	83	105	101	95	93	98	88	105
	resulting from	b	89	87	101	86	105	72	111	102	90	85	97	76	111
	earlier OF	c	85	82	102	80	108	63	116	103	86	80	96	67	116

Light absorption a



Canopy photosynthesis b



Partitioning of assimilates to the seeds c

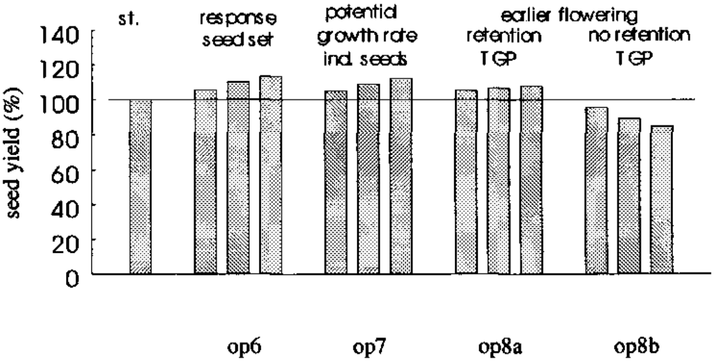


Figure 5.3 Simulated response of average seed yield to changes in various canopy traits for sowings in the period 1974/75-1988/89 using climatic data from Swifterbant (see text and Tables 5.1 and 5.8 for further details).

Table 5.9 Three components of yield, related crop characters and options for increasing seed yield discussed in this paper (Table 5.1). Options with * had a distinct positive influence on seed yield (≥ 3 %) of winter oilseed rape through the indicated component of yield (≥ 3 %), related crop characters and through given increases in related parameter values (Table 5.8).

Component of yield	Related crop character	Related option
Cumulative light absorption	- Duration of the growth cycle from early spring until maturity	2b, 8b, 4*
	- Fraction of light absorbed:	
	+ $LAI_{\max}$	1, 2a, 2b, 8a, 8b
	+ Petal size, apetalous flowers	3*
	+ Clustering of pods and pod angle distribution	5
Light use efficiency	- Photosynthetic capacity of individual pods and leaves	
	- Clustering of pods and pod angle distribution	5*
Harvest index	Sink capacity for seed filling	
	- Seed density (m^{-2}):	
	+ $LAI_{\max}$	1, 2a, 2b, 8a, 8b
	+ Petal size, apetalous flowers	3*
	+ Clustering of pods and pod angle distribution	5
	+ Response seed set to crop growth during CP	6*
	- Daily potential growth rate of seeds:	7*
	- Duration of the seed filling period (d)	4*, 8a*, 8b
	Source capacity for seed filling	
	- $LAI_{\max}$	1, 2a, 2b, 8a, 8b
	- Clustering of pods and pod angle distribution	5
	- Duration of the seed filling period (d)	4*, 8a*, 8b
	- Duration of the total growth period	4*, 2b, 8b

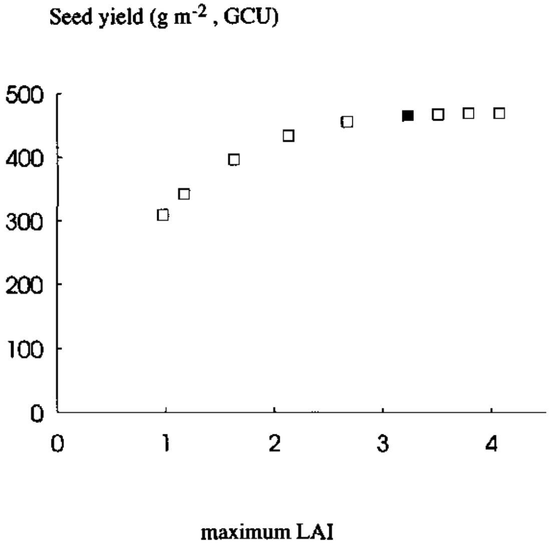


Figure 5.4 Simulated response of average seed yield to maximum *LAI* for sowings in the period 1974/75-1988/89 using climatic data from Swifterbant. The solid symbol represents the average values obtained with the standard parameter set in LINTUL-BRASNAP (Habekotté, 1996c).

Table 5.10 Simulated seed yield (in percentages of the standard seed yield of 466 g m^{-2}, Table 5.8) for combined options for seed yield improvement of winter oilseed rape (1974/75-1988/89, Swifterbant). The ranges of seed yield result from calculations with the lowest and highest values of the relevant parameters described in Table 5.1. (^{n} : combined options without change in the developmental pattern of the crop).

Sink		Source		
		Later maturity (4)	Earlier flowering (8a)	Clustered upright pods (5)
		110-139	105-108	102-103
Later maturity (4)	110-139	x	115-142	111-144
Improved response seed set (6*)	106-114	116-155	112-125	107-118^{n}
Petal size, apetalous flowers (3)	101-113	112-155	107-123	102-117^{n}
Improved potential seed growth (7*)	105-112	115-154	111-124	106-116^{n}
Earlier flowering (8a)	105-108	115-142	x	107-112

Ideotypes for higher seed yields

Based on the insights gained in yield formation of winter oilseed rape, the most promising crop type for high-yielding winter oilseed rape in North-West Europe under optimal growth conditions was formulated: a variety that matures late, combines early flowering with an LAI_{max} of about 3 and has erect clustered pods to maximize the source for seed fill. To take full advantage of this source capacity, further sink increase has to be attained through a high rate of seed set, a large sink capacity of individual seeds, apetalous flowers, or a combination of these characteristics.

Table 5.11 Simulated potential seed yields and components of yield at different locations in North-West Europe for a standard variety (st), and for hypothetical high-yielding varieties (hv) without and with delay in maturity of about one week up to 2 weeks (see text). The results of the hypothetical varieties are given in percentages of the standard values per location. Symbols used are described in Table 5.3.

Location	W_{s}		HI		$I_{\mathrm{a,\,cum}}$		$\mathrm{LUE_{tot}}$	
	st	hv	st	hv	st	hv	st	hv
	t ha^{-1}	%	t t^{-1}	%	MJ m^{-2}	%	g MJ^{-1}	%
No delay of maturity								
Copenhagen	463	130	0.34	120	665	106	1.81	104
Hamburg	456	130	0.33	121	638	105	1.84	104
de Bilt	450	130	0.34	120	578	105	1.87	104
London	513	127	0.36	114	594	110	1.90	103
Paris	472	132	0.34	121	551	108	1.86	103
Toulouse	466	132	0.34	120	480	106	1.80	105
Delay of maturity								
Copenhagen		148-167		129-137		113-122		104-102
Hamburg		148-166		131-139		113-121		102-102
de Bilt		147-164		128-136		114-122		103-102
London		143-159		122-129		119-127		102-102
Paris		151-170		130-139		118-128		102-102
Toulouse		151-169		130-138		118-130		103-102

The relative effect of this crop ideotype on seed yield and on related yield components was calculated for six different locations in North-West Europe (Table 5.11). For these calculations an LAI_{max} of at least 2.8 was considered as sufficient for almost maximum light absorption (Fig. 5.4). Flowering was advanced by 3-6 d ($a_{T,2}$ increased by 5-10 %, Table 5.1) and maturity was delayed by 6-9 d ($a_{T,4}$ decreased by 20 %, Table 5.1) and by 13-17 d ($a_{T,4}$ decreased by 35 %, Table 5.1), respectively. With a further increase in sink size through apetalous flowers, a stronger response of seed set (up by 15 %) and larger sink capacity of individual seeds (an increase of 15 %), the source capacity was almost completely used (≥ 95 %) for both delays in maturity. When maturity was delayed by about one week, potential seed yields rose by 43-51 %, cumulative absorption of PAR ($I_{a,cum}$) by 13-19 %, HI by 29-31 % and LUE_{tot} by 2-4 % (Table 5.11). Delaying maturity by about two weeks increased potential seed yields by 59-70 %, cumulative absorption of PAR ($I_{a,cum}$) by 21-30 %, HI by 29-39 % and LUE_{tot} by 2 % (Table 5.11).

With the same modifications in sink size and source capacity, except the changes by a delay in maturity, the increases in potential seed yield varied between 27-32 %. This crop type also shows higher values for cumulative absorption of PAR (5-10 %), HI (14-21 %) and LUE_{tot} (3-5 %) (Table 5.11).

The values of LUE_{tot} were only slightly higher, because increased canopy photosynthesis (5-10 %, Table 5.7) was only introduced during the seed filling period and the delay in maturity, accompanied by a prolongation of the seed filling period, partly offsets this increase, as pods are less photosynthetically active than leaves.

Irrespective of maturity class, similar relative yield increases were found when the same measures were taken to increase source capacity and sink capacity solely by increasing seed set by 45 %.

