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Introgression in *Brassica napus* for adaptation to the growing conditions in Bangladesh *

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Summary. Among the oleiferous *Brassicas, B. napus* has the highest seed and oil productivity. As it is a species adapted to the temperate regions, its spring type is either unable to flower or flowers too late in the short – day winter (rabi) season of the subtropics. *B. napus* (genome AACC) is an amphidiploid between *B. campestris* (AA) and *B. oleracea* (CC), and shares one genome with the other allotetraploids *B. juncea* (AABB) and *B. carinata* (BBCC). While *B. napus* lacks ecotypes adapted to the subtropics, the other four species are well represented in this climatic zone. Reciprocal crosses with or without one direct backcross to *B. napus* have been carried out with the intention of transfering short-day adaptability. The aim was to introgress the A genome of carefully selected early representatives of *B. campestris* and *B. juncea* with the corresponding genome in *B. napus*, and similary the C genome from *B. oleracea* and *B. carinata* with the analogous genome in *B. napus. B. campestris, B. juncea* and the clearly later species, *B. oleracea* var 'alboglabra' and *B. carinata,* seem to be almost equally effective in introgressing the appropriate earliness necessary for growth in Bangladesh. One backcross sligthly delayed segregation of early types. Convergent crosses did not result in the transgression of earliness, which was unexpected since the inheritance of flowering and maturity indicated a polygenic regulation. This result is partly explained by assuming dominant oligogenic control of the photoperiodic response. Introgression of earliness with the C genome doesn't seem to be necessarily related with the earliness of the donor species. Intergenomic interactions may be important. Interesting new lines were selected with high yield. Thus there is a good probability that Bangladesh will have a new oil crop. As these lines were observed to be early in Sweden as well, they could potentially push rapseed cultivation further north in temperate regions where the growing period is limited by short summers.

Key words: *Brassica napus* – Introgression – Adaptation to short day – Photo-insensitivity – Oligogenic control

Introduction

The oleiferous *Brassica*, an important source of vegetable fats, is mainly represented by rape (*B. napus*), turnip rape (*B. campestris*) and mustards (*B. juncea* Czern and Cross and *B. carinata* Braun), and has a total world production of about 19 million tons annually (FAO Prod Year Book 1985). The Indian subcontinent encompasses about 30% of the total world acreage, but its yield per hectare is the lowest in the world (FAO Prod Year Book 1985). The reasons for this low yield are insufficient precipitation when the crops are cultivated under rainfed conditions, the primitive crop husbandary methods and, especially, the lower yielding varieties of *B. campestris* and *B. juncea* that are commonly used. These two species are the main oil crops on the Indian subcontinent, whereas in Europe and Canada, an advanced breeding programme has enabled farmers to use the higher yielding rape (*B. napus*) as the main oil crop. According to Kariya and Tsunoda (1972, 1973, cited by Tsunoda 1980), *B. napus* has a physiological constitution that makes it more productive than *B. campestris*. In Japan, *B. napus* has been bred for earliness (Shiga 1970) and has consequently replaced *B. campestris*, a shift that has helped to increase the average national yield. Also in China, the introduction of *B. napus* and high input management has initiated a trend towards higher productivity (FAO Prod Year Book

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Table 1. Parents selected for introgression of earliness; trait here characterized by days to flowering and maturity in Bangladesh and Sweden

Species	Source and origin	Accession	Days to flowering		Days to maturity	
			Bangladesh	Sweden	Bangladesh	Sweden
B. campestris	2 Bangladesh	cam 1*	30	21	78	76
	2 Bangladesh	cam 5	33	22	78	76
	1 Malaysia	cam 38	42	25	89	84
	1 Taiwan	cam 39	43	25	91	84
B. juncea	2 Bangladesh	jun 1	33	28	81	78
	2 Bangladesh	jun 5	32	26	81	85
	2 Bangladesh	jun 6	32	26	82	84
	2 Bangladesh	jun 10	34	24	79	85
	2 Bangladesh	jun 11*	33	30	81	86
B. oleracea var *alboglabra*	2 China	albo 2*	62	52	118	132
	4 Italy	albo 10	93	67	–	136
B. carinata	4 Zambia	car 6*	76	45	138	100
B. napus	2 Bangladesh	nap 2	43	40	100	100
	3 Sweden	nap 34*	80	43	135	104

* Studied carefully to understand the process

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1985). However, the *B. napus* of the temperate regions remains constantly in the vegetative stage or is too late in maturing to be a crop in Bangladesh. In an attempt to increase vegetable oil production in Bangladesh, the breeding and introduction of *B. napus* is considered a realistic approach.

