Apidologie, 1988, **19** (1), 51-72

RAPESEED (*BRASSICA NAPUS* L.) PRODUCTIVITY : THE EFFECT OF HONEYBEES (*APIS MELLIFERA* L.) AND DIFFERENT POLLINATION CONDITIONS IN CAGE AND FIELD TESTS

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SUMMARY

Effect of different pollination treatments on aspects of development and production of winter rapeseed were studied. Tests involved plants caged with honeybees, bumblebees (*Bombus terrestris*), flies (*Calliphora* spp.) or electric fans to discriminate between pollinating agents, and comparisons with cages only and uncaged field plots as controls. Measurements were made of branch and flower number, flower life, duration of flowering and levels of pod set and also certain yield components of winter rapeseed. An effect of insects on pollination reduced flower life and duration of flowering. In the absence of insects an overt pollination deficit was not apparent due to increased shoot, flower and pod production, and this prevented detection of statistically significant effects of honeybees or other conditions affecting pollination on seed production.

INTRODUCTION

It is known that honeybees (*Apis mellifera* L.) play an important role in pollination of some cultivated plants, notably allogamous species for which cross pollination is essential. Insect mediated cross pollination may be, only of secondary importance for oilseed rape (*Brassica napus* L. var *oleifera* Meztger) which is self fertile and mainly autogamous (70 %, SYLVEN, 1920 ; OLSSON, 1952 ; RIVES, 1957).

Nevertheless, oilseed rape flowers attract large numbers of honeybees which abundantly exploit their nectar and pollen for food, and for progeny. The consequence is that honeybee frequentation of rapeseed can then become constant and persistent.

While honeybees make up about 90 % of the effective insect pollinating fauna (Belozerova, 1960 ; Mesquida and Renard, 1979), several species of solitary bees (Andrenidae, Halictidae, Megachilidae and lower Apidae) and bumblebees (*Bombus* spp) are as efficient. Some Diptera (Syrphidae, Anthomyiidae, and Calliphoridae in particular), Lepidoptera (Pieridae), Hemiptera, and Coleoptera (*Meligethes* and *Ceuthorynchus*) (Belozerova, 1960 ; Radchenko, 1964 ; Benedek *et al.*, 1972 ; Williams, 1976 ; Pawlikowski, 1978 ; Mesquida and Renard, 1979 ; Eisikowitch, 1981 ; Banaszak, 1982 ; Langridge and Goodman, 1982) are less abundant, and less efficient. It should also be noted that several authors consider that wind may play an appreciable role in rapeseed pollination, shaking plants and carrying pollen between flowers (Nicolaisen, 1943 ; Olsson, 1955 ; Williams, 1978 ; Mesquida and Renard, 1982).

Bee pollination of oilseed rape has been studied by numerous workers who have demonstrated more or less appreciable effects, and sometimes drawn contradictory conclusions. While some consider that oilseed rape autogamy suffices for good yield, independently of entomophilous pollination, given non significant bee effects (Ewert, 1928 ; Nicolaisen, 1943 ; Becker, 1951 ; Harle, 1951 ; Personn, 1956 ; Free and Nuttall, 1968 ; Williams, 1976 ; Van Praagh *et al.*, 1979), others believe that entomophilous pollination is important for yield. (Ewert, 1929 ; Fujita, 1939 ; Zander, 1952 ; Jenkinson *et al.*, 1953 ; Vesely, 1962 ; Barbier, 1978 ; Kubisova *et al.*, 1980 ; Kamler, 1983 ; Williams, 1984).

It is unlikely that yield can be improved for oilseed rape currently cultivated in France, composed of « pure » lines, given the low level of cross fertilisation. (Morice and Renard, pers. comm.). Moreover, oilseed rape is relatively insensitive to inbreeding depression (Olsson, 1955 ; Rives, 1957).

The aim of work described here, undertaken at Rennes (France), is to assess the « bee-effect » on oilseed rape pollination, and its consequences for plant development and yield. Results are presented for tests undertaken from 1982 to 1984 on a variety of oilseed rape currently grown in France.

MATERIALS AND METHODS

A. Plants

The winter rapeseed variety, Jet neuf, was used for all tests.

B. Tests

Tests were made in a complete block design, five treatments and four blocks, at the I.N.R.A. Experimental Station (Rennes, France).

Each test invariably involved three principal treatments, compared with two others to assess the effects of different conditions on pollination. Cages with honeybees were compared with cages without insects (main control), and field crop situation (second control). Other treatments were cages with electric fans and cages with fans and honeybees for 1982 tests. Cages with bumblebees and cages with electric fans were used for comparison in 1983. In 1984 cages with bumblebees and cages with flies were the alternative treatments.

Cages were 18 m^3 (3 m × 3 m × 2 m) covered with a 2 mm mesh plastic netting used in previous work (Mesquida and Renard, 1981 ; 1982). Each cage enclosed a 9 m^2 plot including eight 3 m rows of oilseed, with 0.3 m spacing. A mechanical drill was used, with 5 kg seed/ha (50 to 60 plants/m^2). Between plot distances were 3 m. Cages were present over the whole flowering period.

In the cages with honeybees complete colonies (workers + queen + brood) were held in 5 frame Dadant hives.

In cages without insects, pollination was effected by wind alone. Windspeed under cages was reduced by 90 % for an external windspeed of 2 750 m/hr, and by 60 % for 4 500 m/hr (Mesquida and Renard, 1982).

Founder *Bombus terrestris* females captured in the field, were used in the « cages-with-bumblebees », provided with artificial burrows (two founders females per cage).

Artificially bred *Calliphora* flies, hatched in an incubator (20 °C), were used in the cages with flies. Several hundred flies were regularly introduced once per week.

The electric fans used were horizontal Vent Axia ventilators used in insect suction traps by Johnson and Taylor (see Johnson, 1950) with the following specifications : diameter 23 cm, speed 8 m/sec, suction rate 176 1/sec, motor 220 V-1 200 W. Four fans were placed vertically, in each cage, at 1.8 m, spaced at 0.60 m. The vertical ventilation of the oilseed flowers was designed to ensure permanent agitation. This affected plants within a circular area of nearly 2 m diameter in the centre of the plot. These were the plants sampled after marking.

In the field plots wind and local insect fauna were responsible for pollination.

