

# The damage caused by *Meligethes aeneus* F. (Coleoptera, Nitidulidae) and *Dasineura brassicae* Winn. (Diptera, Cecidomyiidae) in winter rape, assessed by computer simulations.

Jørgen Aagaard Axelsen  
Institute of Biological Sciences, Dpt of Zoology  
University of Aarhus  
Universitetsparken, Building 135  
DK-8000 Aarhus C  
Denmark

Present address:  
National Environmental Research Institute  
Dpt. of Terrestrial Ecology,  
P.O., Box 314, Vejlsovej 25  
DK-8600 Silkeborg  
Denmark

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## Abstract

*A supply-demand regulated population dynamical model of the growth and development of winter oilseed rape is used to simulate the effect of the damage caused by 2 pest species, the pod midge (*Dasineura brassicae*) and the pollen beetle (*Meligethes aeneus*). The model distributes the daily supply of photosynthates through a metabolic pool where pods have highest priority followed by buds, stems, leaves and roots.*

*The model captures the well known mechanisms of compensation and offers an explanation for overcompensation for pollen beetle attacks. Further a large source of variation in the ability to compensate for pollen beetle attacks was found to be the rate of budsetting per plant per degree-day. The model suggest, that oilseed rape is able to compensate to some extend for damage caused by the pod midge by increasing the size of the pods.*

## Introduction

The pollen beetle (*Meligethes aeneus* F.) is a serious pest of both oilseed rape (*Brassica napus* L.) and turnip rape (*Brassica campestris*) in large parts of Europe. A large input of pesticides is often necessary to keep this pest under control. Pollen beetles cause damage by destroying the immature buds in search for pollen, which is the food source of this beetle. They also feed on pollen of other plant species but rape is a preferred species for oviposition, which causes the pollen beetles to seek rape fields with plants in the bud stage.

In several countries damage thresholds are used (Andersson, 1988; Nilsson, 1987; Graham, 1982; Viettinghoff & Daebler, 1986), but very often their scientific foundations appear to be weak. Damage thresholds in winter rape range from 1.0 beetle/plant in spring rape in the former DDR (Viettinghoff & Daebler, 1986) to 15 - 20 beetles/plant in winter rape in England (Graham, 1982). Free and Williams (1979) believe that the damage caused by pollen beetles is overestimated. This confusing picture is mainly due to 3 reasons. Firstly, climatic differences between the countries and years. Secondly, different plant densities. Thirdly, rape plants have a strong capacity for compensation (Williams and Free, 1979; Tatchel, 1983; Lerin, 1987, Axelsen & Nielsen, 1990), which makes it very difficult to assess the damage. The latter is the main reason why it is difficult to establish reliable damage thresholds.

The pod midge (*Dasineura brassicae* Winn.) is also a well-known pest of rape in north-western Europe, but its status as a pest is more uncertain than the status of the pollen beetle. The pod midge oviposits in the pods of rape or other closely related plants, but rape is the preferred species (Åhman, 1988). The growth of the larvae, up to 200 per pod (Sylvèn, 1949) cause the pods to dry up and eventually to open and the seeds drop out. In Denmark and southern Sweden winter rape are often sprayed once or twice during bloom to keep this midge under control. In Denmark in 1992 the damage threshold has been exceeded if 7 - 8 % of the pods have been damaged (Nielsen, pers. comm.) This threshold is only based on the cost of insecticide, application of the insecticide and wheel damage and does not take any kind of compensation into consideration.

Thus there is a need for scientifically based damage thresholds, which can be used in different climates, at different plant densities and take compensation into consideration. When a bud or a pod has been damaged it is not a photosynthetic sink anymore and the resources are allocated to other pods, buds or vegetative growth. This process is described well by simulation models using a metabolic pool. Gutierrez et al. (1984) and Gutierrez et al. (1991a+b) have been able to model successfully the growth of a several crop species under very different climatic conditions and therefore a model that can simulate growth of rape crops may quantify the compensation in response to pest injury. The model described in this paper does not give exact damage thresholds for the insect pests on oilseed rape, but gives an scientifically well founded estimate of the compensation to pest injury.

### *The model*

The driving forces in the model are temperature, solar radiation and the demands of the different parts of the rape plant. The daily production of assimilates is placed into a metabolic pool from which it is distributed first to reproductive organs and then to vegetative growth (Gutierrez, 1988, Graf et al., 1990). In detail, the priorities in this model were pods, buds, stems, leaves and roots. Assimilates used by the flowers were neglected. The production of assimilates by the pods did not contribute to the metabolic pool, since they are known to retain their own production for their own development (Allen & Morgan, 1972; Major et al, 1978).

The model makes daily calculations of the dry weight of leaves, stems, pods, seeds and oil; the surface area of leaves, stems and pods; and the numbers of buds, flowers and pods.

#### *Pods*

The development of every single pod was modelled in the same way as the development of the entire plant. The production of photosynthate was based on demand, temperature and solar radiation. The production entered a metabolic pool, from which it first was distributed primarily to oil production, second to seed growth and finally to growth of the husks. If the production of photosynthates by a pod could not satisfy the demand, it received supplies from the plant metabolic pool. Calculations always started with the largest pods, i.e. if there was a shortage of supplies the smaller ones received no supplies from the plant metabolic pool. If a pod had received less than twice its respiration during 20 °D, abscission occurred.

#### *Buds*

The development of the buds was also modelled individually, but not as detailed as the development of the pods. Their supplies came from the plant metabolic pool and the largest buds received their supplies first, leaving smaller buds without supplies if a shortage occurred. The rule for abscission was similar to that for the pods. Buds were modelled to burst when their dry weight exceeded 0.01 g (Field measurements of mature buds: average from 10 buds from winter rape = 0.102, S.E. = 0.006, N = 10).

#### *Nitrogen balance.*

The nitrogen balance is demand driven and the nitrogen demand was assumed to be proportional to the demand for chlorophyll in the different plant organs(1):

$$ND = \sum_{k=0}^n p^* C_k^* M_k - NP_k \quad (1)$$

where ND is the total daily nitrogen demand,  $NP_k$  is the amount of nitrogen already present in the plant organ,  $p$  is a constant defining the relation between nitrogen and chlorophyll,  $M_k$  is the mass of the plant organs (leaves, stems etc.),  $C_k$  is the maximum concentration of chlorophyll and  $k$  symbolise the plant organ. The constant  $p$  was found by simulation and  $C_k$  was measured in the laboratory. (results reported in this paper). The plants were assumed to take up nitrogen from the soil according to their demand as long as the soil was not depleted. The amount of nitrogen in the soil was assumed to stem exclusively from artificial fertiliser and leaching was ignored.