Allopolyploidy has been shown to be an important factor in the evolution of domesticated plants (Stebbins 1950; MacKey 1987). This kind of evolutionary process has also played an important role in *Brassica* (Shiga 1970). *B. napus* (AACC) is an amphidiploid of two elementary species, i.e. *B. campestris* carrying the A genome and *B. oleracea* carrying the C genome. *B. campestris* and *B. juncea* with the genomic constitution, A and AB, respectively, possess homology with the A genome of *B. napus*. They are indigenous species and should thus have the potential to enrich the A genome of *B. napus*. Likewise, *B. oleracea* var 'alboglabra' (CC), which is endemic to the Asiatic countries, should also be able to enrich the C genome of *B. napus*. *B. carinata* (BBCC) is usually cultivated in moisture deficient regions of Africa, and as such may be an important resistant source for moisture stress as well.

Materials and methods

The search for the early *Brassica* types for this project was facilitated by generous donations from various institutes (Table 1). The collections were evaluated for earliness during the winter season in Bangladesh (1980–81 and 1981–82) and during the summer at two locations in Sweden (Central and Southern Sweden, 1981). Fortunately, indigenous and adapted representatives from Bangladesh proved to be among the earliest accessions and were, therefore, selected as introgression sources. Nap 34 (cv 'Olga'), an advanced representative of *B. napus* developed through conventional breeding in Sweden, was chosen as a late parent, which allowed the introgression process in general and the genetical control of earliness in particular to be studied directly.

Whenever possible, about 400–500 F_1 seeds were produced from each cross to be used in a final experiment aimed at studying the process of species introgression. Some F_1 seeds were used for the production of F_2 seeds in isolation chambers; the remaining F_1 seeds were held under cool storage conditions until used. The F_1 hybrids from the interspecific crosses were expected to show severe sterility. For that reason, the F_1 was handled in two different ways: (1) The production of F_2 plants increasing the risk of a high proportion of fertility disorder was weighed against a maximum probability of introgressing earliness genes. (2) Immediately backcrossing the F_1 to the *B. napus* parent allowed fertility to be improved but with the risk of losing some genes for earliness.

The study of the *Brassica* collections revealed that what was early in Bangladesh was usually early in Sweden as well. Some genotypes do not flower, or flower too late, to be a crop in Bangladesh. Considering this phenomenon, the experiments were conducted especially for early generations in Sweden (55° 55′ N lat) and advanced generations in Bangladesh (24° 0′ N lat). The day length and temperature of the corresponding growing period of the two countries are presented in Fig. 1.

Results

F_1, Bc_1, F_2 and Bc_2 generations grown in Sweden

The Latin square design of the experiment in a rich, black and very homogenous soil at the Weibullsholm Plant

Table 2. Treatments in each interspecific cross trial

Cross combinations							
B. napus × *B. campestris*		*B. napus* × *B. juncea*		*B. napus* × *B. oleracea* var alboglabra		*B. napus* × *B. carinata*	
nap 34	P_1	nap 34	P_1	nap 34	P_1	nap 34	P_1
nap 34 × cam 1	F_1	jun 11 × nap 34	rc F_1	nap 34 × albo 2	F_1	nap 34 × car 6	F_1
cam 1 × nap 34	rc F_1	(nap 34 × jun 11) × nap 34	Bc_1	(nap 34 × albo 2) × nap 34	Bc_1	nap 34 × car 6	F_2
(nap 34 × cam 1) × nap 34	Bc_1	(jun 11 × nap 34) × nap 34	rc Bc_1	nap 34 × albo 2	F_2	car 6 × nap 34	rc F_2
(cam 1 × nap 34) × nap 34	rc Bc_1	nap 34 × jun 11	F_2	nap 34 × albo 2	F_2	(nap 34 × car 6) × nap 34	Bc_2
nap 34 × cam 1	F_2	jun 11 × nap 34	rc F_2	albo 2 × nap 34	rc F_2	(nap 34 × car 6) × nap 34	Bc_2
cam 1 × nap 34	rc F_2	jun 11 × nap 34	rc F_2	(nap 34 × albo 2) × nap 34	Bc_2	(car 6 × nap 34) × nap 34	rc Bc_2
(nap 34 × cam 1) × nap 34	Bc_2	(nap 34 × jun 11) × nap 34	Bc_2	(nap 34 × albo 2) × nap 34	Bc_2	(car 6 × nap 34) × nap 34	rc Bc_2
(cam 1 × nap 34) × nap 34	rc Bc_2	(jun 11 × nap 34) × nap 34	rc Bc_2	(albo 2 × nap 34) × nap 34	rc Bc_2	nap 34	P_1
cam 1	P_2	jun 11	P_2	albo 2	P_2	car 6	P_2