For crop types and locations mentioned above the numbers of seeds per pod varied between 12 and 21 and simulated pod density did not limit seed set.

DISCUSSION

Comparison with winter wheat

Seed yields simulated with SUCROS-WHEAT were slightly higher than actual seed yields in the central part of the Netherlands (Table 5.2). Model testing also showed higher simulated seed yields than recorded in field experiments under optimum growing conditions (Stol, 1995). This suggests that either the model slightly overestimates potential seed yields or that the experimental growth conditions were not optimal as assumed. The lower actual seed yield for the Netherlands as a whole (6.66 t ha^{-1}) is a consequence of sub-optimal growing conditions in part of the area, such as water and nutrient deficits and the influence of pests and diseases.

Actual seed yields of winter oilseed rape in the Netherlands are similar to the simulated standard potential seed yield (Table 5.4). This indicates that in general terms, the crop is grown under near optimum conditions and that increased seed yields can only be attained by introducting higher-yielding varieties.

Comparison with winter wheat showed that the relatively low potential seed yield of winter oilseed rape is due to relatively low values of cumulative light absorption, light use efficiency and harvest index (Table 5.5). The low light absorption is mainly the result of harvesting winter oilseed rape about three to four weeks before winter wheat (Habekotté 1989; Fig. 5.1). The relatively low average LUE of winter oilseed rape may partly be attributable to stems and pods having less photosynthetic capacity then the leaves (Rode et al., 1983; de Boer and Langenhuysen, 1985; Habekotté, 1996c). The highest values of LUE in winter oilseed rape were observed near the onset of flowering (on average 2.62 g MJ^{-1}, Habekotté 1996c), with leaves being the main source for assimilate production. From flowering onwards, leaf area index declines and stems and pods take over assimilate production, which decreases average light use efficiency. More efficient light use may be attained by improving light distribution within the canopy through erect clustered pods, as analysed in this study.

Harvest index is the result of various processes determining the sink and source capacity for seed filling and may be increased by modifying various traits, i.e. increased seed set, increased potential growth rate of the seeds, apetalous flowers and an increase in the relative duration of the seed filling period (Tables 5.8 and 5.9).

Light distribution and canopy photosynhesis

Leaf and pod angle distribution and the clustering of leaves and pods affect light distribution within the canopy and canopy photosynthesis and were therefore analysed in this study. The angle distributions of the leaves and pods of current varieties are not well known, and were assumed to be neither extremely planophyl nor extremely erectophyl (Thompson and Hughes, 1986). As a reference, the intermediate spherical leaf and pod angle distribution is used in the calculations with DAYASS (Spitters et al., 1989). The relatively high value for the measured K_{dif} of winter oilseed rape (0.903) may be due to a rather planophyl leaf angle distribution or to the preferential formation of leaves in gaps within the canopy, which is also found in other dicotyledons (Spitters et al., 1989). As the 'standard' leaf angle distribution is assumed to be spherical, the relatively high value of K_{dif} was assumed to be due to distribution of leaves directed to fill in gaps in the canopy. The K_{dif} of the pod layer was not available and the cluster factor was assumed to be one.

DAYASS assumes that light is homogeneously distributed within a leaf or pod layer (Spitters et al., 1989). However, when leaves and pods cluster, shading may be more intense near the stems and this may reduce canopy photosynthesis (Goudriaan, WAU, 1995, pers. comm.). As a result, canopy photosynthesis and light use efficiency calculated with DAYASS for clustered leaves or pods attain theoretical maxima.

Although many assumptions have been made, the results indicate the potential change in canopy photosynthesis and LUE brought about by a change in light distribution in the canopy resulting from more erect leaves and pods and increased clustering.

The analysis with DAYASS showed that having leaves that are more erect may increase the LUE of the leaf canopy, but canopy photosynthesis does not increase at *LAI*s below 4, which are common before flowering (Table 5.6). For these *LAI*s, the advantage of more favourable light distribution is offset by reduced light absorption. Under conditions of low *LAI*, therefore, planophyl or spherical leaf angle distributions are more favourable than erectophyl or erect leaf angle distributions, as found previously in studies on leaf angle distributions only (De Wit, 1965; van Keulen, 1976; Goudriaan, 1988).

In contrast with a leaf layer alone, erect clustered pods above a standard leaf layer may increase canopy phtosynthesis by maximally 10 %, compared to pods that are not clustered and have a spherical angle distribution.

Options for increasing seed yield

Sink and source capacity for seed filling

Yield components such as pods per m^{-2}, seeds per pod and mean seed weight have been studied extensively in relation to seed yield (Geisler and Henning, 1981; Mendham et al., 1981a; Thompson and Hughes, 1986; Sierst et al., 1987; Pouzet et al., 1988; Grosse et al., 1992a). Because of the compensatory effects among these yield components, their use in breeding programmes as selection criteria for yield improvement is limited (Thurling, 1991; Grosse et al., 1992a). This study showed that the compensatory effect between simulated seed density and mean seed weight can be broken by simultaneously increasing sink and source capacity for seed filling (Figs 5.2b and 5.2c). This provides the best prospects for boosting seed yield.

Single crop traits

Various options for increasing the potential seed yield of winter oilseed rape (Table 5.1) have been suggested (Thurling, 1974, 1991; Mendham et al., 1981a,b; Thompson, 1983; Yates and Steven, 1987; Keiller and Morgan, 1988; Rao et al., 1991; Thurling, 1991; Richards, 1991; Marshall, 1991; Grosse et al., 1992a; Léon, 1993; Habekotté, 1996b). In this study a number of options were ranked according to their effect on seed yield, by analysing the effect of relative changes in crop characters on potential seed yield. Larger simulated seed yields resulted from (in descending order of improtance): later maturity (Richards, 1991; Marshall, 1991); increased seed set (Keiller and Morgan, 1988; Habekotté, 1993); smaller petals or apetalous flowers (Mendham et al., 1981a; Yates and Steven, 1987; Rao et al., 1991); increased potential growth rate of individual pods (Habekotté 1993); earlier flowering with retention of the duration of the total growth period (Thurling, 1991); and clustered erect pods (Mendham et al., 1984; Thompson and Hughes, 1986), in descending order of importance (Fig. 5.3; Tables 5.8 and 5.9).

Simulated pod densities did not limit simulated seed set and will not limit seed set until the maximum number of seeds per pod is reached (in this study 35, Habekotté, 1996c). This number varies from 18 up to 35 seeds, depending on variety (Pechan and Morgan, 1983; Mendham et al., 1994). This variety-specific maximum number of seeds per pod determines whether increased seed densities can be obtained with moderate numbers of pods, as has also been shown by Mendham et al. (1981a), or whether pod densities have to increase concomittantly.

Accelerated leaf area development until onset of flowering (Thurling, 1974; Mendham et al., 1981a,b; Thompson, 1983; Grosse et al., 1992a; Léon, 1993) hardly increased light absorption, total dry matter production and seed yield (range 1-2 %, option 1, Table 5.8). A simulated maximum *LAI* of about 3 m^2 m^{-2} sufficed for nearly maximum light absorption during the critical period for seed set and the seed filling period (Fig. 5.4), assuming that light absorption during the seed filling phase is similar to that at maximum leaf area (Mendham et al., 1981a; Habekotté 1996b). However, data recorded by Grosse (1989) for ten varieties grown in three growing seasons, showed that LAI_{max} (range: 2.4-5.4) correlated positively with leaf area index duration after flowering (LAID), which in turn correlated positively with total dry matter production from the onset of flowering until maturity and with seed yield. This could indicate that at higher LAI_{max}, leaves are productive longer, which may boost total dry matter production and seed yield. The possible physiological effects of LAI_{max} on leaf area index duration and of the latter on canopy photosynthesis were not included in LINTUL-BRASNAP. Thus, no conclusions could be drawn on the relative effect of LAI_{max} on seed yield via its effect on LAID on the basis of this study.

The explorations indicate that a modified developmental pattern is highly desirable for higher seed yields. If the maturity of winter oilseed rape is delayed, the harvest may overlap with the harvest of cereals and some farmers may lose in growing it (Mendham et al., 1981a; Almond et al., 1986; M.J.J. Pustjens, Van der Have, pers. comm., 1995). However, farmers of large farms find it an advantage to have differences in maturity to match the harvesting capacity of the farm, and to reduce yield losses by harvesting the crop close to attaining maturity (F. Grosse, Saaten Union, pers. comm, 1995).