Due to the large mobility of nitrogen (Salisbury & Ross, 1978, Ogunlela et al., 1989), a nitrogen pool containing all nitrogen in the plant was established and redistributed every day. The distribution priority was primarily pods, buds and stems sharing the resources and if anything was left the leaves got their share.

In the model the nitrogen concentration was assumed to control leaf senescence by aid of following criteria (2):

$$\frac{NS_{leaves}}{ND_{leaves}} = 1 \quad (2)$$

where  $NS_{leaves}$  is the nitrogen supply in the leaves and  $ND_{leaves}$  is the demand for nitrogen in the leaves. If the criteria (2) was not satisfied the leaf mass was reduced to obtain satisfaction. 80% of the nitrogen of senescing leaves was retrieved (Zhang et al., 1991).

In the case of nitrogen shortage after the leaves had fallen off, available chlorophyll was distributed among pods, buds and stems relative to their maximum chlorophyll concentration, which reduced the assimilation efficiency of these organs.

#### *Assimilation*

The assimilation of solar radiation was modelled as a predation process depending on the leaf area index (Gutierrez et al., 1987; Graf et al., 1990). Total leaf area index was calculated by equation (3) where the areas of stems and pods were converted to "leaf equivalents".

$$LA = \sum_k SA_k * \frac{C_k}{C_{leaves}} \quad (3)$$

where LA is the total leaf area,  $SA_k$  is the surface area,  $c$  is the chlorophyll concentration mass by a constant ( $p$ ) and for pods by multiplying the square root of the mass by a constant (Appendix 1).

#### *Pests*

The damage caused by the pod midge was simulated by coupling this model with an already existing model (Axelsen, 1993a) and choosing the destroyed pods randomly from the pods present at any time. Pollen beetle damage was simulated by letting the pollen beetles destroy 3 buds/day (Axelsen, 1993b). This is the only parameter that is expressed in calendar time in stead of degree-days. Developmental thresholds are shown in table 1. The immigration of pollen beetles was simulated by a normal distribution and started in the early bud stage and ended in early bloom.

#### *Climatic data*

The climatic data used was hourly measurements of temperatures (10 cm depth and 2 m height) and global solar radiation obtained from the automatic meteorological station at Ødum, 20 km north of Århus, Denmark

Input parameters are shown in appendix 1. In the simulations these parameters are used if nothing else is specified.

## *Plant analysis*

The growth analysis was carried out in 1991 and 1992. Plant material was obtained from a research plot (22m \* 50m) at the edge of a rape field (variety Topas, double low) that was cultivated according to normal agricultural practice. In both years the research plots were situated less than 100 m from the meteorological station at Ødum. The field was fertilised by 160 kg Nitrogen/ha on 20 of April and ? in 1991 and 1992, respectively.

Weekly samples of 15 randomly chosen plants were taken from early September to late October and again from mid May to harvest. In the winter samples were only taken monthly. Plants were cut at ground level, i.e. roots were not included in the growth analysis. Plants were dissected into leaves, stems, buds, flowers and pods. The analysis consisted of :

1. Counting buds, flowers and pods.
2. Measurements of the areas of leaves, stems and pods (measured by an area meter).
3. Determinations of dry weight of leaves, stems, buds and pods. (Dried at 105 °C for 24 h)

During early bloom 100 buds, ready to burst, were collected and their dry weight determined. Finally, at harvest 100 pods were chosen randomly for an investigation of the relation between pod dry weight and seed dry weight. Results from the growth analysis are presented together with charts of simulation results. Results from 1991 were used to estimate maximum growth rates and for model fitting, while the results from 1992 were used for validation only.

During summer 1991 2 plants were chosen every week for chlorophyll analysis of pods, stems and leaves, performed according to Gyldenholm (1968). The maximum chlorophyll content was 0.128, 0.160 and 0.350 mg/g fresh weight for leaves, stems and pods, respectively.

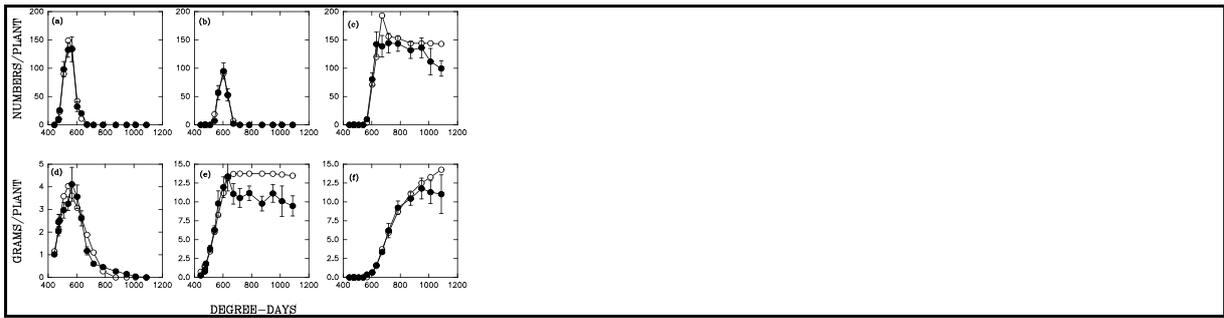
## *Model fitting*

In the model the development of plant parts is dependent on the growth rate and their initial weight. These initial weights are very hard to determine exactly from experiments because it is difficult to decide when e.g. the stem has begun to develop from the leaf rosette and when a pod is a pod and not only the pistil of a flower with senescing petals. Consequently these parameters were found during the fitting process. In rape, the time when stem elongation is initiated is closely tied to the vernalisation, since tiny buds can be found shortly after the stem elongation can be recognised. The mechanism controlling vernalisation is unknown and consequently it was not possible to incorporate a calculation of this parameter into the model.

Thus the time of vernalisation had to be fitted to observations in both 1991 and 1992.

Due to a lack of quantitative data on frost damage in relation to climatic data, no attempt was made to simulate frost damage in the model. It was therefore necessary to fit the dry weight of leaves and stems to observations for both years. This fitting was done in early spring before the growth season commenced.

