

Table 1
Genotypes used in each experiment and a brief summary of their origin and pedigree where available

Genotype	Experiment	Origin	Pedigree or description
<i>B. napus</i>			
79NO13-364	2, 3 & 4	Australia	78NO39/75N107
82N128N9×36	3 & 4	Australia	75N313-L270/RU14
Maluka	1, 2, 3 & 4	Australia	RV3/BLN 227-2(OJ)
Taparoo	2, 3 & 4	Australia	Mutu/3/Chisaya//Zephyr/Bronowski
<i>B. juncea</i>			
CPI61680	1, 2, 3 & 4	India	Indian identification number IB683
JE8	2, 3 & 4	Australia	ZEM2/CPI61694
WA5	2, 3 & 4	Australia	82N022.67
Z.E. Sporospelka	3 & 4	Russia	Zero erucic acid cultivar

tivars, has lead to an interest in mustard as a replacement for canola in low-rainfall environments (Kirk and Oram, 1981). However, high levels of glucosinolates in mustard cultivars have so far precluded their commercial use. The recent discovery of a low glucosinolate trait in mustard (Love et al., 1990) suggests that this problem may soon be overcome and cultivars of canola quality may become available.

The present study compared the growth, seed yield, water use and plant water relations of both *Brassica* species using genotypes matched for development patterns. Comparative seed yield responses from four experiments with differing levels of soil water deficit are reported.

2. Material and methods

2.1. Genetic material

The Victorian Institute of Dryland Agriculture (Horsesham) supplied the genotypes used in this study; the material included established cultivars, unreleased breeding lines and plant introductions (Table 1). The *Brassica napus* material met canola requirements, namely erucic acid concentration less than 2% of total fatty acids in the oil and glucosinolates less than 30 μmol per gram in the meal. The mustard cultivar, ZE Sporospelka, was chosen because its erucic acid content meets the canola quality standard.

To improve the validity of the experiments, the selected genotypes were of dissimilar pedigree but similar maturity type. Peak flowering occurred within a period of four days for all experiments and all geno-

types reached maturity within a three-day period except in Experiment 4 where maturity was spread over five days. Genotypes were also matched for height with no obvious differences occurring in any of the experiments.

2.2. Experiment 1

A glasshouse experiment was conducted at the University of New England, Armidale (152°E, 31°S, elevation 980 m above sea level) using 12 containers each 0.58 × 0.58 m × 1.2 m tall and holding approximately 0.5 t of dry soil. The soil was a sandy clay loam of high fertility packed to a bulk density of 1.3 g cm⁻³. An access tube for the neutron water meter was placed slightly off centre within each container not closer than 0.25 m to the container wall. A complete trace element mixture was dissolved in water and applied two days before sowing combined with the major elements N, P, S, and K, also in solution at rates to supply totals of 30 kg N ha⁻¹, 42 kg P ha⁻¹, 74 kg S ha⁻¹ and 8.5 kg K ha⁻¹. Soil evaporation was minimised by covering the soil surface with a 2-cm layer of upholsterer's foam over a 5-cm layer of polystyrene beads.

The experiment was sown on 17 June 1989, half the containers to *B. napus* cv. Maluka and half to *B. juncea* genotype CPI61680. Nine plants were grown in each container. The experiment also included two water treatments, a low and a high water deficit. A completely randomised factorial design was used with two species by two water treatments replicated three times. Watering of the low-deficit treatment occurred at least weekly. The amount of water applied was calculated to restore the water in the profile to the level initially

Table 3

Above-ground dry matter (AGDM), seed yield (SY), harvest index (HI), number of pods per plant (PN), number of seeds per plant (SN), number of seeds per pod (SN/PN) and seed weight (SW) for Experiment 1 (glasshouse trial)

Treatment	AGDM (g plant ⁻¹)	SY ^a (g plant ⁻¹)	HI (%)	PN	SN × 1000	SN/PN	SW ^a (mg)
Low deficit							
<i>B. napus</i>	110	34	30.9	576	12.1	20.7	2.58
<i>B. juncea</i>	133	26	19.6	1024	10.4	9.9	2.82
High deficit							
<i>B. napus</i>	42	8	19.4	269	3.0	11.9	2.71
<i>B. juncea</i>	46	14	29.9	389	4.1	10.8	3.46
Watering	***	***	ns	***	***	*	ns
Species	ns	ns	ns	*	ns	**	ns
Interaction	ns	†	***	ns	ns	*	ns
CV%	21	27	15	35	41	22	25

† $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

^aCorrected to 8% moisture.

seed yield in both species. There was a suggestion ($P < 0.1$) that high water deficits reduced yield in canola more than in mustard.

Harvest index increased in mustard at high water deficit whilst the reverse occurred in the canola. There were more pods plant⁻¹ in mustard than in canola and there were more pods at the low compared to the high deficit. Seed number per plant was higher for both species at the fully watered site. Average seed weight was not influenced by species or watering treatment. Seed number per pod was severely reduced by high soil water deficit in canola whilst there was no effect in mustard; though under low-deficit conditions the number of seeds pod⁻¹ in canola was twice that in mustard.

3.2. Experiment 2

Dry matter production was greater ($P < 0.1$) in mustard than in canola irrespective of moisture regime, though this did not result in increased seed yield (Table 4). High rainfall during the season resulted in only small differences in dry matter production between the sites, and yields were close to those recorded in low-deficit environments, e.g. Tasmania (Mendham et al., 1984) and Europe (Mendham et al., 1981). Trends in these data are similar to those in Experiment 1. Mustard plants had more pods ($P < 0.18$) with fewer seeds per pod ($P < 0.2$), however, there was no evidence of more seeds per unit area. Differences in oil yield were not significant at either moisture level. While harvest index, average seed

weight and oil concentrations were all lower in mustard compared to canola at both moisture levels.