The crosses, nap 34 × jun 11 (F_1), albo 2 × nap 34 (rc F_1), (albo 2 × nap 34) × nap 34 (rc, Bc_1), car 6 × nap 34 (rc F_1), (nap 34 × car 6) × nap 34 (Bc_1) and (car 6 × nap 34) × nap 34 (rc Bc_1) did not produce enough seeds to be included as a treatment in their respective experiment

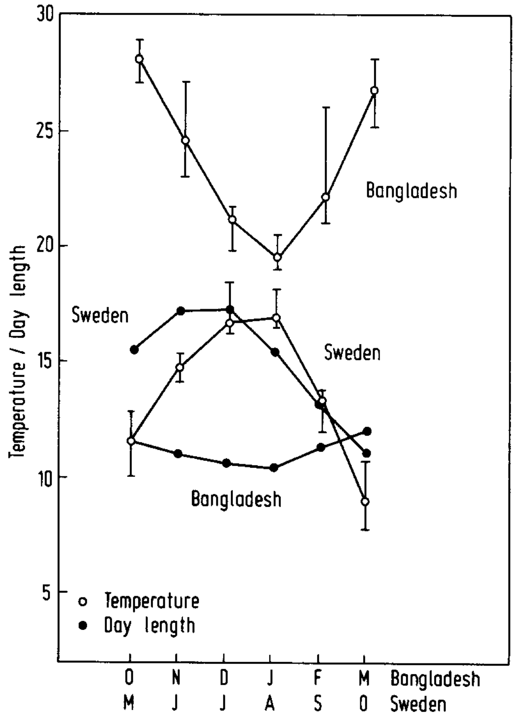

Fig. 1. Monthly average temperature (°C) and day length (h) in corresponding growing period (1979–1985) for oleiferous *Brassica* in Bangladesh and Sweden

Breeding Institute, Landskrona, Sweden helped to maximally eliminate all variances other than those of genetic origin. Insignificant differences were observed for row and column for all major characters. Therefore, the results obtained could be interpreted mainly as being due to genetic factors. No differences were found among progenies from reciprocal crosses for the characters studied. The data from reciprocal crosses and different plots of the same treatments were, therefore, pooled to increase the population size and to avoid repetitions.

A complete experimental set comprised ten treatments (Table 2). Due to a strong hybridization barrier, some treatments were not possible to carry out. In those cases, other treatments were repeated for maintaining the same design in the different sets of experiments. The experiments were laid out in the Latin square (10 × 10) design. The plots in each experiment comprised two rows, 45 cm apart, 1.5 m long. The distance between the plots was 90 cm. Fifty seeds per plot were sown, and after germination, the plots were thinned to 30 plants as evenly spaced as possible over the whole plot. The number of days from the date of emergence to the opening of the first flower, from now on referred to as "days to flowering", was recorded in order to characterize the genotypes for reproductive earliness on an individual plant basis. Days to maturity was later noted for each plant when the main raceme of the plant developed yellow pods and brown seeds.