The fitting was done by eye by aid of graphics at the end of the simulation program and the fitting process was ended when the coincidence between observed and simulated data was satisfactory for all the parameters estimated by the plant analysis ( number of buds, flowers and pods and dry weight of leaves, stems and pods)(Fig. 1).



**Figure 1.** Comparison between observed (closed circles) and simulated (open circles) values of number of a) buds, b) flowers, c) pods/plant, and dry weight of d) buds, e) stems and f) pods/plant. Data from 90/91.

### *Simulations of plant growth in 1992*

There was one parameter, that was necessary to adjust in 1992 relative to 1991 and this parameter was the bud creation rate. This parameter is a constant in the model and the plant analysis from 1992 showed a bud creation rate of 1.4 per °D, while the 1991 value was 2.7 per °D. With this adjustment the ability of the model to simulate the development of winter rape in grown in 1991/1992 is rather good for most parameters (Fig 2.). Only the peak number of flowers differs considerably. The model overestimates the stem weight slightly and underestimates the final number of pods. Further the simulated curve for the development is a little humped relative the observed one, but the coincidence is rather good at harvest.

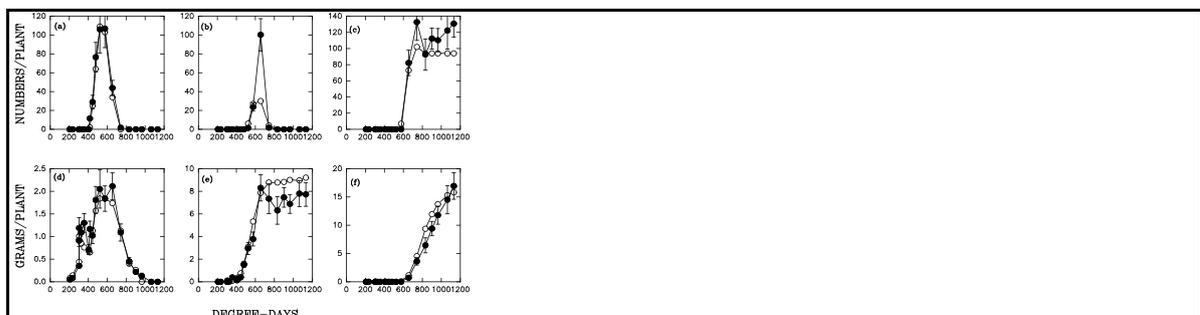
The concurrence between observations and simulations is improved if the pod growth rate is reduced to 50% (not shown). This reduction is confirmed by observations from 1992 and may be due to shortage of water.

When considering the differences between simulations and observations in 1992 the large climatic differences between the 1991 and 1992. In 1991 May and June were extremely cold while July was very warm. In 1992 temperatures were very low until the first week of May where temperatures became very high for the time of the year and a drought period began. This drought lasted throughout May and June and the first rain came in the first week of July. Taking the climatic differences into consideration the simulation of the development in 1992 is a strong support of the model.

### *Simulation results*

The model was used to investigate the effect of the damage caused by pod midges and pollen beetles, when the compensatory power of rape is taken into consideration.

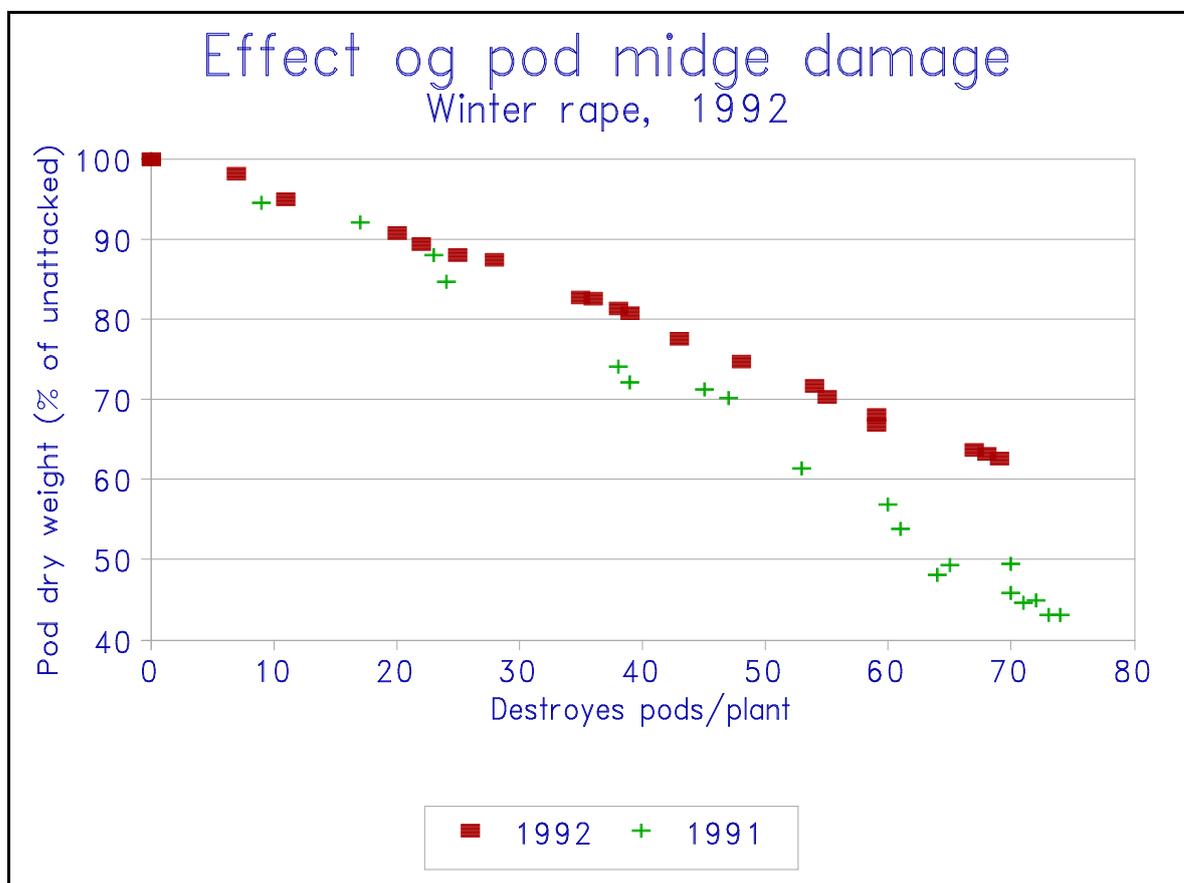
#### *Pod midge*



**Figure 2.** A comparison between observed and simulated values of number of a) buds, b) flowers, c) pods per plant and dry weight of d) buds, e) stems and f) pods per plant during the growth season 1991/1992.