In terms of climate, later maturity is only desirable at locations where there is no the risk of water shortage during later stages of crop growth (Thurling, 1991). Earlier flowering may result in flowers being damaged by frost in early spring (Merrien and Pouzet, 1988; Thurling, 1991; Richards, 1991). However, some damage to early flowers may be compensated by later flowers, therefore, early flowering seems to be a feasible option at locations with occasional frosts in late spring and will probably not lead to lower average seed yields (Richards, 1991; M.J.J. Pustjens, Van der Have, pers. comm., 1995).

Crop characters such as petal size or apetalous flowers, time of maturity, clustering and pod angle distribution of pods and time of flowering are easily recognizable and directly applicable in breeding programmes (M.J.J. Pustjens, Van der Have, pers. comm., 1995). Other crop characters such as the response of seed set to the availability of assimilates during the critical period of seed set and potential growth rate of the seeds cannot be directly derived from field observations and are not recorded in current breeding programmes (M.J.J. Pustjens, Van der Have, 1995, pers. comm.). Seed set is related to seed density (numbers m^{-2}), which is easily calculated from seed yield and mean seed weight. Selection for seed density excludes the compensation effect between pod set (m^{-2}) and seed set per pod and is therefore more suitable as a selection criterion. However, it can only be used during the later stages of selection when varieties/lines are sown in plots (Thompson and Hughes, 1986). Studies on spring rape seed (Chay and Thurling, 1989) suggest that pod length may be a suitable character for early generation selection for seed density and seed yield. Promising results were obtained crossing a selection with long pods with an inbred line with short pods, to combine the long pod character with an increase in seeds per pod and with minimum reduction in pod density (Chay and Thurling, 1989; Léon and Becker, 1992). Potential seed growth rate is related to final weight of the seeds under sink-limited growth conditions divided by the duration of the seed filling period, which may be approximated by the duration of the period from the end of flowering until maturity. Thus, indications of potential seed growth rates may be obtained under conditions with limited seed set, which can be manipulated.

Genetic variation has been observed or is probable for the crop characters considered (Grosse et al., 1992a; Léon and Becker, 1992; A.P. Sørensen, Cebeco, pers. comm., 1995). Moreover, there is an enormous reservoir of genetic diversity for the improvement of winter oilseed rape, in its own gene pool and in the gene pools of genetically related Brassica species and therefore genetic variability will not easily limit the scope for change in these crop characters.

Ideotypes for higher seed yields

A combination of physiological insight and experimental evidence can lead to a model of the ideal crop morphology, often called the 'ideotype' (Sedgley, 1991; Diepenbrock and

Becker, 1992). In this paper it is suggested that ideotype characters be combined with the aim of simultaneously increasing sink and source capacity for seed filling, provides best prospects for boosting yield increase. The effect of proposed crop types on potential seed yield was quantified for six locations in North-West Europe. The breeding value of the formulated crop types will further depend on ranges of genetic variability and genetic control of single or combined characters, which need further research (Diepenbrock and Becker, 1992; Mahon, 1983). Moreover, higher-yielding varieties should also include other characteristics related to crop management, e.g. higher seed yields may demand increased nitrogen application and varieties should be resistant to lodging as was found for winter wheat (Austin et al., 1980; Spiertz and van Keulen, 1980; de Vos and Sinke, 1981). Cold tolerance, resistance to diseases and seed retention also need further attention, if full advantage is to be taken of the improved yield potential.

CONCLUSIONS

The results presented in this paper indicate routes for increasing the seed yield of winter oilseed rape grown under potential growth conditions. Higher values of light absorption, light use efficiency and harvest index of winter oilseed rape are necessary to obtain seed yields closer to equivalent potential seed yields of winter wheat. Crop traits were identified quantitatively for obtaining higher values of these yield components. Combinations of traits based on a simultaneous increase in sink and source capacity for seed filing, provide the best prospects for increasing seed yield. Finally, the crop types proposed, show good prospects for increasing seed yield potential in North-West Europe.

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CHAPTER 6

GENERAL DISCUSSION

Higher seed yield, breeding and production ecology

One of the important objectives when breeding winter oilseed rape is to increase the crop's seed yielding ability. Understanding the physiology of yield formation can be helpful at two stages of breeding work: in the beginning, when choosing the parental material, and later, when selecting a few of the superior genotypes from a large amount of material (Diepenbrock and Becker, 1992; Aggarwal, 1995). However, so far the application of knowledge of the crop's physiology in breeding programmes has been limited, because the proposed strategies are not always unambiguous, the quantitative effects of various crop traits on seed yield and their mutual interactions have often not been clearly identified. Moreover, studies are frequently based on a limited number of existing varieties which do not represent the biologically possible strategies of yield formation, and the recording of some of the proposed characters in breeding programmes is considered to be too laborious and expensive (Diepenbrock and Becker, 1992; Link et al., 1992; M.J.J. Pustjens, Van der Have, pers. comm., 1995; A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995).

Research on plant and crop physiology has improved understanding of different aspects of yield formation and provides starting points for yield increase. However, studies that integrate the findings of such research at crop level are lacking, and therefore the relative importance of yield-determining processes and crop traits and their mutual interactions remain unclear. The identification of key processes of yield formation and related crop characters based on comparative crop growth analyses involving various varieties is hampered because varieties always differ in many characters simultaneously. Such identification based on crop growth analysis of one variety in different growing seasons is hampered because both crop performance and environmental conditions change with growing season. Correlation studies may identify the effects of various factors and their combinations on seed yield and are useful to identify yield-determining crop characters. However, causal relationships based on underlying interacting processes of yield formation and their relationships with the environment often remain unclear and limit the extrapolation of the results to other growing seasons and locations.

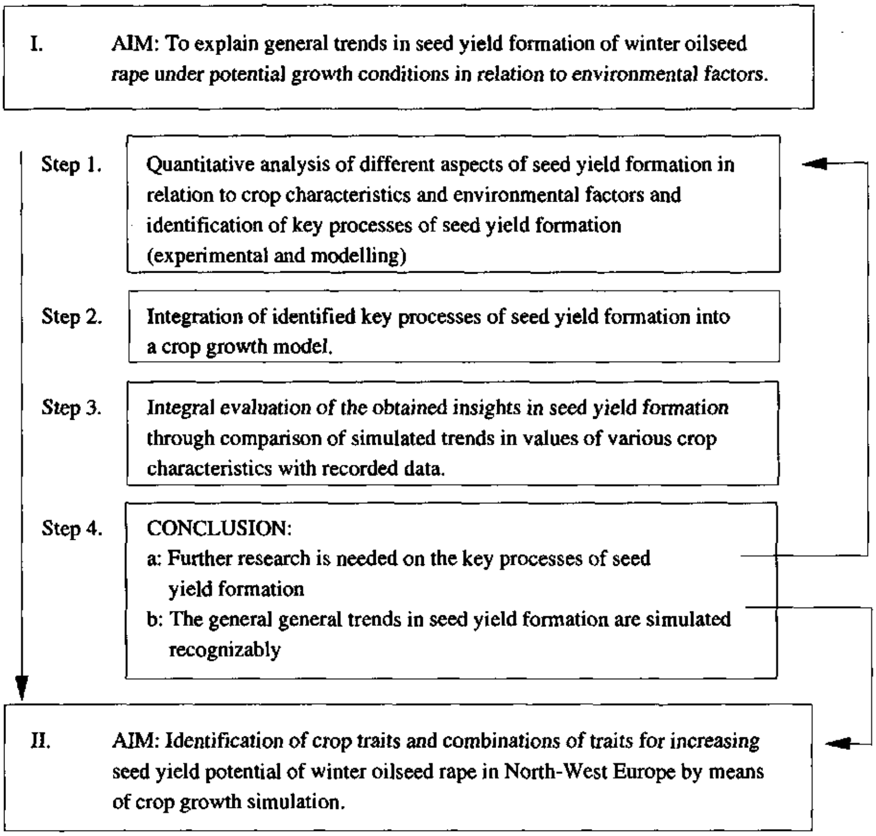
The present study aimed at combining the objectives of the approaches mentioned above and contributing to these approaches. The goal was to integrate existing knowledge on seed yield formation by using a crop growth simulation model, and to identify and fill in important gaps in this knowledge in order to explain general trends in seed yield formation in dependence of the environment under potential growth conditions. This integrated knowledge of yield formation was then used to identify crop traits for increasing seed yield, to analyse interactions between crop traits, to design hypothetical high-yielding crop types and to test these crop types for different locations in North-West Europe (Chapter 5). The measurability and genetic variability of crop characters were taken into consideration. The attempt to quantify and integrate key processes of seed yield formation and to explain how seed yield formation is influenced by the environment makes the present study an example of production ecology research (Rabbinge, 1986).