C. Observations

1. Activity and behaviour of foragers

Numbers of pollinators and nectar foragers with and without pollen were recorded on a 3.0 × 0.5 m area for three minutes, on one day.

2. Influence of pollination

a) On production of secondary and tertiary branches (1982 test) : number of « stage E » branches, at least 1 cm as specified by C.E.T.I.O.M. (*), I.N.R.A. and P.V. (**), prior to flowering, and stage G 4 branches with at least one flower after flowering for 20 plants/plot.

(*) CETIOM : Centre technique Interprofessionnel des Oléagineux Métropolitains.

(**) PV : Protection des Végétaux.

b) On flower life (1984 test) : 20 flowers from 20 plants per plot, from opening of the flower to petal fall (stage 5 and 13 respectively, Peniaud, 1984).

c) On total duration of flowering : density and number of open flowers per branch over a circular area (50 cm diam), per week, throughout the flowering period.

d) On flower production : total flowers produced per whole plant (1982 test) and per main branch (tests 1982, 1983, 1984), for 20 plants/plot.

e) On pod set, ((number of pods/total flowers) × 100) : pod set/whole plant (1982 test) and/main branch (tests 1982, 1983, 1984) ; level of pod set/sector (25 flowers/sector) from 20 plants/plot (1984 test).

f) On yield components : number of seeds/pod (four samples of 50 pods) ; weight of 1000 seeds (four samples of 300 seeds per plot from the total harvest) and total yield per plot.

D. Data analyses

Means are given with standard errors ($\bar{x} \pm s/\sqrt{n}$). Analyses applied were :

- after a Bliss angular transformation of percentages, a two way analysis of variance followed by a Duncan's multiple range test was performed for each variable ; a posteriori analysis of residuals were not undertaken because of the small number of measurements (20 per variable) ;
- discriminant analysis for treatments, taking account of several variables : number of flowers, number of pods, level of pod set, number of seeds per pod, weight of 1000 seeds and yield, to assess effects of different pollination conditions.

ANVARM and ROUV program of « AMANCE » Software Package (Bachacou *et al.*, 1981) were applied for these two analysis.

RESULTS

1. Bee behaviour

Honeybee activity was always satisfactory in cages throughout the oilseed rape flowering period during days when climatic conditions were favourable for foraging. It could be twice to seven times that recorded outside cages, according to time of day. Figure 1.1 shows that this activity was generally greater between 14 h and 16 h (the hottest period) than in the morning (9 h to 12 h). However, honeybees collected significantly more pollen in the morning than in the afternoon (mean percent pollen gatherers 47.7 (± 8.8) to 53.5 (± 9.0) in the morning compared with 19.3 (± 2.4) to 27.0 (± 3.6) in the afternoon, for honeybees in cages. For honeybees in field plots (outside cages) corresponding levels were 9.5 (± 2.4) to 12.0 (± 2.6) compared with 3.8 (± 0.6) to 8.3 (± 2.5), the differences being non-significant.

During full flowering there were large numbers of bee foragers in the cages and intense overexploitation of flowers. With a maximum of 180 honeybees (or 20/m^2, range 7 to 43) foraging simultaneously at a rate of 12 flowers visited/min (range 10 to 16) and a total of 3 645 flowers, the estimated rate of visits/flower/hr is 36.

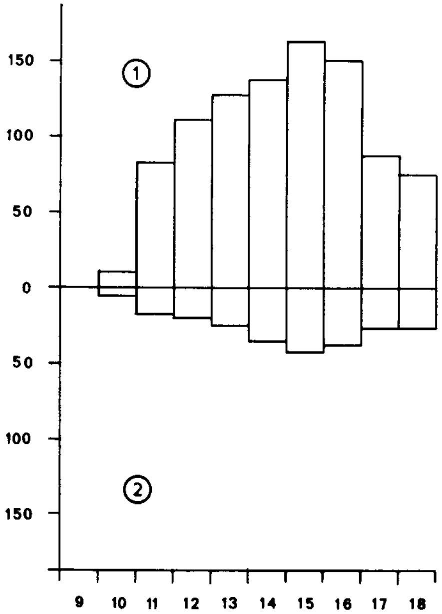

FIG. 1. — *Daily behaviour of honeybees in cages and field plots over rapeseed flowers.*

(*abscissa* - Times of count (GMT + 2hr)
(1) Flowers under cages with honeybees
(2) Flowers in field plots
ordinate - number of bees/9 m^2 plot (3m × 3 m) of rapeseed).

Bumblebees were twice as active as honeybees (20 flowers/min, range 16 to 24), but less numerous in the cages (Fig. 2.1), 0.2-1.6/m^2.

Flower visiting rate was then only 0.4 visit/flower/hr, far lower than for honeybees.

In field crops bee density never exceeded 7/m^2, and visits/flower/hr was estimated at 6.5. Honeybee foraging intensity was therefore about six times greater in cages than in the field plots.

2. *Bee effects*

2.1. *On number of secondary and tertiary branches*

No significant effect of honeybees on number of secondary and tertiary branche production is apparent in Table 1. Nevertheless, some differences in means might reflect a potential effect. A lower production of tertiary branches (23 % in cages with honeybees and 17 % in field crops, as compared with 34 % in cages without honeybees), and of secondary branches (72 % in cages

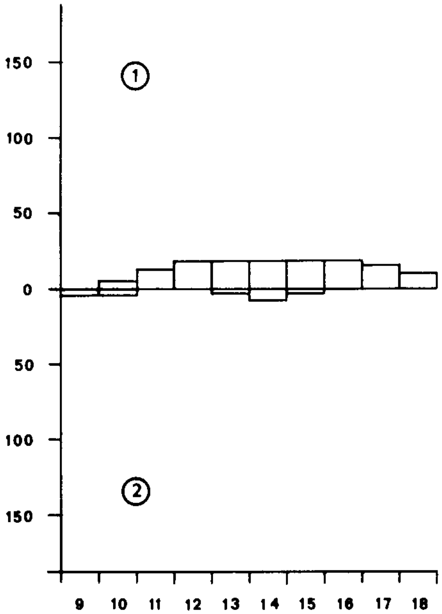

FIG. 2. — *Daily behaviour of bumblebees over rapeseed flowers in cages and in field plots.* Legend : see figure 1.