Simulations of pod yield versus pod midge damage show a reduction of about 5% per 10 destroyed pods (Fig. 3) for climatic input from both growth seasons at low attack levels. For 1992 data this figure lasts for higher attack levels also, but an increased effect of the damage is seen using 1991 climatic data.

Simulations of the pod yield versus pod midge damage at different plant densities are shown in fig. 6. The slopes at the different densities are almost identical, i.e. the effect of pod midge damage is independent of plant density (Fig. 4).

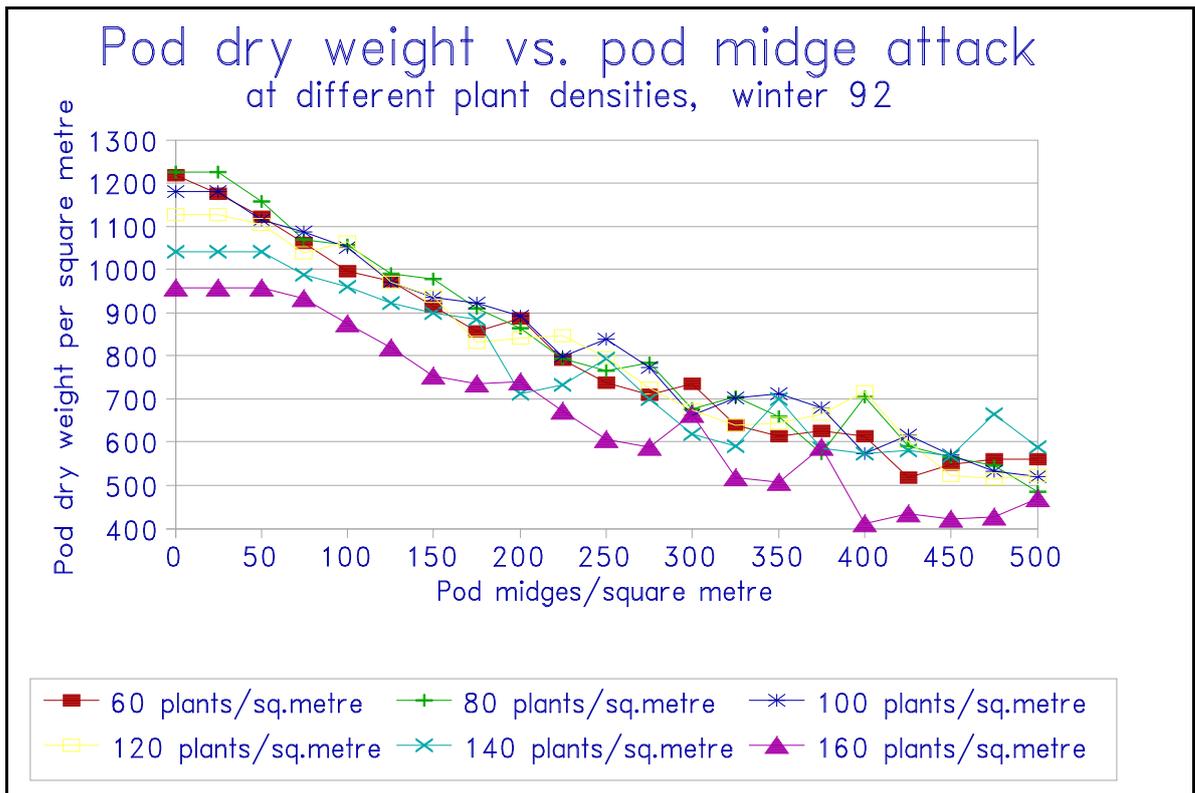


**Figure 3.** Simulations of the loss in pod dry weight at different levels of pod midge damage using climatic measurements from the growth seasons 1990/1991 and 1991/1992.