Seed yield formation

To quantify and explain the general trends in potential seed yield formation of winter oilseed rape in North-West Europe in response to environmental factors, which was the focus of the study, the analysis proceeded in various steps, combining experimental research with crop growth modelling. These steps are illustrated in Fig. 6.1. Experimental research was needed to provide more quantitative data on pod and seed set, seed filling and crop growth (step 1, Fig. 6.1). A model was used to simulate the phenological development of the crop in relation to environmental factors (step 1, Fig. 6.1). A crop growth simulation model was needed to integrate the identified key processes of seed yield formation (step 2, Fig. 6.1) and to integrally evaluate the insights obtained in relation to environmental factors (step 3, Fig. 6.1). The integral evaluation of seed yield formation by comparing simulated values of various crop characteristics with observed values resulted in new questions on seed yield formation (step 4, go back to step 1, Fig. 6.1). Finally, it was concluded that the first objective of this study had been partly achieved and that the insights obtained as described in the model developed, were applicable for the second objective (step 4, go to II, Fig. 6.1). The steps of analysis followed are discussed in more detail in the text below.

Pod formation and seed set

To increase quantitative insight into pod formation and seed set, questions were addressed concerning: 1) the period in which final numbers of pods and seeds are defined, 2) the effect of pod position in the canopy, defined by branch order and height, and time of pod initiation on pod and on seed set per pod and 3) the relation between pod and seed set and assimilate availability during relevant periods. To answer these questions, treatments were applied to ascertain the variation in canopy structure, number of pods, total dry matter production and seed yield in two growing seasons. Pod density (m^{-2}) and seed density appeared to be fully determined just after the end of flowering. The potential number of pods (i.e. the number of flower buds) did not appear to be a limiting factor for pod set, as at all positions in the canopy it was much higher than the number attained. Potential and actual pod density were linearly related to cumulative dry matter production of the crop until the onset and end of flowering, respectively, i.e. to total assimilate availability over that period. The number of seeds per pod did not vary with height in the canopy. Primary branch number and the time of pod initiation during flowering had some effect on the number of seeds per pod.



I. AIM: To explain general trends in seed yield formation of winter oilseed rape under potential growth conditions in relation to environmental factors.

Step 1. Quantitative analysis of different aspects of seed yield formation in relation to crop characteristics and environmental factors and identification of key processes of seed yield formation (experimental and modelling)

Step 2. Integration of identified key processes of seed yield formation into a crop growth model.

Step 3. Integral evaluation of the obtained insights in seed yield formation through comparison of simulated trends in values of various crop characteristics with recorded data.

Step 4. CONCLUSION:
a: Further research is needed on the key processes of seed yield formation
b: The general general trends in seed yield formation are simulated recognizably

II. AIM: Identification of crop traits and combinations of traits for increasing seed yield potential of winter oilseed rape in North-West Europe by means of crop growth simulation.

Figure 6.1 Stepwise analysis of seed yield formation of winter oilseed rape as followed in this study, as a basis for identifying options to increase seed yield potential in North-West Europe.

However, this had little influence on the overall mean number of seeds per pod of the whole canopy and did not affect the differences among treatments. It is argued that pod set did not limit seed set as the potential number of seeds per pod were not reached, and seed density (m^{-2}) could be explained by total crop growth during the flowering period without interference of pod set. Previous research indicated the importance of pod and seed set for seed yield. This study contributed quantitative insight into pod and seed set.

Seed filling

Once seed has set, the potential for final seed yield is defined. Conditions during seed filling determine to what extent this potential is reached. Daily seed growth appeared to be determined either by daily assimilate availability (source) or by the potential growth rate of the seeds (sink). Experimental research in this study showed that individual seed weight followed a sigmoidal pattern when plotted against the temperature sum from the onset of flowering per flower bud, until maturity (Chapter 2). Such a curve, derived under conditions of ample assimilate availability for seed filling was later used to derive potential growth rates of individual seeds during different phases of development.

Previous research had indicated that carbohydrate reserves accumulated before onset of seed filling may contribute to final seed weight. However, this contribution had not been definitively quantified. The experimental research in this study confirmed that carbohydrate reserves continued to accumulate until the end of flowering, and then declined during seed filling. The contribution to final seed weight varied between 7-12 % (Chapter 2).

Phenological development

During the period from sowing until the onset of flowering, yield potential is set by the number of flower buds and by the leaf area index at onset of flowering. Conditions during flowering are particularly important for pod formation and seed set, and the duration of the seed filling phase partly determines availability of assimilates for seed filling. Previous research had shown that variation in seed yield in different growing seasons and at different sowing dates was partly attributable to differences in developmental patterns of the crops (Mendham et al., 1981). Thus, phenological development needed to be quantified in relation to environmental factors in order to explain seed yield variation in different growing seasons at various locations. The literature was examined to identify key factors that influence phenological development of winter oilseed rape (Chapter 3), i.e. temperature, photoperiod and vernalization requirement for flowering. A model was developed to simulate the phenological development of the crop in response to environmental factors. The basic structure of the model and the ranges in parameter values were derived from literature. Predictions of various developmental stages were compared with data recorded at locations in the Netherlands, Germany and France, which differ in photoperiod and temperature regimes. The results showed that much of the variation in duration of the periods from sowing until onset of flowering, until end of flowering and until maturity are attributable to the interactive effect of temperature, vernalization and photoperiod. The resulting model is therefore useful for simulating various developmental stages of winter oilseed rape in North-West Europe.

Total dry matter production

Light absorption, light use efficiency and total dry matter production were analysed experimentally in this study (Chapter 4). Light use efficiency appeared to change with the phenological development stage of the crop. The concept of light absorption and light use efficiency largely explained differences in total dry matter production in the experiments. As reflection and absorption of incoming light by the yellow flowers distinctly reduces availability of intercepted light for crop growth during flowering, cumulative light absorption was used instead of cumulative light interception, to explain differences in cumulative crop growth.

Quantitative evaluation of seed yield formation

The identified and quantified key processes of seed yield formation mentioned above (step 1, Fig. 6.1) were integrated in a simple crop growth model (Chapter 4, step 2, Fig. 6.1) in order to integrally evaluate the insights obtained (step 3, Fig. 6.1). The LINTUL model, which bases crop growth and seed yield on cumulative light interception, light use efficiency and harvest index, was used as a starting point (Spitters, 1990). This basis was extended as far as necessary to attain the first objective of this study and as far as possible on basis of the information available. This involved extending the model to calculate 1) light reflection and absorption by the green canopy and flower layer, 2) total dry matter production based on light absorption and light use efficiency by the green canopy 3) pod and seed density, 4) partitioning of dry matter to the seeds based on whether seed growth is limited by source or sink, 5) accumulation and remobilization of reserve carbohydrates and 6) crop phenological development in relation to temperature and photoperiod. Model parameterization was partly based on literature and partly on research in this study. Model's performance was first evaluated, by comparing simulated values of various crop characteristics with recorded data used for parameterization (variety Jet Neuf). The model appeared to explain much of the variation in various crop characteristics such as total dry matter production at various stages of development, seed density, pod density and seed yield (Chapter 4). When the model's performance was evaluated by comparing the simulated trends in values of various crop characteristics with values of early and late sown crops in the UK observed over a period of 5 years, statistically significant correlations were found between the simulated and experimental data of various crop characteristics such as total dry matter production at various stages of crop development, seed density, pod density and seed yield. The differences between sowing dates were simulated better than the differences between years per sowing date. Seed set appeared to be crucial for the differences in observed and simulated trends in seed yields. These results focused attention again on the process of seed set (step 4, Conclusion: go back to step 1, Fig. 6.1) and a new hypothesis was formulated for the duration of the critical period of seed set, introduced in Chapter 4 as the second hypothesis for the duration of this period. The trends in observed seed densities and seed yields were simulated better under this hypothesis. It was concluded that the model is applicable for identifying options for increasing seed yield potential, as general trends in seed yield formation were simulated recognizably (Step 4, Conclusion: go to II, Fig. 6.1). Further research was advised to attain a more explanatory description of seed set, as will be discussed in the following section.

It can therefore be concluded that the approach followed appeared to be effective in attaining partly the first objective of the present study: '*To integrate existing knowledge on seed yield formation of winter oilseed rape and to identify and fill in important gaps in this knowledge in order to explain seed yield formation in relation to environmental factors under potential growth conditions'*.