TABL. 1. — *Effect of honeybees and other pollination factors on mean number of secondary and tertiary branches.*

		Number of branches				
		NB/1	NB/2	NB/3	NB/3 – NB/2 / NB/2	NB/2 / NB/1
1982	+ B	7.75 (± 0.22)	5.58 (± 0.33)	6.85 (± 0.79)	23 %	72 %
	– B	7.95 (± 0.47)	6.33 (± 0.29)	8.50 (± 0.99)	34 %	80 %
	+ EF	7.70 (± 0.34)	5.28 (± 0.43)	6.58 (± 0.88)	25 %	69 %
	+ EF + B	7.90 (± 0.34)	6.03 (± 0.45)	7.78 (± 0.81)	29 %	76 %
	FP	7.68 (± 0.35)	5.15 (± 0.21)	6.05 (± 0.09)	17 %	67 %
Between treatments		NS	NS	NS		
Between blocks		NS	NS	NS		

Means ($\pm s/\sqrt{n}$)
NB/1 Number of secondary branches prior to flowering
NB/2 Number of secondary branches after flowering
NB/3 Number of secondary and tertiary branches after flowering
+ B Cages with honeybees
– B Cages without honeybees (control n° 1)
+ EF Cages with electric fans
+ EF + B Cages with electric fans + bees

FP Fields plots (control n° 2)
+ BB Cages with bumblebees
+ F Cages with flies
NS Non significant differences
S* Differences significant at 5 %
S** Differences significant at 1 %
S*** Differences significant at 1 ‰
Means marked by same letter do not differ significantly

with honeybees and 67 % in field crops as compared with 80 % in cages without insects) is suggestive in this respect. Plants in cages with electric fans had intermediate branch production, 25 % to 29 % for tertiary branches, and 69 % to 76 % for secondary branches.

2.2. *On length of flower life and flowering cycle*

There was a highly significant honeybee effect on length of flower life (Table 2), 3.2 (± 0.3) days for insect-pollinated plants in cages with honeybees, and 5.6 (± 0.2) days for non-insect pollinated plants in cages without insects.

TABL. 2. — *Mean flower life relative to different pollination conditions.*

	Flower life (days)
+ B	3.21 (± 0.25) (A)
− B	5.63 (± 0.23) (B)
+ BB	5.13 (± 0.15) (B)
+ F	5.21 (± 0.13) (B)
FP	4.44 (± 0.09) (C)
Between treatments	S***
Between blocks	NS

Legend : see table 1.

In field plots, flower life was intermediate, while it did not differ appreciably between plants in cages with flies or bumblebees and cages without insects. Short flower life in cages with honeybees may be attributed to overexploitation.

Total duration of flowering cycle was slightly shorter, and total production of flowers slightly lower for plants in cages with honeybees as compared with cages without insects but no differences were significant (Table 3, 1983 test).

2.3. *On levels of pod set*

Tables 4 and 5 show that levels of pod set varied according to whether whole plants, the whole main shoot, or sectors of the main branch are considered.

TABL. 3. — *Effect of honeybees and other pollination factors on mean number of flowers on main branches and whole plants.*

		Number of flowers	
		Main branches	Whole plants
1982	+ B	88.0 (± 4.31)	349.0 (± 44.1)
	− B	91.3 (± 1.34)	429.0 (± 45.0)
	+ EF	84.4 (± 2.22)	330.9 (± 34.3)
	+ EF + B	86.0 (± 2.17)	367.2 (± 38.4)
	FP	81.0 (± 0.84)	319.3 (± 22.9)
	Between treatments	NS	NS
	Between blocks	NS	NS
1983	+ B	85.3 (± 2.37)	
	− B	84.6 (± 1.51)	
	+ BB	87.2 (± 0.96)	
	+ EF	86.5 (± 1.72)	
	FP	85.3 (± 3.44)	
	Between treatments	NS	
	Between blocks	S*	
1984	+ B	73.3 (± 1.18)	
	− B	74.8 (± 0.94)	
	+ BB	73.1 (± 1.54)	
	+ F	70.8 (± 2.09)	
	FP	76.3 (± 0.53)	
	Between treatments	NS	
	Between blocks	NS	

Legend : see table 1.

For the first two cases (Table 4), there was an appreciable decrease for insect-pollinated plants in cages with honeybees, significant in two tests (1982 and 1984). Under other conditions of pollination, results were comparable to those obtained in cages with honeybees.

For the third case (Table 5) comparisons between sections of main branch bearing equal numbers of flowers, provide a better indication of a bee effect as a function of flowering rhythm. Mean pod set levels for the first section (first 25 flowers) were close to 100 % and significantly higher for insect-pollinated plants in cages with honeybees (+ 11 %) compared with cages without insects, with bumblebees, and with flies, and in field plots. For the second sections the trend is already less pronounced, but when first and second sections are combined (i.e., the first 50 flowers), entomophilous pollination in cages with bees still shows a 4 % lead.

TABL. 4. — *Effect of honeybees and different pollination treatments on mean levels of main branches and whole plants pod set.*

		Pod set (*)	
		Main branches	Whole plants
1982	+ B	81.1 (± 1.94) (A)	61.3 (± 0.62) (A)
	− B	91.2 (± 1.24) (B)	73,5 (± 2.74) (B)
	+ EF	79.1 (± 1.84) (A)	66.5 (± 4.16) (A)
	+ EF + B	78.4 (± 2.67) (A)	64.4 (± 3.15) (A)
	FP	83.9 (± 3.61) (A)	64.9 (± 3.40) (A)
	Between treatments	S**	S**
	Between blocks	NS	S**
1983	+ B	83.1 (± 1.53)	
	− B	86.1 (± 0.58)	
	+ BB	86.1 (± 1.57)	
	+ EF	80.6 (± 3.32)	
	FP	82.3 (± 0.86)	
	Between treatments	NS	
	Between blocks	NS	
1984	+ B	82.0 (± 0.97) (A)	
	− B	87.5 (± 0.78) (B − C)	
	+ BB	89.5 (± 1.19) (D)	
	+ F	85.8 (± 0.82) (B − C)	
	FP	85.2 (± 0.92) (B)	
	Between treatments	S***	
	Between blocks	NS	

Legend : see table 1.