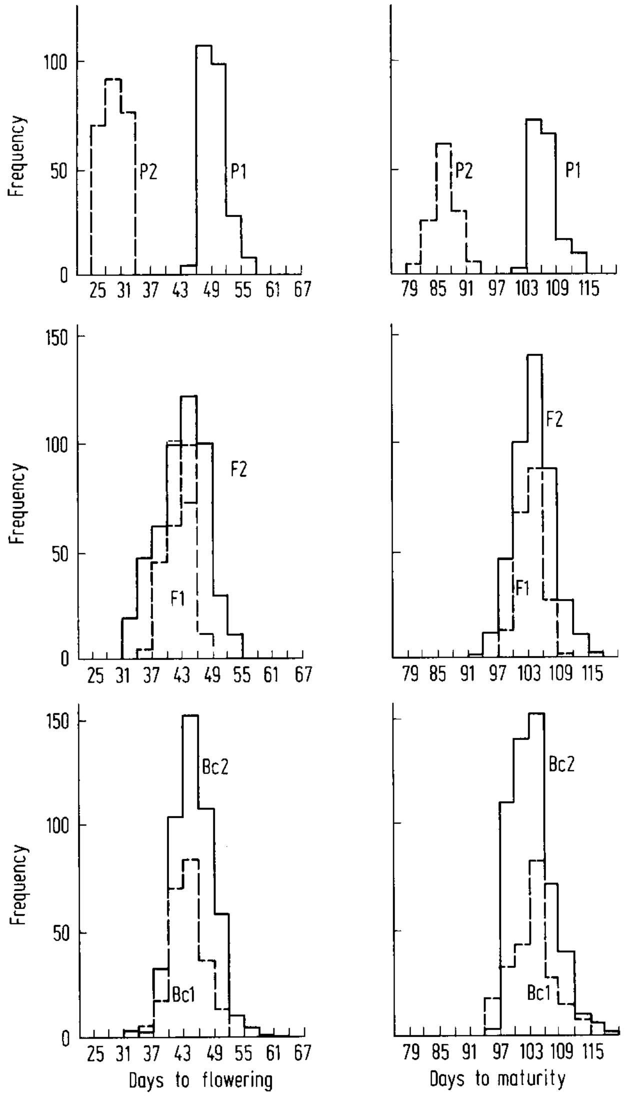

Fig. 2. Distribution and range for days to flowering and maturity in parents (P_1, P_2), F_1, F_2, Bc_1 and Bc_2 of the cross, nap 34 (P_1) × cam 1 (P_2)

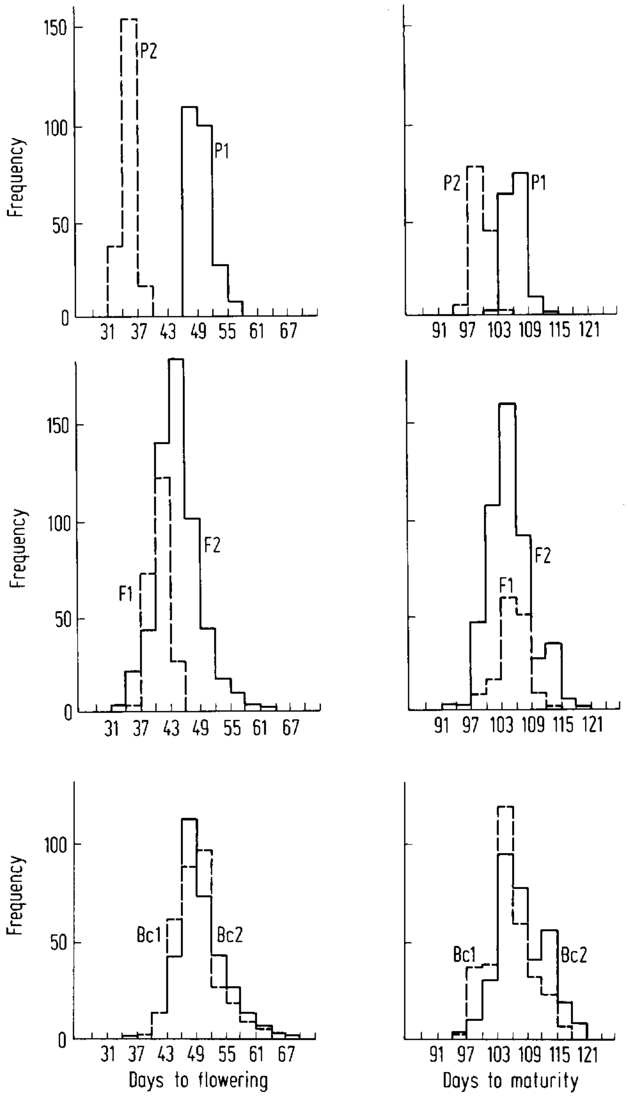

Fig. 3. Distribution and range for days to flowering and maturity in parents (P_1, P_2), F_1, Bc_1, F_2 and Bc_2 of the cross nap 34 (P_1) × jun 11 (P_2)

Introgression of earlines through the A genome. (1) *B. napus* (AACC) × *B. campestris* (AA). The parent, nap 34, represents a late flowering North European type unable to enter the generative phase within a reasonable time in Bangladesh. With respect to time of flowering, the F_1 generation was intermediate to the parents, indicating either polygenic inheritance or a more simple inheritance with incomplete dominance. One backcross of the F_1 generation to the recipient parent nap 34 shifted the population only slightly towards lateness. The F_2 and Bc_2 generations exhibited a transgressive segregation in both directions. Some plants were as early as 31 days to flowering, others as late as 55 days. These are most likely to have arisen from recombinations involving genes or chromosomes contributed by cam 1. The frequency distributions in F_2 and Bc_2 were more or less unimodal. For days to maturity, the F_1, Bc_1, F_2 and Bc_2 showed a trend similar to days to flowering (Fig. 2). Shiga (1970) reported similar positive results in his attempt to introgress earliness in Japanese *B. napus* from *B. campestris*.