The model

Seed set appeared to be a key factor in the explanation of observed seed yields. Differences in simulated and observed variation in seed yields appeared to be attributable to differences in simulated and observed seed densities. In previous research (Leterme, 1985) and in this study (Chapters 2 and 4), a period identical or nearly identical to the flowering period was identified as the period in which seed density is determined. In this study, seed density could be explained on the basis of total crop dry matter production during this critical period (Chapters 2 and 4). In the model, the duration of the critical period was determined solely by temperature, and this caused relatively large variation in simulated seed density compared to observed variation under conditions with maximum light absorption and crop growth rates during flowering. The duration (d) of the critical period might be partly governed by temperature and partly by other factors. Keiller and Morgan (1988a) found that in oilseed rape the end of pod and flower production coincides with a sudden cessation of apical growth and sink strength. In a companion paper they conclude that the pods closer to the base of the plant inhibited the growth and development of the apical regions, possibly because of competition for assimilates or a build-up of inhibitory substances at the apices, or a combination of these (Keiller and Morgan, 1988b). Seed set may be regulated by a mechanism similar to pod set. Further research is needed for a more explanatory and quantitative description of the factors that regulate pod and seed set and that may improve the accuracy of simulating seed density and final seed yield.

The model was evaluated solely with data recorded in the UK and in the Netherlands. The phenology part of the model was also evaluated with data obtained in France and Germany. Further testing of the model is needed to confirm or reject its value for explaining the general trends in seed yield formation in North-West Europe.

The model simulates the phenological development of the crop from sowing until maturity and crop growth from early spring until maturity under potential growth conditions. Extending the model to include crop growth during autumn and winter would extend its applicability to locations were initial conditions in spring are not known. Extending it to include crop growth under conditions of limiting water and nutrients would broaden its applicability for evaluating breeding strategies for these growth conditions.

Identifying options for increased seed yield potential

Comparing the yield formation of a crop with a high-yielding reference crop may result in guidelines for further research to improve yield (Shorter et al., 1991). This was illustrated by comparing the yield formation of winter oilseed rape with that of winter wheat. The following weak yield-determining components were identified: cumulative light absorption, light use efficiency and harvest index (Chapter 5).

Potential options for seed yield increase were derived from Chapter 2 and from the literature. The production ecology approach helped when identifying crop traits that might increase average values of light absorption, light use efficiency and harvest index and concomittantly final seed yields. Interactions between crop traits could be identified by distinguishing their average effect on the source or sink for seed filling. Simultaneously increasing the average source and sink capacity for seed filling, appeared to provide the best propects for increased average seed yield. The approach also enabled hypothetical high-yielding crop types to be designed and tested at various locations in North-West Europe. This revealed that the most promising crop type matures late, combines early flowering with sufficient leaf area index for almost maximum light absorption and has erect clustered pods to maximize average source for seed filling. To take full advantage of the source, further sink increase has to be attained through a high rate of seed set, a high growth rate of individual seeds, apetalous flowers or a combination of these characteristics.

The above mentioned steps in the analysis gave indications of the routes to follow in order to increase the average seed yield of winter oilseed rape grown under potential growth conditions in North-West Europe. The analysis may form a reference frame work for interpretating the yield formation strategies of existing varieties. This may help when identifying suitable parental lines for crosses. For example, lines with ample source for seed filling should be crossed with lines with ample sink for seed filling, to attain higher yielding-varieties and hybrid crops most efficiently. It is concluded that the approach followed appeared to be effective in attaining the second objective of the present study: *'To quantitatively identify crop traits and combinations of traits for increasing seed yield potential of winter oilseed rape in North-West Europe'.*

Usefulness of the study for breeding

The quantitative analysis and synthesis in this study (Chapter 5) yielded promising directions for increasing the potential seed yield of winter oilseed rape. The applicability of the given directions for breeding will depend on the link with breeding practice. In this study the link is based on identifying crop characters that are related to seed yield, and on identifying interactions triggered by changes in different crop characters. The value of crop characters as selection criteria also depends on other aspects such as genetic variability, genetic control and measurability in large scale trials, especially for selection after crosses have been made (Mahon, 1983; Diepenbrock and Becker, 1992).

Winter oilseed rape has an enormous reservoir of genetic diversity in its own gene pool and in genetically closely related Brassica species, such as *Brassica oleracea* L., *Brassica campestris* L. and *Brassica juncea* L. (Thurling, 1991) which can be exploited when breeding for improved varieties. Thus, genetic variability will not easily limit the use of ideotype characters in breeding programmes. Moreover, for most of the promising ideotype characters in this study, genetic variability has already been observed in varieties or is likely to be present (Thurling, 1991; Diepenbrock and Becker, 1992; A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995).

Genetic control, defined e.g. by genetic linkage between crop characters and single or multiple gene-defined characters, has hardly been studied. Research in this field may be a great help for breeders and may promote the use of ideotype characters in breeding programmes (A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995).

An appraisal of the measurability of the characters mentioned indicated that most of these, such as petal size and apetalous flowers, time of flowering and of maturity, clustering of pods and pod angle distribution are easily recognizable and directly applicable in breeding programmes (Diepenbrock and Becker, 1992; M.J.J. Pustjens, Van der Have, pers. comm., 1995; A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995). Incorporating others, such as seed set and potential growth rate of seeds, would require some additional effort (Chapter 5).

This discussion shows that collaboration between crop physiologists, modellers, reseachers in breeding and breeders is highly desirable to make the best use of ideotype characters in breeding programmes.

Consequences for crop management and cropping systems

Higher-yielding winter oilseed rape varieties may demand improved agronomic practices and may influence which varieties and crops are chosen for crop rotations. Winter oilseed rape requires large amounts of nitrogen. When nitrogen supply is ample, total N uptake ranges from 200-300 kg N ha^{-1}, of which 50-70 % is allocated to the seeds (Triboi-

Blondel, 1988; Habekotté and Smid, 1992; Pouzet, 1995). Assuming an N content of the seeds of about 3.3 % (Habekotté and Smid, 1992), a minimum N content of about 1.7 % in the leaves and about 0.7 % in the straw (including roots) (Habekotté and Smid, 1992), total N uptake and N allocation to the seeds were calculated for increased potential seed yields (plus 30-66 %) of the ideotypes designed in Chapter 5. This resulted in an increased total N uptake of 15-35 % and an increased N allocation to the seeds of 13-22 %. Thus, both N supply and N allocation to the seeds have to be improved to attain these increases in potential seed yields.

Current recommendations for N supply refer to the period before onset of flowering, and N supply is most important at the start of regrowth early in spring. When N is applied early in spring, about 70 % of total N uptake occurs in the period between emergence and onset of flowering (Triboi-Blondel,1988; Habekotté and Smid, 1992). Assuming an N content of about 4 % in crop dry matter at the onset of flowering (Habekotté and Smid, 1992), the required crop dry weight at onset of flowering may be calculated for the designed ideotypes: it is 3.8-5.2 t ha^{-1}. Simulations showed that this requirement was fulfilled for all ideotypes. This suggests that with the given timing of N application, potential N uptake up to flowering will not limit the increases in potential seed yields within the calculated ranges. The increased demand for allocation of N to the seeds after flowering has to be mainly provided by reallocation of N from stems, leaves and pod walls. This may accelerate the decrease in photosynthetic capacity of leaves and pods and thus may conflict with the attainment of higher seed yield. However, investigations have also shown that a high seed yield (about 4.5 t ha^{-1}) resulted in a relatively high N efficiency (defined by the ratio of seed yield and N application) compared to that of a lower-yielding crop (about 3.4 t ha^{-1}) for a given N application of 195 kg N ha^{-1} (reviewed by Marquard and Walker, 1995). Thus a high seed yield may coincide with a high N efficiency and profitable allocation of N to the seeds. Higher N efficiency and allocation of N to the seeds may reduce the amount of nitrogen in stubble left on the field after harvest, which subsequently mineralizes. Thus, N application and its efficiency need further attention and research with a view to optimizing seed yield formation and minimizing nitrogen losses to the environment.

In crop rotations winter oilseed rape has to follow crops that are harvested in summer, such as grain crops, as it has to be sown early, to ensure proper establishment before winter. It is a beneficial crop in the rotations because it improves soil structure due to its deep and extensive root system, it provides soil cover in winter and thus prevents erosion, its N uptake in autumn prevents N leaching in autumn and winter, it gives the opportunity to control grass weeds more easily than in cereal crops and it has a beneficial effect in reducing the levels of cereal diseases. However, it is problematic to incorporate in crop rotations with sugar beet, because it is a host for sugar beet nematodes and because oilseed rape plants that have grown from residual seeds are difficult to control in the sugar beet crop.

Currently, winter oilseed rape is mainly grown with cereals in the following rotation: winter oilseed rape, winter wheat and winter wheat or winter barley. The order of harvest in cereal rotations is winter oilseed rape, winter barley and winter wheat. Ideotypes with delayed maturity (Chapter 5) may give rise to problems with labour input during harvest of the crops. However, farmers of large farms find it an advantage to have differences in maturity since this makes it easier to attune the harvest date to the harvesting capacity of the farm, thereby reducing losses in seed yield (F. Grosse, Saaten Union, pers. comm, 1995). Later maturing of current high-yielding winter wheat crops, also gives some scope for delaying the harvest of winter oilseed rape (B. Knollema, DLV-Groningen, pers. comm., 1995).