TABL. 5. — *Effect of honeybees and different pollination conditions on mean levels of main branches pod set according to sector.*

		Pod set (%)		
		1	2	3
1984	+ B	97.8 (± 1.55) (A)	94.3 (± 2.29)	48.2 (± 3.07) (A)
	− B	88.3 (± 2.75) (B)	96.6 (± 0.83)	72.1 (± 2.11) (C)
	+ BB	96.1 (± 0.25) (A)	97.1 (± 0.45)	72.7 (± 4.02) (C)
	+ F	94.4 (± 1.36) (A)	92.4 (± 2.49)	66.6 (± 1.86) (BC)
	FP	98.2 (± 1.32) (A)	98.2 (± 0.36)	58.7 (± 3.50) (B)
	Between treatments	S**	NS	S***
	Between blocks	NS	NS	NS

1. ist sector, ist to 25th flower on main branch.
2. 2nd sector, 26th to 50th flower on main branch.
3. 3nd sector, 51th to 75th flower on main branch.

Legend : see table 1.

A distinct and significant advantage to cages without insects (33 % higher pod set) is apparent when the third section is considered.

2.4. *On some yield components*

There were no significant differences for yield criteria studied (number of seeds/pod, weight of 1 000 seeds, yield - Table 6) between insect-pollinated plants in cages with honeybees and non-insect pollinated plants in cages without insects.

Some differences in means might however be related to entomophilous pollination as, for example, an increase in number of seeds/pod (+ 9 % to 24 %).

TABL. 6. — *Influence of honeybees and other pollination factors on mean seed number per pod, 1 000 seeds weight and production of whole plants.*

		Yield components			
		NSP	W	Y	Y'
1982	+ B			2.750 (± 0.171)	
	− B			2.690 (± 0.117)	
	+ EF			2.482 (± 0.101)	
	+ EF + B			2.436 (± 0.111)	
	FP			—	
	Between treatments			NS	
	Between blocks			NS	
1983	+ B	16.30 (± 0.69) (B)	5.38 (± 0.11)	2.311 (± 0.244)	66.86 (± 1.58)
	− B	16.08 (± 0.56) (B)	5.15 (± 0.09)	2.262 (± 0.197)	49.99 (± 3.88)
	+ BB	14.56 (± 0.58) (A)	5.34 (± 0.11)	2.411 (± 0.102)	65.37 (± 4.89)
	+ EF	14.77 (± 0.64) (A)	5.46 (± 0.28)	2.303 (± 0.287)	55.70 (± 9.47)
	FP	18.21 (± 0.59) (C)	5.21 (± 0.27)	2.910 (± 0.169)	65.68 (± 3.22)
	Between treatments	S**	NS	NS	NS
	Between blocks	NS	NS	NS	NS
1984	+ B	14.95 (± 1.73)	5.55 (± 0.14)	2.886 (± 0.113) (A)	67.86 (± 7.75)
	− B	12.03 (± 1.69)	5.55 (± 0.18)	3.072 (± 0.112) (A)	58.52 (± 9.19)
	+ BB	16.31 (± 1.05)	5.54 (± 0.21)	2.856 (± 0.071) (A)	81.00 (± 6.96)
	+ F	13.51 (± 1.36)	5.46 (± 0.11)	2.944 (± 0.080) (A)	63.26 (± 6.51)
	FP	15.59 (± 0.69)	5.29 (± 0.25)	3.811 (± 0.182) (B)	70.16 (± 4.39)
	Between treatments	NS	NS	S***	NS
	Between blocks	NS	NS	NS	NS

NSP - Number of seeds/pod
W - 1 000 seeds weight (g)
Y - Yield (Tonnes/ha)
Y' - Yield/1 000 flowers (g)

Yields calculated for equal flower number, as a function of pod set, number of seeds/pod, and weight of seeds (Table 6, Y') could be higher in cages with honeybees (16 to 34 % more) relative to cages without insects, as for field crops, but differences were still not significant.

Differences in means, which need not necessarily have been related to presence of bumblebees or flies, and their effects on pollination were also noted. Yields could be greater than for non-insect pollinated plants (6 % for bumblebees) or lower (4 % to 7 % for plants with flies and bumblebees together). Pods could have more seeds (12 to 36 % with flies and bumblebees) or fewer (9 % with bumblebees alone), and seeds could be large or small.

The same differences in means were found for cages with fans as for cages with honeybees.

In field plots pods had more seeds, and while these were smaller, yields were distinctly higher.

A higher real yield of field plots compared with cages with honeybees and without insects (+ 30 %) indicates an appreciable cage effect.

No between cage effect could be demonstrated for the honeybee effect on yield, a result confirmed by factorial analysis.

Discriminant analysis

a) Factor 1 (Fig. 3) was well correlated with the indicator variables of the design (canonical correlation coefficient $P^2 = 0.85$). Bartlett's χ^2 applied to this was significant ($P^2 = 0.05$). Variables associated by this factor were principally yield and number of seeds/pod. Factor 2 was not significant, and only weakly correlated with the indicator variables of the design ($P^2 = 0.52$). However, three groups of results could be relatively well distinguished in the plan formed by the first two factors :

— the first group, on the right of the positive side, is composed of field plots (5, Fig. 3), for which there was higher yield, and significantly higher seed number/pod. (Table 6, 1983 trial) ;

— the second group, bottom centre, results from overlay of treatments, cages with honeybees, cages with fans and cages with bumblebees. (1, 4 and 3, Fig. 3) ;

— the third group, only slightly distant from the second, is the treatment cages without insects.

b) In figure 4, and as opposed to the previous presentation, the two first discriminant factors are strongly and significantly correlated ($P^2 = 0.92$ and 0.87). The third factor is not. Variables associated with the first factor are