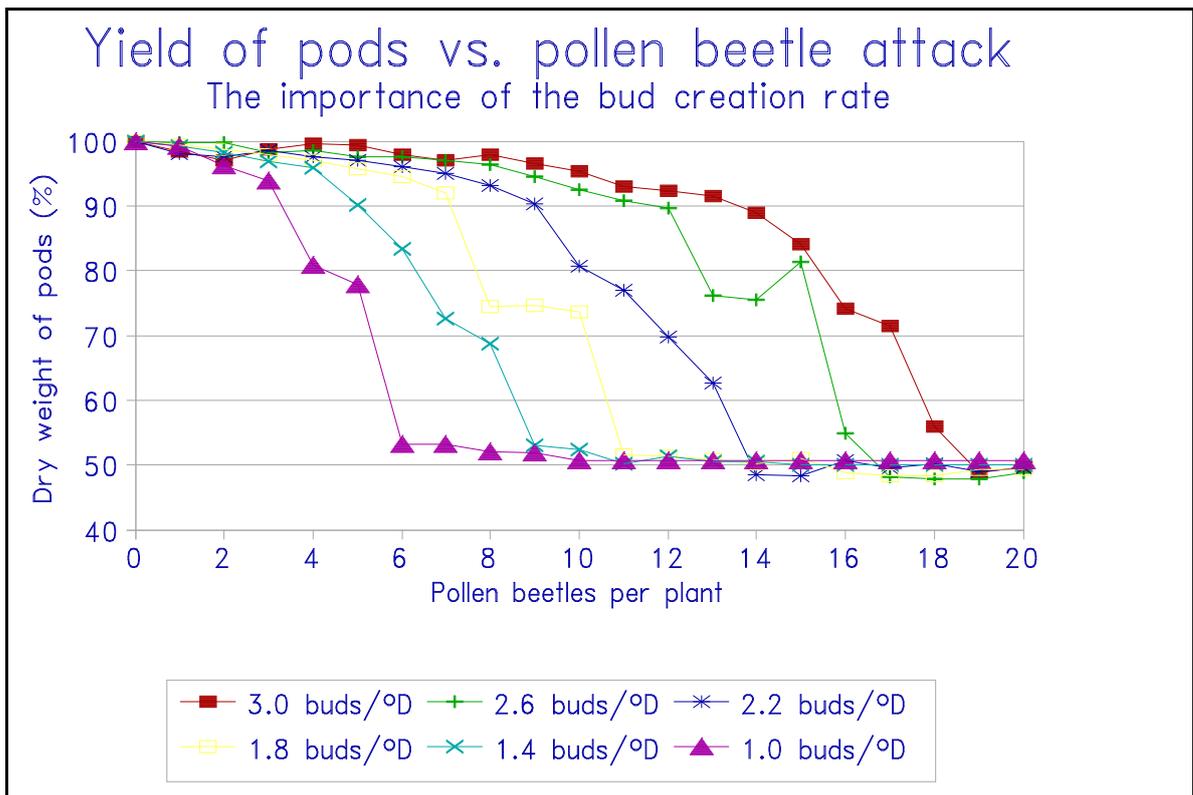
### *The pollen beetle*

The effect of the pollen beetle damage turned out to differ from 1991 to 1992 in simulations. In 1991 an important reduction in yield occurred at more than 10 beetles/plant, while a similar reduction occurred at about 4-5 beetles/plant in 1992. The reason for this difference was the factor, which had to be changed in 1992, relative to 1991, to make the simulation fit observed data, namely the bud creation rate. The importance of this parameter is demonstrated in fig. 5, where the resulting pod weight is shown as a function of the cumulative pollen beetle attack, i.e. the density of pollen beetles when immigration had ended. The ability to compensate for pollen beetle damage is clearly dependent on the rate of bud setting and therefore it was appropriate to investigate which factors control the bud setting rate. Plant analyses was not set up to gain information on this subject but the number of buds on the date when the highest number of buds was observed is correlated with the dry weight of the plant (Fig. 6).

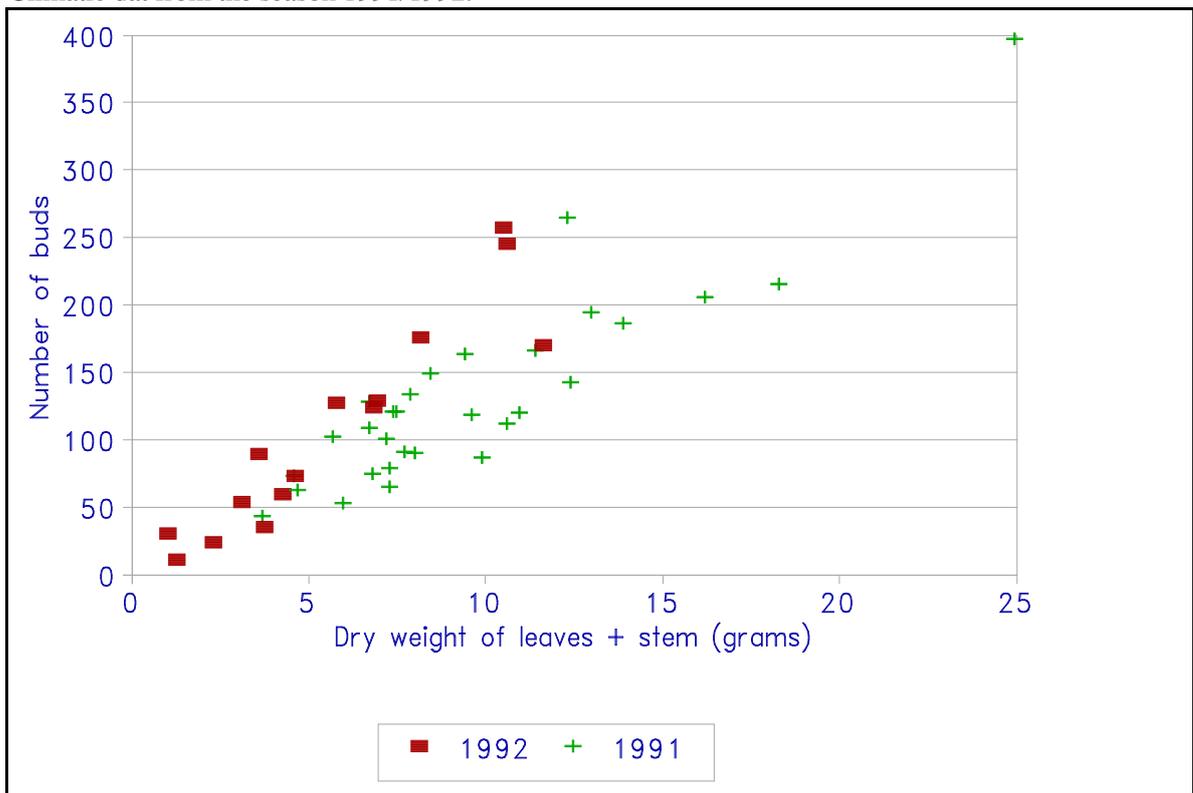
Another important factor is the timing of the pollen beetle attack. The importance of this factor was quantified by changing the average time of arrival from a very early arrival (500 °D) through arrival that coincided well with the bud stage to a very late arrival (600 °D) (Fig 7). The initial parameter 560 °D was chosen to let the start