(2) *B. napus* (AACC) × *B. juncea* (AABB). The population obtained from the cross combination nap 34 × jun 11 reacted in a fashion similar to that of the cross, nap 34 × cam 1. When backcrossing was applied in the F_1, a shift towards lateness also became apparent. The F_2 and Bc_2 frequency distributions for days to flowering and maturity (Fig. 3) were unimodal. There is thus no reason to expect a fundamentally different genetic control of

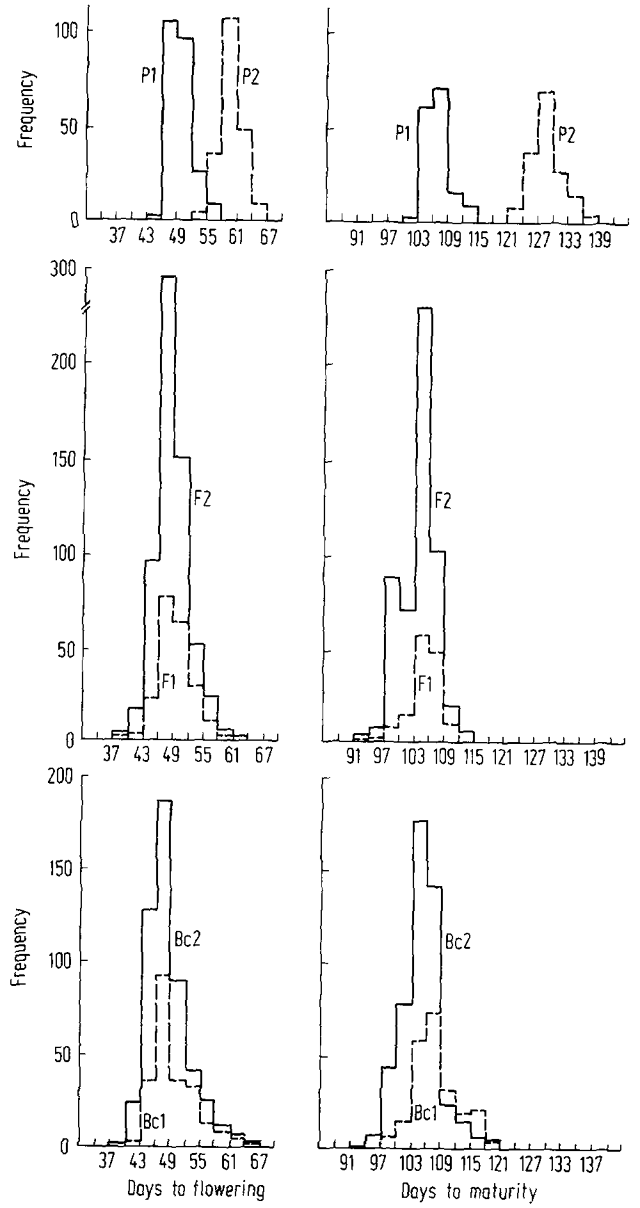

Fig. 4. Distribution and range for days to flowering and maturity in parents (P_1, P_2), F_1, Bc_1, F_2 and Bc_2 of the cross nap 34 (P_1) × albo 2 (P_2)

earliness in the A genome of *B. campestris* compared to that in *B. juncea*. Roy (1984) also observed introgression of earliness in *B. napus* from a cross *B. napus* × *B. juncea*.

Introgression of earliness through the C genome. (1) *B. napus* (AACC) × *B. oleracea* var 'alboglabra' (CC). In comparison to the A genome donors, albo 2 must be characterized as very late in flowering and maturity, in fact, even later than nap 34. It was thus promising to observe an earliness in the F_1 which was similar to that of the nap 34 parent. In Bc_1, the population shifted towards lateness. An additive gene effect best explains the wide segregation observed in the F_2 and Bc_2 generations where some quite early transgressions were found. The cross behaved similarly for days to flowering and maturity (Fig. 4).