Oilseed rape is currently often grown on shallow, stony soils with low water holding capacity, as the more profitable crops such as sugar beet and potatoes are not grown on these soils. Ideotypes with delayed maturity will need more water and therefore are certainly not suitable for growth on these soils.

Applications of production ecology in breeding

Knowledge of ranges of genetic variance of crop characters and of genetic linkage between crop characters may be taken into account in the design of ideotypes by means of systems analysis (Aggarwal, 1995). Then, the approach not only integrates knowledge of plant and crop growth and development processes and their relations with the environment, but also knowledge about the genetics of crop characters. This enables physiologically and genetically based contraints for improved seed yields to be evaluated in an integrated way, and thus may improve the identification of suitable characters for selection.

In this study, ideotypes for increased seed yield were formulated in general terms. No distinction was made in location-specific requirements for increased seed yields. The next step could be to define such location specific requirements and to consider them in the design of ideotypes (Shorter et al., 1991), because the demand for varieties adapted to different locations is increasing (A.P. Sørensen, Cebeco Zaden B.V., pers. comm., 1995). Production ecology research and the application of crop growth modelling may also be useful for analysing multi-locations evaluation of crop breeding lines (Elings, 1995). Both applications require crop growth models that are sensitive to relevant varietal differences.

Biotechnology is seen as a promising science for achieving improvement in varieties and hybrid crops (F. Grosse, Saaten-Union, pers. comm., 1995; Murphy and Mithen, 1995). New techniques make it possible to detect loci of genes affecting crop characters which have a positive effect on e.g. seed yields (Quantitative trait loci, QTLs). This may lead to marker-aided selection instead of phenotypical selection. Eco-physiological models may be useful to bridge the gap between genetic information on useful characters and the performance of the crop in different environments. The challenge is to determine whether the yielding ability can be predicted on the basis of genetic mapping of QTLs in combination with eco-physiological models (M.J. Kropff, WAU/AB-DLO, pers. comm., 1995).

The present study provides an example of an application of production ecology research in support of breeding. The approach followed appears to be helpful in integrating of existing knowledge on seed yield formation in winter oilseed rape, and in identifying and filling in important gaps in this knowledge in order to evaluate general trends in seed yield formation of the crop. The insights obtained, integrated in a crop growth model, appears to be useful for evaluating and synthesizing options for increasing the seed yield potential of winter oilseed rape in North-West Europe.

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SUMMARY

Oilseed rape is the most important oilseed crop of temperate climates. The name 'oilseed rape' refers to two Brassica species, *Brassica napus* L. and *Brassica campestris* L. In this thesis autumn-sown varieties of *Brassica napus* L. grown in Nord-West Europe are studied. Demand for the products of oilseed rape is increasing, making higher production per ha desirable. Seed yields of winter oilseed rape have been increased by improved agronomic practices and breeding. By optimizing agronomic measures, such as sowing rate, sowing date, nutrient application, and protection against pests and diseases it has become possible to attain potential seed yields, i.e. seed yields defined by genetic characteristics of the crop and the climatic factors radiation, temperature and photoperiod. Breeding has resulted in higher seed yields by selecting for high-yielding lines and by eliminating constraints e.g. susceptibility to low temperatures in winter, to diseases, to lodging or to shattering of pods. Despite these efforts, the potential seed yields of winter oilseed rape are still low compared to a high-yelding reference crop winter wheat (Chapter 1). Breeding for yield *per se* might be more effective if more were known about desirable traits to select for, to obtain a crop type which is expected to give higher yields because of greater efficiency in canopy structure and in allocation of resources within the plants.

In the first chapter it is argued that production ecology research may contribute to the identification of desirable crop traits and combinations of traits for increasing the seed yield potential of winter oilseed rape. The present study is an example of such research. The approach followed is based on two steps. The first was the aim of integrating knowledge on the seed yield formation of winter oilseed rape grown under potential growth conditions, and on identifying and filling important gaps in this knowledge, in order to elucidate seed yield formation in response to environmental factors (Chapters 2, 3 and 4). Secondly, this integrated knowledge was used to identify crop traits and combinations of traits for increasing seed yield potential of the crop in North-West Europe (Chapter 5). This involved combining experimental research with crop growth simulation.

In Chapter 2 different aspects of pod set, seed set and seed filling are studied, to increase quantitative insight into these components. For this purpose questions are addressed with respect to: 1) the period in which final numbers of pods and seeds are defined, 2) the effect of pod position in the canopy, defined by branch order and height, and time of pod initiation on pod and seed set per pod, 3) the relation between pod and seed set and assimilate availability during relevant periods, 4) the potential growth rates of individual seeds and 5) the contribution of reserve carbohydrates to seed filling. Treatments were applied to ascertain variation in canopy structure, number of pods, number of seeds, total dry matter production and seed yield. Pod density (m^{-2}) and seed density appeared to be

fully determined just after the end of flowering. The potential number of pods (defined as the number of flower buds) did not appear to be a limiting factor for pod set, as at all positions in the canopy it was much higher than the number realized. Potential and actual pod density were linearly related to cumulative dry matter production of the crop until the onset of flowering and until the end of flowering, respectively, i.e. to total assimilate availability over that period. The number of seeds per pod did not vary with height in the canopy. Primary branch number and the time of pod initiation during flowering had some effect on the number of seeds per pod. However, this had little influence on the overall mean number of seeds per pod of the whole canopy and did not affect the difference among treatments. Pod set did not limit seed set, and seed density could be explained by dry matter production of the crop during flowering, without interference of pod set. Individual seed weight followed a sigmoidal pattern when plotted against the temperature sum from the onset of flowering per flower bud, until maturity. Such a curve, derived under conditions of ample assimilate availability for seed filling, was later used to derive the potential growth rates of individual seeds during different phases of development. The maximum levels of reserve carbohydrates were attained just after the end of flowering, followed by a decline during seed filling. Remobilization of reserve carbohydrates contributed at most 12 % to final seed yield. The research in this chapter formed the basis for simulating pod set, seed set and seed filling in relation to crop characteristics and environmental factors.

The research presented in Chapter 3 aimed at developing an empirical model to simulate the phenological development of winter oilseed rape in relation to environmental factors. Literature was examined to elucidate the key factors that influence the phenological development of winter oilseed rape, i.e. temperature, photoperiod and vernalization requirement for flowering. The basic structure of the model and the ranges in parameter values were derived from literature. Predictions of various developmental stages were compared with data recorded on locations in the Netherlands, Germany and France, which differ in their photoperiod and temperature regimes. The results showed that much of the variation in duration of the periods from sowing until onset of flowering, until end of flowering and until maturity are attributable to the interactive effect of temperature, vernalization and photoperiod. The resulting model is useful for simulation of various developmental stages in North-West Europe.

In Chapter 4 experimental research on light absorption, light use efficiency and total dry matter production is presented. The light use efficiency appeared to be different in various phenological developmental stages of the crop. The concept of light absorption and light use efficiency largely explained differences in total dry matter production in the experiments.

Key processes of crop growth, crop phenological development and partitioning of assimilates to the seeds were integrated in a simple crop growth model (Chapter 4). A basic concept of light interception, light use efficiency and harvest index was extended to calculate 1) light reflection and absorption by the green canopy and flower layer, 2) total dry matter production based on light absorption and light use efficiency by the green canopy 3) pod and seed density, 4) partitioning of dry matter to the seeds based on whether seed growth is limited by source or sink, 5) accumulation and remobilization of reserve carbohydrates and 6) crop phenological development in relation to temperature and photoperiod. Model parameterization was partly based on literature and partly on own research. The model's performance was first evaluated by comparing simulated values of various crop characteristics with recorded data used for parameterization (variety Jet Neuf). It appeared to explain much of the variation in various crop characteristics such as total dry matter production at various stages of development, seed density, pod density and seed yield. Its performance was then evaluated by comparing the simulated trends in values of various crop characteristics with observed trends for early and late sown crops in the UK over a period of 5 years. Statistically significant correlations were found between the simulated and experimental data of various crop characteristics, such as total dry matter production at full flowering, seed density, pod density and seed yield. The differences between sowing dates were simulated better than the differences between years per sowing date. Seed set appears to be crucial for the differences in observed and simulated trends in seed yields and therefore further research is advised, to attain a more explanatory description of seed set. It is concluded that the model is applicable for identifying options for increasing seed yield potential, as it simulates general trends in seed yield formation recognizably.