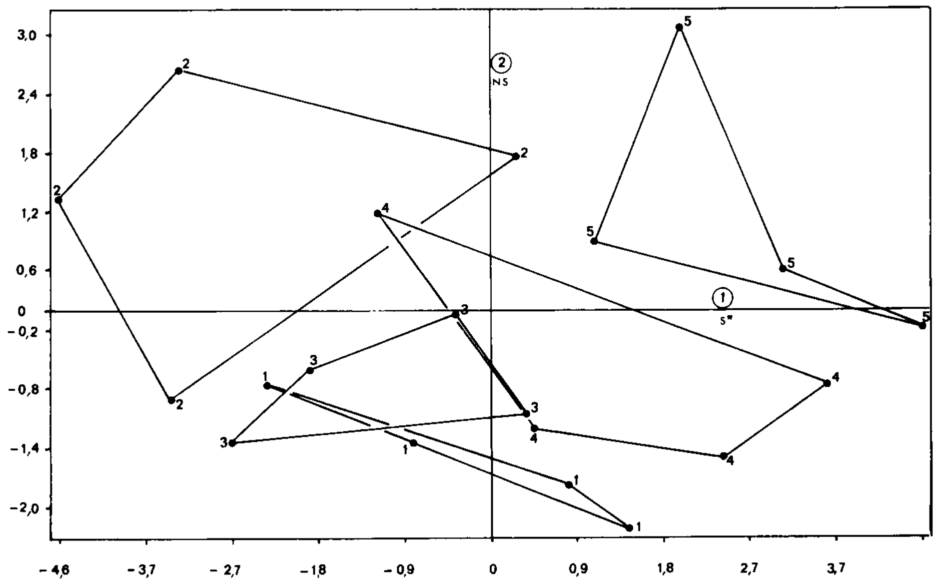

FIG. 3. — *Discriminant analysis of effect of honeybees and other pollination conditions on rapeseed production.* Projection for components of factor 1 and 2 (1983 trial).

Abscissa : (1) - Components of factor 1.
Ordinate : (2) - Components of factor 2.

1 - Cages with honeybees.
2 - Cages without honeybees.
3 - Cages with bumblebees.
4 - Cages with electric fans.
5 - Field plots.
NS Chi square (BARTLETT) non significant components of factor 2.
S* Chi square (BARTLETT) significant at 5 % components of factor 1.

again yield and number of seeds/pod. For factor 2, dominant variables are this time pod set and number of pods.

Taken as a whole Figure 4 reveals three groups significantly separated :

— the group in the right half of the positive side of the plane is made up of the field plots (5, Fig. 4) distinguished in the projection on factor 1 ;

— the group in the upper part on the negative side is made up of cages without insects, cages with flies and cages with bumblebees (2, 4 and 3, Fig. 4) which overlap in the projection on factor 1 relative to field plots (5, Fig. 4) and on factor 2 relative to cages with honeybees (1, fig. 4) ;

— a group of cages with honeybees (1, Fig. 4) distinguishable relative to the first group in projection on factor 1, and to the two first groups in projection on factor 2.

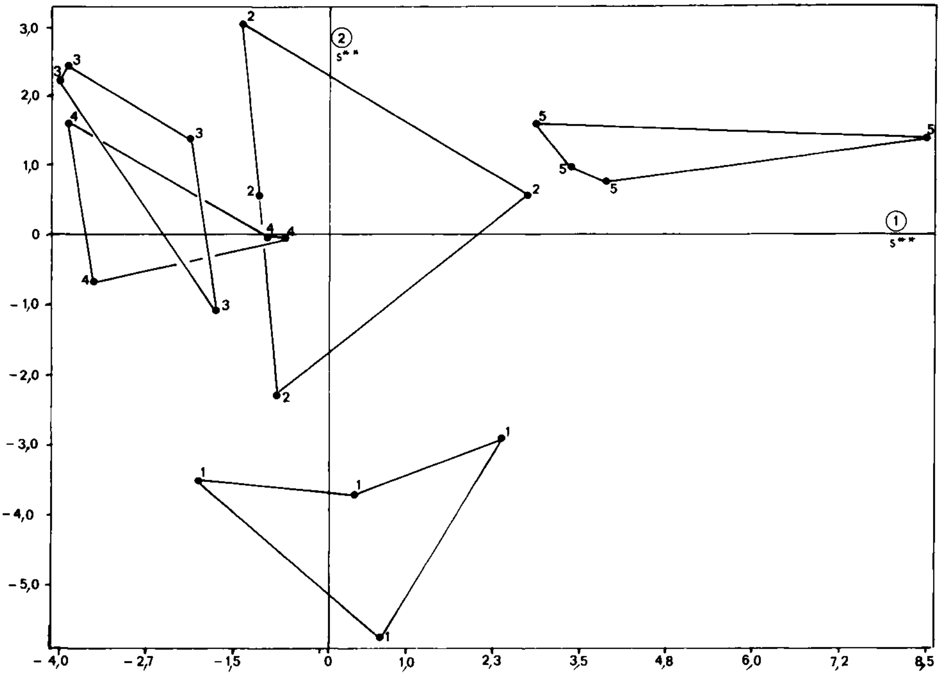

FIG. 4. — *Discriminant analysis of effects of honeybees and different pollination conditions on rapeseed productivity.* Projection components of factors 1 and 2 (1984 trial).

Abscissa : (1) - Components of factor 1.
Ordinate : (2) - Components of factor 2.

1 - Cages with honeybees.
2 - Cages without honeybees.
3 - Cages with bumblebees.
4 - Cages with flies.
5 - Field plots.
S** Chi square (BARTLETT) significant at 1 % (factors 1 and 2).

Table 6 shows that yield in field plots for the 1984 test was significantly highest. The separation between cages with honeybees and cages without insects was partly due to a highly significant difference in pod set levels (Table 4, 1984 test), the dominant variable for factor 2.

It must be noted that there were fairly strong correlations between pod set and number of pods ($r = 0.74^{**}$), number of pods and number of flowers ($r = 0.78^{**}$) and number of pods and yield ($r = 0.70^{*}$). These results demonstrate the interest of factorial discrimination analysis in extracting meaningful relationships and interactions between several variables.

The separation of field plots from other treatments under cages in the factorial designs (Fig. 3 and 4) confirms the existence of a cage effect already evoked. However a honeybee effect on yield improvement is not apparent. It is possible that the absence of evidence for this may result from insufficient experimental plan, and that such an effect could be revealed if the number of blocks were to be increased.

DISCUSSION

It is interesting to note that honeybee activity in cages was very high, and that flowers visited early (at anthesis) were intensively exploited. However, the results showing an effect of honeybees on pollination of oilseed rape permit the following remarks.

a) The phenomena or rather the trends observed, which were suggestive of a honeybee effect, appeared in a decrease in number of branches, lower flower production, and shorter flower life and flowering period (agreeing with numerous other authors : Ewert, 1929 ; Zander, 1952 ; Vesely, 1962 ; Barbier, 1978 ; Mesquida and Renard, 1981 ; Lerin, 1982 ; Williams, 1984).