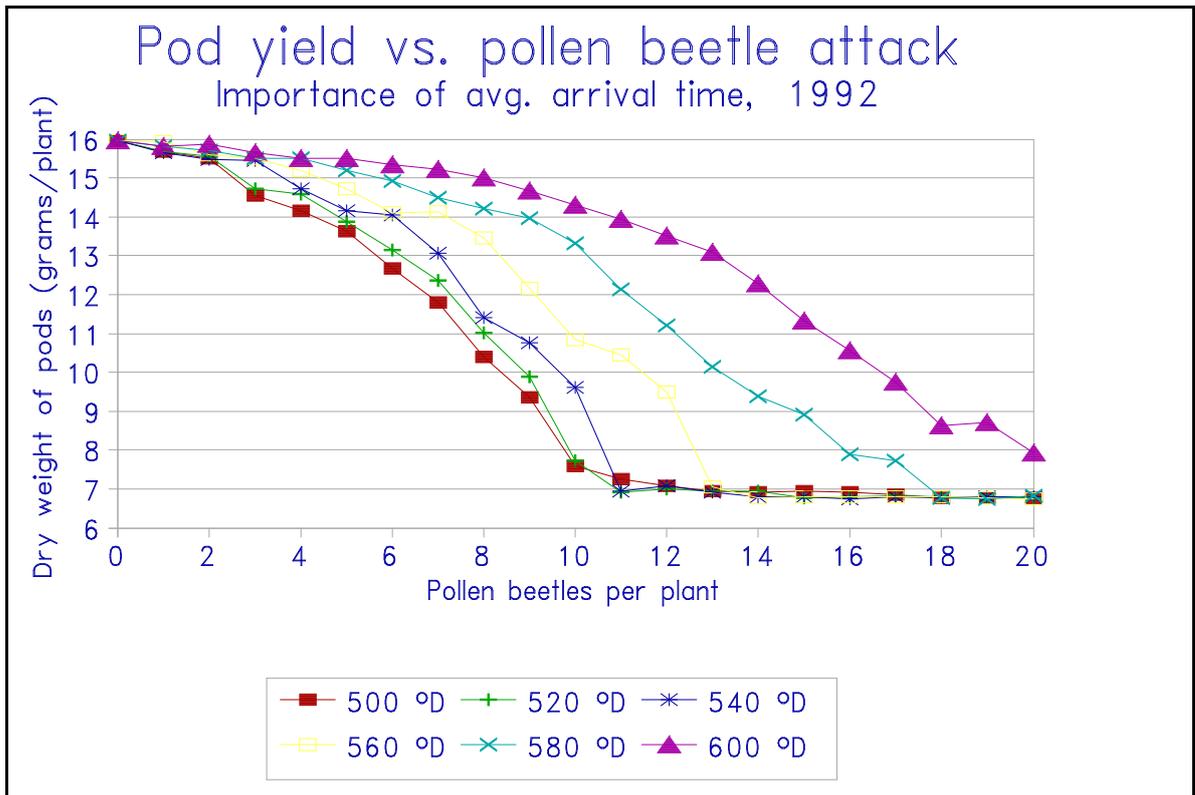
**Figure 4.** Simulations of the impact of pod midge damage at various plant densities on the pod dry weight at harvest, climatic data from the season 1991/1992.



**Figure 5.** Simulations of the pod dry weight per plant after pod midge attacks at various plant densities. Climatic dat from the season 1991/1992.



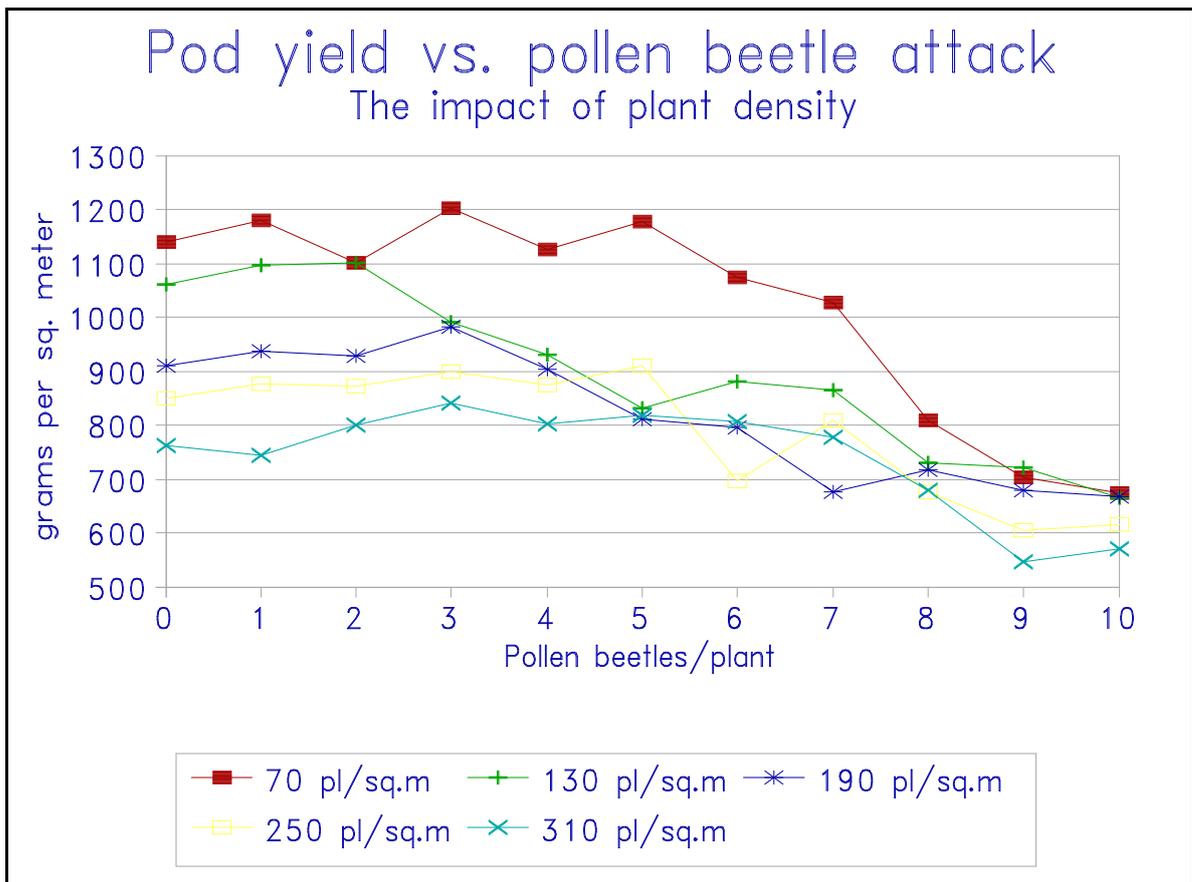
**Figure 6.** Correlation between dry weight of leaves + stem (DW) and bud number shortly before bloom. Regression in 1991:  $-6.67 + 13.4 \cdot DW$ ,  $R^2 = 0.81$ ; and 1992:  $-13.4 + 8.87 \cdot DW$ ,  $R^2 = 0.87$ .