In Chapter 5 the extended crop growth model is used to identify options for increasing seed yield potential. When seed yield formation of winter oilseed rape was compared with that of winter wheat, cumulative light absorption, light use efficiency and harvest index were found to be relatively weak yield-determining components of winter oilseed rape. Crop traits were identified to obtain higher values for these components. An analysis of sink and source capacity for seed filling showed that average potential seed yield can best be increased by increasing the average sink and source capacity for seed filling, simultaneously. Finally, promising crop types for increasing seed yield potential were designed and tested through simulations for various locations in North-West Europe. The most promising crop type matures late, combines early flowering with a maximum *LAI* of about 3 for almost maximum light absorption and has erect clustered pods for source improvement. To take full advantage of the source, further sink increase has to be attained through a high rate of seed set, a large sink capacity of individual seeds, apetalous flowers or a combination of these characteristics. Simulations showed that the cumulative light absorption, light use efficiency, harvest index and potential seed yield of this crop type at different locations in North-West Europe are higher than those of the standard crop type. Without a delay in maturity, the potential increases in seed yield were smaller.

The study concludes with a general discussion in which the methodology of the study, its scientific worth and its usefulness for breeding and implications for the cultivation of winter oilseed rape are evaluated (Chapter 6). It is concluded that the approach followed has been helpful in integrating existing knowledge on seed yield formation in winter oilseed rape, and in identifying and filling in important gaps in this knowledge to quantitatively explain general trends in yield formation of the crop. The insights obtained, integrated in a crop growth model, appear to be useful for evaluating and synthesizing options for increasing the seed yield potential of winter oilseed rape. The applicability of the results of this study for breeding is based on the greater understanding obtained of seed yield formation and on the identification of related crop characters, whose measurability and genetic variance were considered. It is argued that in order to grow higher-yielding varieties it may be necessary to improve agronomical practices such as nitrogen application, and that later maturing varieties may influence the varieties and crops chosen for crop rotations. It is concluded that the study indicates promising routes for increasing the seed yield potential of winter oilseed rape in North-West Europe.

SAMENVATTING

Koolzaad (*Brassica napus* L.) en de nauw verwante soort raapzaad (*Brassica campestris* L.) zijn de belangrijkste olieproducerende gewassen van de gematigde streken. Van beide soorten bestaan zomer- en winter-variëteiten. Onderwerp van dit proefschrift is winterkoolzaad (*Brassica napus biennis* L.), geteeld in Noord-West Europa. Een hogere zaadproduktie per hectare is wenselijk om te kunnen voldoen aan de toenemende vraag naar de produkten van het gewas, de olie in het zaad en het schroot dat overblijft na het persen van het zaad.

In de afgelopen decennia is de opbrengst van winterkoolzaad toegenomen door verbeterde teeltmaatregelen en veredeling. Optimalisering van teeltmaatregelen, zoals bemesting, bestrijding van ziekten en plagen en toepassing van de optimale zaaitijd, zaaizaadhoeveelheid en plantdichtheden, resulteerde in het bereikbaar zijn van potentiële opbrengsten, die alleen bepaald worden door gewaskarakteristieken en de omgevingsfactoren straling, temperatuur en daglengte. Veredeling resulteerde in variëteiten met o.a. een hogere opbrengstpotentie, die resistenter zijn voor ziekten, lage temperaturen in de winter beter kunnen doorstaan, minder snel legeren en waarvan de hauwen minder snel openspringen bij de afrijping en oogst. Ondanks deze inspanningen zijn de potentiële opbrengsten van winterkoolzaad laag vergeleken bij wintertarwe, een produktief referentiegewas. Kennis van plant- en gewaseigenschappen die een positieve invloed hebben op de gewasopbrengst via bijvoorbeeld de structuur van het gewas, de morfologie, de fenologie of de assimilatenproduktie en -toevoer naar het zaad, kan een belangrijke bijdrage leveren aan het verkrijgen van produktievere variëteiten via veredeling.

In hoofstuk 1 wordt beargumenteerd dat produktie-ecologisch onderzoek kan bijdragen aan identificatie van gewaseigenschappen en combinaties daarvan die een positieve invloed hebben op de opbrengstpotentie van het gewas. Het onderzoek beschreven in dit proefschrift is daarvan een voorbeeld. De gevolgde werkwijze is gebaseerd op twee stappen die tevens de twee doelstellingen van het onderzoek weergeven. Ten eerste is het onderzoek gericht op integratie van bestaande kennis over de opbrengstvorming van winterkoolzaad en het identificeren en invullen van kennisleemtes met als doel de algemene trends in de opbrengstvorming van het gewas te verklaren in relatie met de omgevingsfactoren temperatuur, daglengte en straling (Hoofdstukken 2, 3 en 4). Vervolgens is deze kennis gebruikt als basis voor het identificeren van gewaskarakteristieken en combinaties daarvan die kunnen bijdragen aan verhoging van de potentiële opbrengst van het gewas. Gebruik is gemaakt van experimenten en simulatiemodellen.

Experimenteel onderzoek is uitgevoerd om meer kwantitatief inzicht te verkrijgen in hauw- en zaadzetting en zaadvulling (Hoofdstuk 2). Daartoe zijn onderzoeksvragen gesteld met betrekking tot 1) de periode waarin de uiteindelijke aantallen hauwen en

zaden worden bepaald, 2) het effect van de hauwpositie in het gewas (diepte en vertakking) en het moment van hauwinitiatie (gedefinieerd als het moment van bloemopening) op de zaadzetting per hauw, 3) de relatie tussen hauw- en zaadzetting en assimilatenproduktie gedurende de relevante gewasgroeiperioden, 4) de potentiële groei van individuele zaden, 5) de bijdrage van reserve-koolhydraten aan de zaadvulling. Behandelingen werden aangelegd om verschillen te verkrijgen in gewasstructuur, aantallen hauwen en zaden, totale gewasproduktie en zaadopbrengst. De uiteindelijke hauw- en zaaddichtheden (m^{-2}) bleken rond het einde van de bloei bepaald te zijn. Het potentiële aantal hauwen (gedefinieerd als het aantal bloemknoppen) was op alle posities in het gewas veel groter dan het aantal gerealiseerde hauwen en beperkten de hauwzetting niet. De potentiële en gerealiseerde hauwdichtheden vertoonden een duidelijke relatie met het totale drogestofgewicht van het gewas bij respectievelijk begin bloei en einde van de bloei. Het aantal zaden per hauw varieerde niet met de diepte in het gewas. De vertakking en het moment van hauwinitiatie hadden wel enig effect op de zaadzetting per hauw. Echter, door het geringe aantal hauwen met lagere aantallen zaden per hauw, was het uiteindelijke effect op de verschillen in zaden per hauw op gewasniveau tussen de verschillende behandelingen gering. Het aantal zaden per hauw was steeds lager dan het potentieel mogelijke aantal per hauw, hetgeen aangeeft dat op deze wijze, het aantal hauwen niet beperkend was voor de zaadzetting. De uiteindelijke aantallen zaden (m^{-2}) vertoonden een significante relatie met de totale drogestofproduktie van het gewas gedurende de bloeiperiode. Het individuele zaadgewicht vertoonde een logistisch verloop uitgezet tegen de temperatuursom vanaf hauwinitiatie. Een dergelijke curve, afgeleid onder omstandigheden met ruime assimilatenvoorziening voor de vulling van de zaden, is later gebruikt voor het afleiden van potentiële groeisnelheden van individuele zaden in verschillende fasen van de zaadvulling. De bijdrage van reserve-koolhydraten aan de uiteindelijke zaadopbrengst was ongeveer 12 %. Deze onderzoeksresultaten legden een basis voor een kwantitatieve beschrijving van hauw- en zaadzetting en zaadvulling in relatie tot gewaskarakteristieken en de omgevingsfactor temperatuur.

Hoofdstuk 3 beschrijft de ontwikkeling van een empirisch model voor simulatie van de fenologische ontwikkeling van het gewas in relatie tot omgevingsfactoren. Op basis van literatuuronderzoek werd duidelijk dat temperatuur, daglengte en vernalisatie de belangrijkste factoren zijn die de fenologische ontwikkeling van het gewas bepalen onder optimale teeltomstandigheden. De basis van het ontwikkelde model en de mogelijke spreiding in parameterwaarden zijn gebaseerd op voorgaand onderzoek. Simulaties van data waarop verschillende ontwikkelingsstadia worden bereikt, zoals begin en einde van de bloei en afrijping, zijn vergeleken met experimentale data verzameld in Duitsland, Frankrijk en Nederland, onder verschillende omstandigheden van temperatuur en daglengte gedurende het groeiseizoen. De resultaten tonen aan dat veel van de waargenomen verschillen in duur van ontwikkelingsfasen van zaai tot begin bloei, tot einde bloei en tot de afrijping, toegeschreven kunnen worden aan de effecten van temperatuur, daglengte en vernalisatie. Het onderzoek resulteerde in een bruikbaar model voor simulatie van tijdstippen waarop verschillende ontwikkelingsstadia van winterkoolzaad in Noord-West Europa worden bereikt.