The influence of honeybees on oilseed rape flowering may be explained by the fact that flowers are visited early in their development, when the corolla is tubiform and the petals are unfolding, revealing a small opening above the stigma (stage 5, Peniaud, 1984). Such early visiting is immediately followed by deposition of abundant pollen on the receptive stigmas (oilseed rape is protogynous). If this pollen was obtained at dehiscence of anthers on another flower, it has greater germinating potential than that from older flowers (Mesquida *et al.*, 1987). Consequently flowers pollinated in this way wither more quickly. Flower life is then strongly reduced, flowering is shorter, and is more uniform and coordinated than for plants that are not insect pollinated.

The results of this study underline the significance of honeybees for oilseed rape in terms of total branch production, duration of flowering, and flower life. Moreover, bumblebees, flies and even electric fans have effects analogous to those of honeybees.

Wind pollination in cages (i.e., fans + wind) does not appear to differ appreciably in effect from that of insects + wind. Fans therefore compensate to some extent from attenuation of wind speed by cage plastic covering. However, conditions in cages are undoubtedly very far removed from those in field crops, for which wind and insects together contribute more efficiently to pollination, and where there is no cage effect.

b) The effects of insect pollination in terms of oilseed rape production (level of pod set, number of seeds/pod, weight of 1 000 seeds and yield), vary to a greater or lesser extent, depending on whether they are measured for parts of plants, or plants as a whole. This source of difference accounts for differences in conclusions we have drawn using the same or different methods in other work.

LERIN (1982) has already shown an effect of entomophilous pollination on pod production and pod set of main branches for bumblebees, and for honeybees as did BARBIER (1978). However, the effects of insect pollination are more apparent over the first 50 flowers on main branches. This may be accounted for by a compensatory effect. When flowers at the branch base (i.e., the first 25) at least are insect pollinated, their life is short (particularly when honeybees are concerned) because they are visited early. They therefore develop to seed more rapidly. Pod production then proceeding more rapidly on this part of the branch, flowers further up, notably at branch tips, will be subject to physiological abortion. EWERT (1929) had already noted earlier pod formation with insect pollination, and, following LERIN (1982), it can be added that maturation is quicker and more uniform.

Other authors have reported that pods are longer and contain more seeds (EWERT, 1929 ; MEYERHOFF, 1954 ; KOUTENSKY, 1959 ; FORSTER *et al.*, 1973 ; BARBIER, 1978). However, for MEYERHOFF (1954) pods were larger, while they were smaller and more uniform for MEYERHOFF (1958) ; RADCHENKO (1964) ; FREE & NUTTALL (1968) ; BENEDEK *et al.* (1972) ; KUBISOVA *et al.* (1980). Our tests confirm that insect pollinated plants have pods with more seeds, but these are not evidently smaller.

Higher yields have been obtained in tests using cages with and without honeybees for pollinated plants (FUJITA, 1939 ; ZANDER, 1952 ; JENKINSON *et al.*, 1953). However, most of these studies did not use replications, and sometimes concerned old varieties of which some may have been subject to self-incompatibility. BARBIER (1978) obtained yield increases of 36 % to 62 % on main branches of bee pollinated plants, using cages similar to those of the present study, and in tests without replication. It seems that effects of insect pollination on yield may be differently appreciated, according to whether the main branch or the whole plant is considered. LERIN (1982) found that it was precisely on main branches that insect pollination had the greatest effect, because of lesser variation as compared with whole plants, whence more significant differences when means were compared. The increase in number of pods and number of seeds/pod is then translated into a very significant increase in yield for this part of the plant (LERIN, 1982), a finding which can be related to that of BARBIER (1978).

Nevertheless, given the relative importance of secondary branches (80.8 % in non insect-pollinated plants, 71.6 % in insect-pollinated plants), results for whole plants reflect secondary branch production rather than that of primary branch, when competition is not involved (LERIN, 1982). Consequently, any pollination effect attributable to honeybees would have been masked by secondary branch contribution to yield in Lerin's study, in which differences between the two treatments were not significant.

In another context, appreciable, and sometimes considerable differences in yields that have been attributed to a honeybee effect, may be accounted for because they compare field crop yield with that of plants in cages without insects, without considering a cage effect (KAESER *et al.*, 1978 ; WOZNICA, 1979 ; KUBISOVA *et al.*, 1980 ; KAMLER, 1983 ; other references WILLIAMS, 1985).

This study has shown that field crop plots in which wind and insects together ensure good pollination, stand out sharply from other treatments. Confinement under cages without insects, preventing insect exploitation, and limiting wind effects, inevitably results in low pollination levels, to which a cage effect may contribute as well. The latter may, however, induce some compensatory effect which in fact improves productivity.

KOUTENSKY (1959), found that a 65 % yield increase in oilseed rape (*Brassica napus* var. *arvensis*) when hives were placed in a plot was the same (under the same experimental conditions) as for white mustard. This appears to be normal for the latter, given its self incompatibility and its dependence on pollinating agents for cross fertilisation. The result is less easily understood for oilseed rape, unless the variety used also displayed self incompatibility similar to that of mustard, or the author's method of yield measurement was a factor liable to obscure differences.

In conclusion the present study shows that under optimal pollination conditions flower life and total duration of flowering are shorter, but that in the face of a pollination deficit (absence of insects, shelter effect under cages) a compensatory effect involving increased shoot, flower and pod production obscures any significant effects of insects. While the existence of the latter cannot be excluded, our study could not demonstrate this conclusively.

Received for publication in July 1987.
Accepted for publication in October 1987.

RÉSUMÉ

IMPORTANCE DE L'EFFET ABEILLE (*APIS MELLIFICA* L.) ET DE DIFFÉRENTES CONDITIONS DE POLLINISATION DANS DES ESSAIS DE CAGES ET DE PLEIN CHAMP SUR LA PRODUCTIVITÉ DU COLZA OLÉAGINEUX (*BRASSICA NAPUS* L.)

Les fleurs de colza (*Brassica napus* L.) sont très attractives et très visitées principalement par les abeilles domestiques (*Apis mellifica* L.), pour le pollen et le nectar qu'elles prélèvent en abondance.

Cependant, le colza est une plante partiellement autogame pour laquelle environ 70 % de la fécondation est assurée par autofécondation. La pollinisation croisée chez cette plante n'est d'ailleurs pas forcément obligatoire et il est peu probable qu'elle ait un effet significatif sur les rendements, le matériel actuellement cultivé en France étant principalement composé de lignées « pures ».