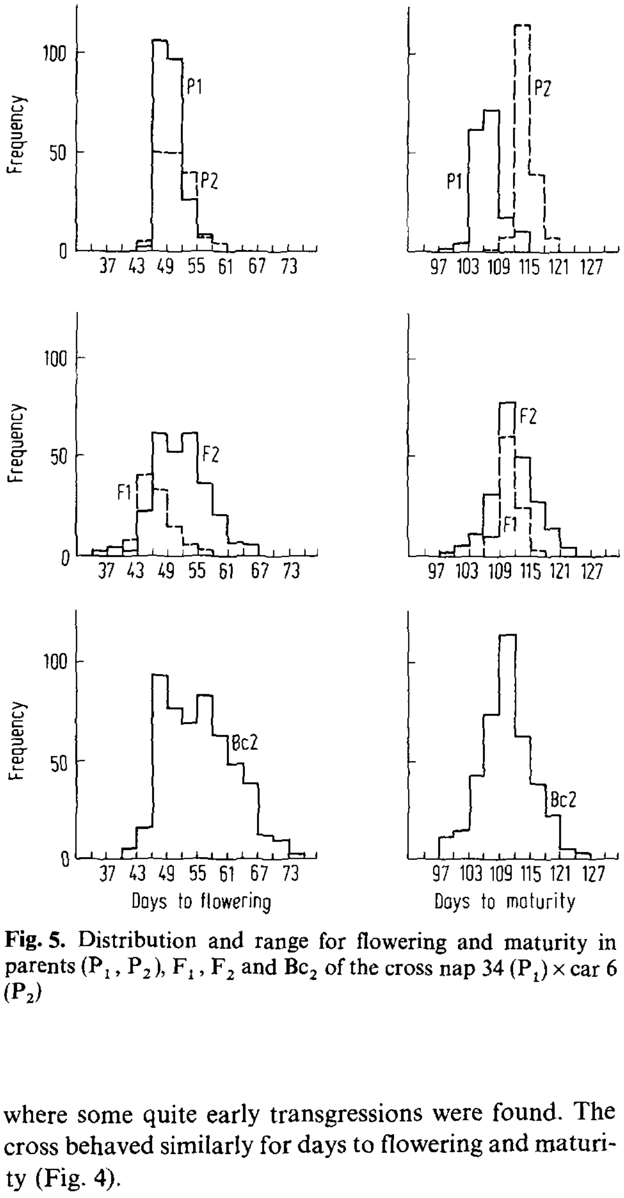

Fig. 5. Distribution and range for flowering and maturity in parents (P_1, P_2), F_1, F_2 and Bc_2 of the cross nap 34 (P_1) × car 6 (P_2)

(2) *B. napus* (AACC) × *B. carinata* (BBCC). *B. carinata*, car 6, proved to have the same lateness in flowering and maturity as nap 34. A slight heterosis for early flowering was observed in the F_1. Transgressive segregation was observed for both flowering and maturity (Fig. 5). The distribution of segregants suggest a polygenic control of the traits in conformity with other crosses.

Earliness pattern in the intraspecific cross. B. napus (AACC) × *B. napus* (AACC). The intraspecific cross, nap 34 × nap 2 was carried out as a comparison to the interspecific crosses. The F_1 showed intermediate behaviour for days to flowering and maturity (Fig. 6), i.e. the same picture as that obtained for crosses nap 34 × cam 1/jun 11/albo 2. No transgressive segregants could, however, be observed in the present combination, suggesting the absence of additive genes.

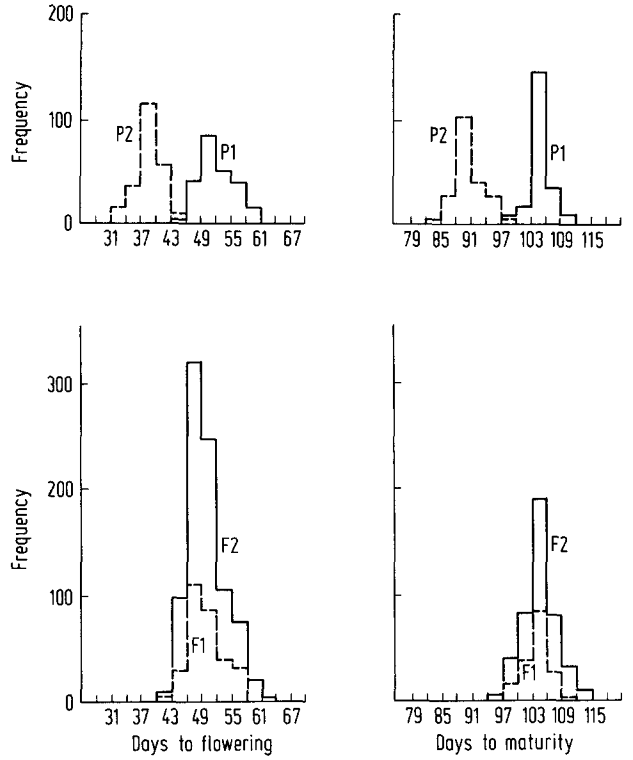

Fig. 6. Distribution and range for days to flowering and maturity in parents (P_1, P_2), F_1, and F_2 of the cross nap 34 (P_1) × nap 2 (P_2)

F_2 and F_3 generations grown in Bangladesh

Twenty five plants progenies from F_1 and 25 early representatives from F_2 were taken from all the combinations described above and tested in Bangladesh in a balanced lattice square design. Almost all progenies obtained from the interspecific crosses proved to be significantly earlier than nap 34. Although albo 2 and car 6 are very late in Bangladesh, some progeny lines derived from the crosses involving these parents were able to flower quite early (Table 3). A similar reaction as to earliness in both Sweden and Bangladesh was observed, which indicates that some of the genes controlling flowering are photoinsensitive.