**Figure 7.** The pod dry weight at harvest vs. pollen beetle attacks at different times during the bud stage. The degree-day value given in the legend is the average arrival time. 500 is early and 600 is late bud stage.

of immigration coincide with the early bud stage. It is clearly seen that the earlier the arrival, the more important is the damage.

The impact of plant density on the ability of the rape plants to compensate for pollen beetle attack is rather weak. (Fig. 8). At all densities the loss begins to be important at 5 - 7 beetles/plant with a tendency to highest values at higher plant densities. It is remarkable, that the simulations show a slight overcompensation at low attack levels.



**Figure 8.** Simulations of the impact of plant density on the compensation after a pollen beetle attack. Notice the overcompensation at low attack levels.

### Discussion

The model is able to simulate in detail the development of the different plant parts in both 1991 and 1992. The plant analysis from 1992 and the simulations for this year are completely independent. Further the model is able to simulate the compensation for damage to winter rape made by flocks of whopper swans (*Cygnus cygnus*) (Laubæk & Axelsen, in prep). When considering the strength of the model it is worth to stress the very large climatic differences between 1991 and 1992. Spring 1991 was rather cold but sunny and the summer was very cold and rainy. The crop was harvested as late as 31. July. Spring 1992 was cold and rainy, often with overcast skies until 10. May when an 8 weeks long period with clear skies, high temperatures and drought began. The crop was harvested on 9. July. Due to these differences the growth of the crop was also very different between the 2 years, with small high yielding plants in 1992 relative to 1991, when plants were large but yield relatively low. The model captures these differences and offers an explanation of the large differences in leaf area per plant between the 2 years (see fig 1 and 2).

Compensation for a pod midge attack has not been described before, but the model suggests that compensation must take place some years. In the simulations the number of pods at harvest is 148 and 97 in 1991 and 1992, respectively. If 50 % of these pods are destroyed it is seen from fig. 3 that the yield is slightly less than 50% in 1991 but about 75% in 1992 (Plant densities were even the two years). This means that compensation by increasing the weight of the remaining pods should take place in 1992 but not in 1991.

The simulations of pod yield at various pollen beetle infestations (fig 5,7 and 8) takes the compensation into consideration and is a good tool, when an economic damage threshold has to be established. Compensation is actually captured by the model with the aid of the metabolic pool concept and the distribution of photosynthates according to the priorities mentioned earlier. When

some buds are damaged by pollen beetles the supplies they would have required are allocated to other buds, stems or leaves. Thus some buds that would otherwise have aborted due to shortage of supplies are retained on the plant, or if the plant has enough supplies for all buds, the stem and/or leaves will get a larger part of their demand satisfied. In the latter case stem size and probably leaf area will be increased by a pollen beetle attack as shown in fig. 9. This may be the background for the overcompensation for a pollen beetle attack, which has been simulated by the model and observed by a few authors (Nilsson, 1980, Boelcke & Vietinghoff, 1987, Axelsen & Nielsen, 1990). Boelcke & Vietinghoff concluded that the plants might overcompensate if the pollen beetle attack did not occur in the early bud stage. In the simulations in fig. 7 the mean arrival time is in the middle of the bud stage, i.e. the Boelcke and Vietinghoff's conclusions are consistent with the simulations. Another mechanism of compensation is to develop more seeds per pod and to produce larger seeds (Tatchel, 1983). The model does neither simulate the number of seeds per pod nor the seed size, but larger seeds and/or more seeds per pod will give a larger pod weight. The simulations with large attacks of pollen beetles and pod midges give larger average pod weight. A third known mechanism of compensation for pollen beetle attack is increasing the number of pods (Axelsen & Nielsen, 1990), which is also captured by the model (Fig. 9).

It is no simple task to establish thresholds in oilseed rape, since the power of compensation depends strongly on the bud creation rate (fig. 5), which seems to vary from year to year. In 1991 the threshold is at about 9 - 10 beetles per plant when the infestation is at maximum and the beetles begin to arrive at the early bud stage (73 plants/m<sup>2</sup>). The corresponding number for 1992 is 4 - 5 beetles per plant. Presently it is not known precisely which mechanism controls the bud creation rate, but based on the results in fig. 6, the size of the plant is an important factor. If the correlation between plant size and bud setting is a general trend, it will be possible to calculate a damage thresholds that might differ considerably from year to year based on plant size after winter.

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**Figure 9.** The mechanisms of compensation in the simulations. (a) The number of pods per plant during the summer 1991, (b) The average dry weight of stem, (c) The average dry weight of pods at harvest.