Cependant, il existe de nombreux travaux faisant état d'effets plus ou moins bien marqués et souvent contradictoires de la pollinisation par les abeilles sur sa production grainière.

C'est en raison de ces divergences d'opinion que, dans des essais de cages et de plein champ, les auteurs ont étudié les effets de différentes conditions de pollinisation (« cages avec abeilles », « cages avec bourdons », « cages avec mouches », « cages avec ventilateurs électriques ») sur le développement de la plante (nombre de ramifications, nombre de fleurs, durée de vie des fleurs, durée de floraison et taux de nouaison) et sur l'élaboration de quelques composantes du rendement.

Les essais ont été effectués à Rennes (Bretagne) sur du colza d'hiver (var. « Jet-neuf ») pendant 3 années consécutives (1982, 1983 et 1984).

Ont été utilisées, des cages (3 × 3 × 2 m) recouvertes d'une toile plastique à mailles de 2 mm. Chaque cage recouvrait une parcelle de 9 m^2 de colza (8 lignes de 3 m de long, interlignes de 0,30 m, densité de 50 à 60 pieds/m^2).

Chaque essai comportait 5 traitements et 4 blocs. Les traitements étaient chaque année invariablement constitués de « cages avec abeilles » *(Apis mellifica)*, de deux témoins : « cages sans insectes » et « extérieur sans cages » et de deux autres traitements : « cages avec ventilateurs électriques » et « cages avec ventilateurs électriques + abeilles » (essai 1982), « cages avec bourdons » *(Bombus terrestris)* et « cages avec ventilateurs électriques » (essai 1983), « cages avec mouches » *(Calliphora)* et « cages avec bourdons » (essai 1984). Dans les « cages sans insectes », la pollinisation était assurée par le vent et, en extérieur, elle était assurée par le vent et les insectes pollinisateurs locaux.

L'influence de la pollinisation a été étudiée sur des critères phénologiques (ramifications, floraisons, siliques) et sur certaines composantes du rendement (nombre de graines par silique, poids de 1 000 grains et rendement parcellaire).

A l'intérieur des cages, le comportement des pollinisateurs a toujours été satisfaisant pendant toute la période de floraison du colza (Fig. 1 et 2).

Dans ces cages, en présence notamment d'abeilles et par rapport aux « cages sans insectes », on a constaté que :

— les plantes ont tendance à produire un peu moins de ramifications secondaires et surtout tertiaires entre le début et la fin de la floraison ; les fleurs ont une durée de vie plus courte (de l'ordre de 2,5 jours en moins) ; la floraison est réduite et les taux de nouaison de la plante entière sont plus faibles, mais ils sont significativement plus élevés sur les premiers secteurs des inflorescences de la tige principale (Tabl. 1 à 5) ;

— les siliques renferment plus de graines qui sont plus grosses ou de même taille, les rendements sont plus élevés, mais, les différences sont non significatives du point de vue statistique (Tabl. 6).

En extérieur, les siliques renferment plus de graines, elles sont généralement plus petites et les rendements sont nettement supérieurs à ceux des « cages sans abeilles » ou « avec abeilles ». Mais ces différences parfois hautement significatives par rapport aux cages s'expliquent par l'existence d'un « effet cage » important (Tabl. 6).

L'effet abeille, en cages, sur le rendement n'a donc pas été mis en évidence. Ce résultat est d'ailleurs confirmé par l'analyse factorielle discriminante (Fig. 3 et 4).

Ainsi, les phénomènes qui affectent plus particulièrement certaines parties de la plante et qui semblent liés aux effets du butinage par les abeilles (diminution de la production des ramifications, du nombre de fleurs, de la durée totale de la floraison et de la vie des fleurs) sont confirmés.

On peut ainsi considérer que l'effet abeille sur le colza se traduit par une floraison et une maturation des siliques plus homogènes. Mais en ce qui concerne la productivité du colza, les effets de la pollinisation se présentent différemment selon qu'on les considère partiellement sur une partie de la plante seulement (inflorescence de la tige principale, par exemple) ou globalement (plante entière).

Sur l'inflorescence de la tige principale, l'effet positif de la pollinisation entomophile a déjà été démontré par LERIN (1982) et BARBIER (1978). Mais cette partie de la plante surestime le phénomène et ne traduit pas l'effet réel de la pollinisation sur le rendement. L'effet abeille est masqué généralement par des phénomènes de compensation liés à d'autres facteurs (milieu principalement). LERIN (1982) a aussi montré que la production totale de la plante s'apparente davantage à celle des ramifications secondaires qu'à celle des inflorescences de la tige principale et les ramifications secondaires, plus nombreuses chez les plantes non pollinisées par les insectes, influent sur le rendement global. C'est pourquoi, si les différences apparaissent significatives au niveau des inflorescences des tiges principales, elles ne le sont plus au niveau de la plante entière.

Par ailleurs, signalons que les résultats divergents rapportés par de nombreux auteurs et attribués à l'effet pollinisation par les abeilles, proviennent des conditions expérimentales ; ils comparent, en effet, des rendements de plantes de plein champ à ceux obtenus sous « cages sans insectes » sans tenir compte des « effets cages » sur le développement végétatif et le rendement grainier. Ces effets, toujours très importants, difficiles à maîtriser, en raison surtout des différences climatiques (l'effet brise-vent, par exemple qui réduit considérablement la probabilité d'une autopollinisation anémophile par transport du pollen et agitation des plantes), rendent les comparaisons aléatoires. Les rendements de plein champ se discriminent inévitablement de ceux des cages.

En conclusion, si certains aspects positifs et non négligeables liés à la pollinisation entomophile sont confirmés, par contre, l'effet sur le rendement global du colza, du fait des phénomènes de compensation, n'est pas démontré dans nos conditions d'expérimentation.

En absence d'insectes, le déficit de pollinisation est donc compensé par une production plus importante de ramifications, de fleurs et de siliques qui s'oppose à la mise en évidence du bénéfice réel que la plante peut tirer de la visite des insectes pollinisateurs, les abeilles en particulier, pour l'amélioration significative de sa production grainière.