Introgression with other genotypes

In addition to the above-mentioned recorded combinations with cam 1 and jun 11, accessions cam 5, cam 38, cam 39, jun 1, jun 5, jun 6 and jun 10 (cf. Table 1) were also used for introgression of earliness into the A genome of nap 34. All these crosses exhibited the same reaction as nap 34 × cam 1 and nap 34 × jun 11 in both the F_1 and advanced generations.

Both albo 2 and albo 10 were used in crosses. Although albo 10 is very late in Bangladesh (cf. Table 1), the lines derived from the cross albo 10 × nap 34 were as

Table 3. Range and mean with significant differences for days to flowering and maturity in Bangladesh from crosses between nap 34 and cam 1/jun 11/car 6/albo 2/nap 2

Cross combinations		Days to flowering			Days to maturity		
		Range	Mean	Adj. mean	Range	Mean	Adj. mean
nap 34	P_1	75–90	81.8	79 b	125–135	128.6	130 a
nap 34 × cam 1	F_2	29–70	46.2	46 i	74–137	104.2	106 def
nap 34 × cam 1	F_3	30–65	39.6	42 i	93–105	92.7	98 gh
cam 1	P_2	27–30	28.8	29 k	79– 86	79.5	78 l
nap 34 × jun 11	F_2	43–86	68.5	73 bc	86–135	112.5	120 abc
nap 34 × jun 11	F_3	30–80	58.2	58 efg	91–134	110.2	102 efg
jun 11	P_2	30–40	36.2	36 jk	90–110	95.6	91 h
nap 34 × albo 2	F_2	31–90	64.5	69 c	79–134	114.2	118 bc
nap 34 × albo 2	F_3	31–80	57.6	48 h	88–130	111.8	104 efg
albo 2	P_2	55–70	62.5	59 defg	95–134	118.3	117 bcd
nap 34 × car 6	F_2	33–78	47.8	49 gh	88–130	102.0	96 gh
nap 34 × car 6	F_3	30–78	48.2	55 efgh	78–130	106.1	105 ef
car 6	P_2	85–95	90.0	90 a	97–108	127.0	124 ab
nap 34 × nap 2	F_2	35–62	43.8	38 ij	86–110	100.0	95 gh
nap 34 × nap 2	F_3	30–67	39.1	40 ij	86–113	96.2	96 gh
nap 2	P_2	30–46	37.1	34 jk	90–110	94.1	92 gh

Values with different letters are significantly different at $P < 0.05$

Table 4. Earliness of some selected lines in advanced generations in Bangladesh

Cross combinations		Days to flowering	Days to maturity
cam 1	check	25	80
nap 34 × cam 1	F_7	28.50 ± 1.5	89.45 ± 1.3
nap 34 × jun 11	F_8	29.15 ± 1.5	89.48 ± 1.3
albo 10 × nap 34	F_7	29.01 ± 2.1	89.86 ± 1.2
albo 2 × nap 34	F_5	34.25 ± 3.1	97.00 ± 3.9
nap 34 × car 6	F_7	30.89 ± 2.0	90.45 ± 1.4
(nap 34 × jun 11) × (albo 10 × nap 34)	F_3	28.82 ± 1.1	85.14 ± 0.8
(nap 34 × albo 2) × (nap 34 × jun 11)	F_2	30.88 ± 1.4	84.39 ± 1.3
(nap 34 × cam 1) × (nap 34 × albo 10)	F_3	30.61 ± 2.3	89.80 ± 1.0
(nap 34 × car 6) × (nap 34 × jun 11)	F_3	29.78 ± 1.2	90.94 ± 0.6

early as the earliest lines derived from any A genome introgression. This suggests that *B. oleracea* var. 'alboglabra' has gene(s) regulating day length neutrality.

Performances of convergent crosses

In order to add further earliness, different early introgressed *B. napus* lines developed from A and C genome sources were crossed together. The range in the F_2 and F_3 progenies from these crosses did not show much promise for selection of further earliness (Table 4) compared to the level already achieved. The lack of further transgression in earliness may indicate exhaustion of the potential due to previous hard selection for earliness or very few genes controlling the trait.