In Hoofdstuk 4 wordt experimenteel onderzoek naar de absorptie van licht, de lichtbenuttingsefficiëntie en totale drogestofproduktie gepresenteerd.

De lichtbenuttingsefficiëntie bleek te veranderen in de loop van de gewasontwikkeling. Met het concept van lichtabsorptie en lichtbenuttings-efficiëntie konden de verschillen in drogestofproduktie in de experimenten goed verklaard worden.

Voortbouwend op identificering en kwantificering van de meest bepalende processen voor de opbrengstvorming van winterkoolzaad, is in hoofstuk 4 deze kennis geïntegreerd in een gewasgroeimodel. Een eenvoudig model, gebaseerd op lichtinterceptie, lichtbenuttingsefficiëntie en oogstindex is daartoe uitgebreid met berekening van: 1) lichtreflectie en -absorptie door het groene gewasoppervlak en de bloemlaag tijdens bloei, 2) totale drogestofproduktie op basis van lichtabsorptie en lichtbenuttings-efficiëntie door het groene gewasoppervlak, 3) hauw- en zaadzetting, 4) toevoer van assimilaten naar het zaad per dag, op basis van de opname-capaciteit van de zaden (sink) en beschikbare assimilaten (source), 5) ophoping en remobilisatie van reserve-koolhydraten en 6) de fenologische ontwikkeling van het gewas in relatie tot de omgevingsfactoren temperatuur en daglengte. Parameterwaarden zijn gebaseerd op voorgaand onderzoek en op het onderzoek beschreven in de Hoofdstukken 2, 3 en 4. Modelberekeningen zijn geëvalueerd door middel van vergelijking van gesimuleerde waarden van verschillende gewaskarakteristieken met gemeten waarden. De evaluatie is eerst uitgevoerd met gegevens van de experimenten die tevens dienden voor parameterizering van het model. Het model bleek de waargenomen variaties in verschillende gewaskarakteristieken zoals totale drogestofproduktie tot verschillende ontwikkelingsstadia, hauw- en zaaddichtheid en zaadopbrengst goed te kunnen verklaren. In een volgende stap zijn de modelberekeningen geëvalueerd met behulp van experimentele data verzameld in Engeland van vroeg tot laat gezaaide gewassen in vijf verschillende groeiseizoenen. Significante correlaties zijn gevonden tussen gesimuleerde en waargenomen waarden van verschillende gewaskarakteristieken zoals totale gewasproduktie tot volle bloei, hauw- en zaaddichtheid en zaadopbrengst. De verschillen in waarden van deze gewaskarakteristieken gevonden bij verschillende zaaitijden werden beter gesimuleerd dan de verschillen tussen groeiseizoenen. De simulatie van het aantal zaden (m^{-2}) speelt hierbij een belangrijke rol. Verder onderzoek is aanbevolen voor een meer verklarende simulatie van de zaadzetting. De waargenomen variaties en trends in de opbrengstvorming zijn herkenbaar gesimuleerd. Dit leidde tot de conclusie dat het model bruikbaar is voor identificatie van gewaskarakteristieken en combinaties daarvan die een positieve invloed hebben op de opbrengstpotentie van winterkoolzaad, de tweede doelstelling van dit onderzoek.

Het ontwikkelde gewasgroeimodel is vervolgens gebruikt voor evaluatie en synthese van opties voor verbetering van de opbrengstpotentie van het gewas (Hoofdstuk 5). Een vergelijking van de opbrengstvorming van winterkoolzaad met die van wintertarwe toonde aan dat cumulatieve lichtabsorptie, lichtbenuttingsefficiëntie en oogstindex relatief zwakke elementen zijn in de opbrengstvorming van winterkoolzaad. Gewaskarakteristieken, die tot hogere waarden van deze opbrengstcomponenten leiden, zijn geïdentificeerd. Analyse van de sink- en source-capaciteit voor zaadvulling toonde aan dat verhoging van de gemiddelde potentiële zaadopbrengst het meest effectief verkregen wordt door verhoging van zowel de gemiddelde source- als van de gemiddelde sink-capaciteit van het gewas. Uiteindelijk zijn gewastypes ontworpen die perspectieven bieden voor verhoging van de potentiële zaadopbrengst. Deze zijn getest door middel van simulaties met klimaatgegevens van verschillende locaties in Noord-West Europa. Het gewastype met het meeste perspectief bloeit vroeg, heeft een maximale blad oppervlak index van circa 3 (m^2 m^{-2}) voor bijna volledige lichtabsorptie, heeft erecte geclusterde hauwen en rijpt laat af. Deze eigenschappen vergroten met name de source-capaciteit van het gewas. Om deze source te benutten zal de sink verder verbeterd moeten worden door een verhoging van de zaadzetting, een hogere sink-capaciteit van individuele zaden en bloemen zonder gele kroonblaadjes of een combinatie van deze gewaskarakteristieken. Simulaties met dit gewastype voor verschillende locaties in Noord-West Europa resulteerden in hogere waarden voor cumulatieve lichtabsorptie, lichtbenuttingsefficiëntie, oogstindex en zaadopbrengst ten opzichte van het standaard gewastype. Zonder latere afrijping waren de opbrengstverhogingen geringer.

In Hoofdstuk 6 wordt het onderzoek afgesloten met een discussie over de gevolgde methode, de bereikte onderzoeksresultaten, de bruikbaarheid van de onderzoeksresultaten voor veredeling en mogelijke consequenties voor de teelt van het gewas. Geconcludeerd wordt dat de gevolgde methode heeft bijgedragen tot integratie van bestaande kennis van de opbrengstvorming van winterkoolzaad en tot identificatie en vermindering van kennisleemtes ter verklaring van de opbrengstvorming van het gewas in relatie tot de omgevingsfactoren straling, temperatuur en daglengte. De verkregen inzichten vormden een goede basis voor het ontwikkelen van een gewasgroeimodel, dat een handig hulpmiddel bleek voor evaluatie en synthese van opties voor opbrengstverbetering van winterkoolzaad. De verkregen inzichten in de opbrengstvorming, de hieraan gerelateerde vrij eenvoudig waar te nemen gewaskenmerken en het aanwezig zijn van genetische variatie in deze kenmerken, vormen een basis voor toepassing van de onderzoeksresultaten in de veredeling. Ten aanzien van de teelt wordt aangegeven dat met introduktie van produktievere variëteiten mogelijk de stikstofgift aanpassing behoeft en dat met name later afrijpende variëteiten de gewas- en variëteit-keuze in gewasrotaties kunnen beïnvloeden. Geconcludeerd wordt dat met deze studie richtingen zijn aangegeven voor verbetering van de opbrengstpotentie van winterkoolzaad in Noord-West Europa.

CURRICULUM VITAE

Barbara Habekotté werd geboren op 11 oktober 1958 te Amsterdam. Na het behalen van het diploma Atheneum-B aan de Openbare Scholengemeenschap te Epe, begon zij haar studie aan de Landbouwuniversiteit te Wageningen. In 1981 behaalde ze het kandidaatsdiploma Biologie. Haar doctoraal voltooide ze in de period 1982-1986 met de doctoraalvakken Theoretische Produktie Ecologie, Onkruidkunde, Microbiologie, Didaktiek, Milieukunde en Milieurecht. Aansluitend werkte zij als student-assistente bij de cursus Systeem Analyse en Simulatie by de vakgroep Theoretische Produktie Ecologie (TPE) van de Landbouwuniversiteit (1986) en bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde aan de modellering van Knolcyperus (*Cyperus Esculentus* L.) ten dienste van de bestrijding van dit onkruid (1986-1988). In maart 1988 werd zij aangesteld bij het Nederlands Graan Centrum (NGC) voor het onderzoek aan winterkoolzaad beschreven in dit proefschrift. De uitvoering van het onderzoek vond plaats bij het toenmalige Centrum voor Agrobiologisch Onderzoek (CABO), het huidige DLO-instituut voor Agrobiologisch en Bodemvruchtbaarheids-onderzoek (AB-DLO). In 1991 continueerde zij dit onderzoek via een aanstelling bij het AB-DLO. In de periode vanaf januari 1992 tot juli 1995 verrichtte zij onderzoek ten behoeve van het project 'Introductie Geïntegreerde Akkerbouw' in dienst van het AB-DLO. Bij dit project waren verschillende onderzoeksinstellingen betrokken. Tevens besteedde zij in deze periode tot begin 1996 tijd aan het afronden van het proefschrift.

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