ZUSAMMENFASSUNG

DIE BEDEUTUNG DER HONIGBIENEN (*APIS MELLIFERA* L) UND VERSCHIEDENER BEDINGUNGEN DER BESTÄUBUNG AUF DEN ERTRAG VON ÖLRAPS (*BRASSICA NAPUS* L) BEI KÄFIG- UND FREILANDVERSUCHEN

Die Blüten des Rapses (*Brassica napus* L.) werden von Honigbienen stark besucht und sie liefern ihnen große Mengen Nektar und Pollen. Raps ist jedoch teilweise autogam und etwa 70 % des Samenansatzes erfolgt durch Selbstbefruchtung. Kreuzbestäubung ist bei dieser Pflanze nicht obligat und sie wirkt sich wahrscheinlich nicht auf den Ertrag aus, da die gegenwärtig in Frankreich kultivierten Sorten aus « reinen » Linien bestehen. Demgegenüber gibt es aber eine Anzahl von — oft widersprüchlichen — Arbeiten, in denen über einen deutlichen Einfluß der Bestäubung durch Bienen auf die Samenproduktion berichtet wird. Deshalb wurden von den Autoren Versuche in Käfigen und im Freiland unter verschiedenen Bedingungen durchgeführt (« Käfig mit Bienen », « Käfig mit Hummeln », « Käfig mit Fliegen », « Käfig mit elektrischem Ventilator »), um deren Einfluß auf die Entwicklung der Pflanzen (Zahl der Verzweigungen und Blüten, Lebensdauer der Einzelblüte und Gesamtblühdauer, Samenansatz) und auf verschiedene Ertragskomponenten zu untersuchen. Die Versuche wurden in Rennes (Bretagne) mit Winterraps (Sorte « Jet-neuf ») in drei aufeinanderfolgenden Jahren (1982-1984) durchgeführt.

Für die Versuche wurden Käfige (3 × 3 × 2 m) aus Kunststoffnetz mit einer Maschenweite von 2 mm benutzt. Jeder Käfig überdeckte eine Fläche von 9 m^2 Raps (8 Reihen von 3 m Länge mit 0,30 m Abstand, Saatdichte 50-60 Pflanzen/m^2). Jeder Versuch umfaßte 5 Ansätze in 4 Blöcken. Die Versuche bestanden jedes Jahr unverändert aus « Käfige mit Honigbienen », aus zwei Kontrollen « Käfige ohne

Insekten » und « Freiland ohne Käfige », und aus zwei anderen Ansätzen : « Käfige mit Ventilator » und « Käfige mit Ventilator und Bienen » (1982) ; « Käfige mit Hummeln » *(Bombus terrestris)* und « Käfige mit Ventilator » (1983) ; « Käfige mit Fliegen » *(Calliphora)* und « Käfige mit Hummeln » (1984). In den « Käfigen ohne Insekten » erfolgte die Bestäubung durch den Wind, im Freiland durch Wind und freifliegende Insekten.

Die Folgen der Bestäubung wurden mittels phänologischer Kriterien (Verzweigung, Bildung von Blüten und Schoten) und auf Grund von Ertragskomponenten (Körnerzahl pro Schote, 1 000 Korngewicht, Ertrag pro Parzelle) untersucht.

In den Käfigen war das Verhalten der Bestäuber während der gesamten Rapsblüte durchaus zufriedenstellend (Abb. 1, 2). Besonders beim Vergleich der « Käfige mit Bienen » mit « Käfige ohne Insekten » ergaben sich folgende Beobachtungen :

— Die Pflanzen zeigten die Tendenz zwischen Beginn und Ende der Blüte etwas weniger Sekundärverzweigungen zu bilden ; die Öffnungszeit der Einzelblüte war um mindestens 2,5 Tage kürzer ; die Gesamtblühdauer ist verkürzt und der Samenansatz der ganzen Pflanze ist verringert, aber er ist am ersten Abschnitt des Hauptstammes signifikant erhöht (Tabelle 1 bis 5) ;

— Die Schoten enthalten mehr und meist größere Körner und der Ertrag ist höher, aber der Unterschied ist statistisch nicht gesichert (Tab. 6).

Im Freiland enthalten die Schoten mehr (aber kleinere) Körner und die Erträge sind deutlich höher, aber diese Unterschiede lassen sich durch den bedeutenden « Käfigeffekt » erklären (Tab. 6).

Ein Einfluß der Bienen im Käfig auf den Ertrag konnte demnach nicht nachgewiesen werden. Dieses Resultat wird auch durch Diskriminanzanalysen bestätigt (Fig. 3 und 4). Es wurden jedoch Einflüsse der Sammeltätigkeit der Bienen auf gewisse Teile der Pflanze nachgewiesen, wie Verringerung der Verzweigung, Anzahl der Blüten, Dauer der Gesamtblühzeit wie der Einzelblüte. Der Bieneneinfluß auf den Raps zeigt sich auch in einer einheitlicheren Blüte und Reifung der Schoten. Hinsichtlich des Ertrags kommt man in der Bewertung der Bestäubung aber zu unterschiedlichen Ergebnissen, je nachdem ob man nur die Blüten des Hauptstammes oder ob man die ganze Pflanze bewertet. Wie schon Lerin (1982) gezeigt hat, hängt der Gesamtertrag hauptsächlich von dem Samenansatz der Nebenzweige ab, selbst wenn deren Blüten nicht von Insekten bestäubt wurden. Durch deren stärkere Ausbildung bei Abwesenheit von Bienen wird der höhere Ertrag der Hauptrispe als Folge der Bestäubung überdeckt.

Die abweichenden Ergebnisse anderer Autoren über der Effekt der Rapsbestäubung durch Bienen läßt sich dadurch erklären, daß sie Pflanzen im Freiland mit Pflanzen im Käfig ohne Insekten verglichen und dabei den wichtigen « Käfig-Effekt » außer acht gelassen haben. Dieser sehr wichtige Effekt hängt stark von unkontrollierbaren meteorologischen Faktoren ab, wie z.B. die Stärke von Windbrisen, wichtig für die Selbstbestäubung. Die Bedingungen im Freiland und im Käfig sind zwangsläufig immer verschieden.

Unter unseren Versuchbedingungen konnten also gewisse Effekte der Bienenbestäubung bestätigt werden, die keineswegs vernachlässigt werden dürfen. Als Folge kompensatorischer Vorgänge (zusätzliche Produktion von Verzweigung, Blüten und Schoten) konnte jedoch ein Einfluß des Bienenbefluges auf den Gesamtertrag des Rapses nicht nachgewiesen werden.

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