Discussion

Somatic chromosome analyses in *Brassica* suggest that six basic types of chromosomes exist within the genus (Richharia 1937 a, b). From his analysis of the pachytene chromosomes, Röbbelen (1960), proposed that the genetical constitution of the three basic genomes is AABCDDEFFF for *B. campestris*, ABCDDEFF for *B. nigra* and ABBCCDEEF for *B. oleracea*. This implies two tetrasomic (A, D) and one hexasomic (F) set in *B. campestris*, two tetrasomic sets (D, F) in *B. nigra* and three tetrasomic sets (B, C, F) in *B. oleracea*. Such an interpretation implies that all three species should be secondarily balanced polyploids derived from a common prototype.

Intergenomic homology in *B. campestris*, *B. nigra* and *B. oleracea* has been confirmed by the different number of allosyndetic pairing in allohaploids, *B. juncea* (U et al. 1937; Ramanujam and Srinivasachar 1943; Olsson 1960; Prakash 1973), *B. napus* (U 1935; Olsson and Hagberg 1955; Morinaga and Fukushima 1933), *B. carinata* (Mizushima 1950 a, b; Kuriyama and Wantanabe 1955) and in the hybrids between *B. carinata* and *B. campestris*, and *B. napus* and *B. nigra* (Mizushima 1950 a, b)

The genomic constitutions and interrelationships of the diploid *Brassica* species indicate possibilities of intra- as well as intergenomic pairing when crossed together. Thus, it is possible to introgress A genome chromosome(s) or gene(s) from *B. campestris*/*B. juncea* not only into the A genome of *B. napus* but also into the C genome in the F_1s having AAC and AABC constitutions produced from the cross *B. napus* (AACC) × *B. campestris* (AA) and *B. napus* (AACC) × *B. juncea* (AABB), respectively. Correspondingly, similar possibilities exist for introgression from the C genome of *B. oleracea* var 'alboglabra' or *B. carinata* in the F_1s having ACC and ABCC constitutions produced from the crosses, *B. napus* (AACC) × *B. oleracea* var 'alboglabra' (CC) and *B. napus* (AACC) × *B. carinata* (BBCC), respectively, not only into the C genome of *B. napus*, but also into its A genome as well. Such heterogenetic recombinations may explain some of the positive results in obtaining early progenies in the present investigation.

The materials especially selected for earliness reacted similarly in the Bangladesh winter with its short days and in the Swedish summer with its long days. This trend is true for all studied interspecific crosses. Since the receptor parent and late segregants from the interspecific crosses were able to flower in Sweden, but not in Bangladesh, some photoperiodic sensitivity control must be involved. Phenotypically, the gene or genes involved will have this function only under the Bangladesh short-day condition. In the long days of the Swedish summer, they will act solely as genes for earliness. In a control experiment, Friend and Helson (1966) observed that photosensitive *B. campestris* will switch over more quickly to the generative phase during long days. Similarly, photoinsensitive wheats are found to be quite early in Northern Europe, while cultivars from this region are extremely late and vegetatively luxuriant when grown in the short days of the South (Martinic 1973, 1975). Since the ability to flower or not to flower in Bangladesh was quite distinct with similar patterns independent of the interspecific cross examined, it is likely that the essential control of the photoperiodic sensitivity is simply inherited and same independent of the donor species.

The existence of genes which influence only earliness and not photoperiodic response appears very likely. It is, however, puzzling and disappointing that transgression was not obtained after making convergent crosses between early lines selected from the different interspecific crosses. Experience from Bangladesh clearly shows that differences in earliness do occur both in *B. campestris* and *B. juncea* even though all indigenious cultivars have the ability to flower and set seed in due time. Except for the possibility that this outcome depends on genetic drift, it is difficult to find a good explanation for this uniform pattern that is independent of donor species. The outcome could, however, be taken as more evidence that the gene pool within the U triangle shows a high degree of homology. Considering the different earliness of the C genome compared with that of the A genome donor lines, but similarity of earliness in their crosses, some kind of epistatic involvement must occur under such circumstances.

The present study is another demonstration of the potential of hybrid introgression as a means of improving the agronomic traits of *B. napus*. In attempts to widen the gene pool, it is an interesting alternative to resynthesis through amphidiploidization of *B. campestris* and *B. oleracea*. As shown by the present investigation, not only the diploid progenitors but also the two allotetraploids, *B. juncea* and *B. carinata*, can be explored with similar gains. In the past, this wide exploration of the *Brassica* gene pool has been neglected. In addition, introgression by interspecific crosses offers, at least in *Brassica*, fewer technical obstacles than resynthesis. Chromosome disturbances are only a problem in the very early generation.

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