## Literature

- Allen, E.J. and Morgan, D.G. 1972. A quantitative analysis of the effects of nitrogen on the growth, development and yield of oilseed rape. *J. agric. Sci., Camb.* 78, 315 - 324.
- Andersson, K. 1988. Möjligheter att minska den kemiska bekämpningen i oljeväxtodlingen. *Sveriges utsädesforenings tidsskrift.* 98 (3): 125 - 136.
- Axelsen, J. 1992. The population dynamics and mortalities of the pod gall midge (*Dasyneura brassicae* Winn.) (Dipt., Cecidomyiidae) in winter rape and spring rape (*Brassicae napus* L.) in Denmark. *J. appl. Ent.* 114, 463-471.
- Axelsen, J. 1993a. Analysis of the population dynamics of the pod gall midge (*Dasyneura brassicae* Winn) in winter rape and spring rape by computer simulation. *Ecological modelling*, 69, 43 - 55.
- Axelsen, J. 1993b. The damage caused by single specimens of the pod weevil (*Ceutorrhynchus assimilis* Payk) and the pollen beetle (*Meligethes aeneus* F.). *IOBC/WPRS-Bulletin on Integrated Control in Oilseed Crops. Vol. 166(9).*
- Axelsen, J. & Nielsen, P. S. 1990. Compensation in spring sown oilseed rape after attack by pollen beetles (*Meligethes aeneus* F.). *Tidsskrift for Planteavl*, 94, 195 - 199.
- Boelcke, B. & Vietinghoff, J. 1987. Kompensationseffekte an Winterrapspflanzen nach Verlust generative Organe im Knospenstadium. In: 7. *International rapeseed congress, May 1987 i Poznan, Polen. Instytut Hodowli i Aklimatyzacji Roslin.* 3, 630 - 638.
- Graf, B.; Baumgaertner, J. and Gutierrez, A.P. 1990. Modelling agroecosystem dynamics with the metabolic pool approach. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 63, 465 - 476.
- Graham, C. W. 1982. Insect pests of oilseed rape. *Leaflet Ministry of Agriculture, Fisheries and Food, U.K. nr. 780.*
- Gutierrez, A.P.; Baumgaertner, J.U. and Summers, C.G. 1984. Multitrophic models of predator-prey energetics. *Can Ent.* 116, 923 - 963.
- Gutierrez, A. P.; Schulthess, F.; Wilson, L T.; Villacorta, A. M.; Ellis, C. K. and Baumgaertner, J. U. 1987. Energy acquisition and allocation in plants and insects: A hypothesis for the possible role of hormones in insect feeding patterns. *Can. Ent.* 119, 109 - 129.
- Gutierrez, A.P.; Wermelinger, B.; Schulthess, F., Baumgaertner, J.U.; Herren, H.R.; Ellis, C.K. and Yaninek, J.S. 1988. Analysis of biological control of cassava pests in Africa. I. Simulation of carbon, nitrogen and water dynamics in cassava. *J. appl. Ecol.*, 25, 901 - 920.
- Gutierrez, A.P.; dos Santos, W.J.; Villacorta, A.; Pizzamiglio, M.A.; Ellis, C.K.; Carvalho, L.H. and Stone N.D. 1991. Modelling the interaction of cotton and the cotton boll weevil. I. A comparison of growth and development of cotton varieties. *J. Appl. Ecol.* 28, 371 - 397.
- Gutierrez, A.P.; dos Santos, W.J.; Pizzamiglio, M.A.; Villacorta, A.; ; Ellis, C.K.; Fernandes, C.A.P. and Tutida, I. 1991. Modelling the interaction of cotton and the cotton boll weevil. II. Bollweevil (*Anthonomus grandis*) in Brazil. *J. Appl. Ecol.* 28, 398 - 418.
- Gyldenholm, A.O. 1968. Macromolecular physiology of plastids V. On the nucleic acid metabolism during chloroplast development. *Hereditas* 59, 142 - 168.
- Lerin, J. 1987. Compensation in winter rape following simulated pollen beetle damage. *IOBC/WPRS*

- Major, D.J.; Bole, J.B. and Charnetski, W.A. 1978. Distribution of photosynthates after  $^{14}\text{CO}_2$  assimilation by stems, leaves and pods of rape plants. *Can. J. Plant Sci.* 58, 783 - 787.
- Morrison, M.J.; McVetty, P.B.E. and Shaykewich, C.F. 1989. The determination and verification of a baseline temperature for the growth of westar summer rape. *Can. J. Plant Sci.* 69, 455 - 464.
- Nilsson, C. 1987. Yield losses in summer rape caused by pollen beetles (*Meligethes spp.*). *Swedish J. Agric. Res.* 17, 105 - 111.
- Nilsson, C. 1980. Rapsbaggans, *Meligethes aeneus* F. (Col.), inverkan på höstrapsens avkastning. Fältforsög 1969 - 1971. *Växtskyddsnotiser.* 44, 109 - 114.
- Ogunlela, V.B.; Kullmann, A. and Geisler, G. 1989. Leaf growth and chlorophyll content of oilseed rape (*Brassica napus* L.) as influenced by nitrogen supply. *J. Agronomy & Crop Science* 163, 73 - 89.
- Salisbury, F.B. and Ross, C.W., 1978. *Plant Physiology*. Wadsworth Publishing Company, Belmont California, 422 pp.
- Sylvén, E. 1949. Skidgallmyggen, *Dasyneura brassicae* Winn. *Växtskyddsanst. Medd* 54, 120pp.
- Tatchell, G. M. 1983. Compensation in spring sown oil-seed rape (*Brassica napus* L.) plants in response to injury to their flower buds and pods. *J. agric. Sci., Camb.* 101, 565 - 573.
- Viettinghoff, J. & Daebler, F. 1986. Neuere Gesichtspunkte bei der Handhabung des Bekämpungsrichtwertes für den Rapsglanzkäfer. *Nachrichtenblatt für den Pflanzenschutz in der DDR.* 40(3), 58 - 61.
- Williams, I. & Free, J. B. 1979. Compensation of oil seed rape (*Brassica napus* L.) plants after damage to their buds and pods. *J. agric. Sci., Camb.* 92, 53 - 59.
- Zhang, Q.Z.; Kulmann, A. and Geisler, G. 1991. Nitrogen transportation in oilseed rape (*Brassica napus* L.) plant during flowering and early siliqua developing. *J. Agronomy & Crop Science* 167, 229 - 235.
- Åhman, I. 1988. Wild and cultivated crucifers as hosts for *Dasyneura brassicae* Winn. (Dipt., Cecidomyiidae). *J. appl. Ent.* 105, 420 - 424.

## Appendix 1

Table of the input parameters used in the oilseed rape model.

### Developmental times ( $\square D$ )

Leaves (nitrogen controlled);	
Roots = 1157;	Morrison et al. 1989
Stem = 1157;	-
Flower = 35;	Fitting parametre
Pod = 600;	Morrison et al. 1989
Temperature threshold = 5 $\square C$	-

### Growth parameters

Bud creation rate(1991) = 2.7 ( $\text{plant}^{-1} \square D^{-1}$ )	Field data
Bud creation rate (1992) = 1.5 ( $\text{plant}^{-1} \square D^{-1}$ );	-
Max growth rate (all organs) = 0.025 ( $\text{g g}^{-1} \square D^{-1}$ )	-
Prime bud weight = 0.0004;	Fitting parameter
Prime pod weight = 0.003;	Fitting parameter
Prime leaf weight = 0.010;	Fitting parameter
Prime root weight = 0.022;	Fitting parameter
Prime stem weight = 0.05	Fitting parameter
Extinction = 0.34;	Field data
Dates of vernalisation: 3 Oct. 1990, 18 Oct. 1991	Fitting parameter
Delay between vernalisation and bud initiation = 105 $\square D$	Fitting parameter
Plant density = 74 $\text{m}^{-1}$ ;	Field data

### Factor (p) to convert from mass to surface area

$p_{\text{Leaves}} = 172 \text{ cm}^2/\text{g}$	Field data
$p_{\text{Stems}} = 53 \text{ cm}^2/\text{g}$	Field data

"Field data" means that the parameter estimation was based on the growth analysis described in this paper.