3.3. Experiment 3

Mustard produced more dry matter than canola in Experiment 3 (Table 5). Mustard also yielded more seed, had a larger harvest index and produced more pods m⁻² and seeds m⁻² than canola. There was no significant difference between the species in seed weight or seeds pod⁻¹, though the number of seeds pod⁻¹ was greater in mustard ($P < 0.1$). No differences in oil or protein concentration were evident while oil production per unit area was greater in mustard. However, insufficient seed was available to determine oil concentration in the seed and protein concentration in the meal from all the replicates of the canola cultivars. Hence, the value presented for canola may be an overestimate because it represents an average for the best replicates with no determinations being made from the worst replicates.

Some late-season insect damage occurred in this experiment, however damage appeared to be equal in both species.

3.4. Experiment 4

Mustard produced 17% more dry matter than canola at the irrigated site but this was not reflected in seed yield because mustard's harvest index was lower (Table 6). There were more pods m⁻² in mustard but

Table 6

Above-ground dry matter (AGDM), seed yield (SY), harvest index (HI), number of pods per square metre (PN), number of seeds per square metre (SN), number of seeds per pod (SN/PN), seed weight (SW), oil concentration (OC), protein concentration (PC) and oil yield (OY) for Experiment 4, $n = 16$

Site and species	AGDM (g m^{-2})	SY ^a (g m^{-2})	HI (%)	PN \times 1000	SN \times 1000	SN/PN	SW ^a (mg)	OC (%)	PC (%)	OY (g m^{-2})
Irrigated site										
<i>B. napus</i>	520	160	30.4	3.4	46	13.5	3.44	46.5	39.2	74
<i>B. juncea</i>	610	138	22.7	6.0	52	8.8	2.63	47.6	40.1	66
Significance	*	ns	***	***	ns	***	***	*	ns	ns
CV%	23	27	8	21	24	9	6	3	6	28
Rainfed site										
<i>B. napus</i>	232	66	27.5	1.5	17	11.2	3.87	44.0	47.0	29
<i>B. juncea</i>	350	79	22.0	3.5	26	7.6	3.00	44.5	50.5	35
Significance	***	ns	***	***	**	***	***	ns	*	ns
CV%	35	40	8	34	38	13	6	4	8	40
Rain-exclusion site										
<i>B. napus</i>	165	30	16.7	0.8	9	10.4	3.31	40.1	52.9	12
<i>B. juncea</i>	364	68	18.5	3.2	26	8.2	2.69	42.5	51.1	29
Significance	***	***	ns	***	***	***	***	***	ns	***
CV%	26	46	35	37	44	21	9	4	10	46

* $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

^aCorrected to 8% moisture.

largest is as follows; irrigated site Experiment 2, rainfed site Experiment 2, irrigated site Experiment 4, rainfed site Experiment 4, rain-exclusion site Experiment 4 and Experiment 3. Data from the glasshouse experiment, converted to an area basis, are also included in Fig. 1. The high level of productivity in the glasshouse experiment suggests that edge effects were present; however, trends present in the data are similar to those in the other experiments and are included to allow a general comparison across all experiments. The comparison made is a relative one, using the ratio of mustard to canola for each component, e.g. a ratio above one indicates that mustard has more of that component than canola at that site.

Factors other than water deficit, such as soil compaction, can influence site-mean dry-matter production. However, care was taken in these experiments to limit such extraneous influences. The extent to which this was achieved can be seen from the fact that variation in a supply/demand stress index (water supply/pan evaporation) accounted for 93% of the variation in site-mean dry matter (Fig. 2) in those experiments where such data were available (Experiments 3 and 4).

When comparing the two species, the response of components of yield to different levels of soil water deficit can be classified into three types: (1) compo-

nents that favour one species across all conditions, (2) components that are similar between the species regardless of the moisture regime and (3) components that favour one species under one set of soil moisture conditions but the other species under other conditions.

Dry matter production of mustard is in the first group as it exceeded that of canola at all sites. This advantage was largest (greater than twofold) at sites with the highest water deficits (Fig. 1a). Similarly, pod number (Fig. 1d) and total seed number per unit area (Fig. 1e) were always greater in mustard with the exception of seed number in the well-watered treatment of the glasshouse experiment and, as with dry matter, the differences were largest at the highest-deficit sites. These results suggest that mustard is better adapted than canola to high-deficit conditions. However, there are other yield components that favour canola across conditions including seed number per pod (with the exception of Experiment 3, Fig. 1f) and individual seed weight (except under glasshouse conditions, Fig. 1g). Components of yield that fall into the second group (showing no comparative advantage to either species regardless of moisture regime) were seed oil (Fig. 1h) and protein (Fig. 1i) concentrations. Harvest index (Fig. 1c) was the only component that fell into the third

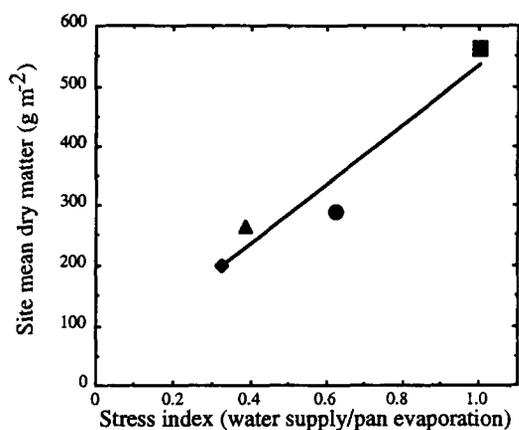


Fig. 2. Relationship between a stress index (soil water plus rainfall divided by class A pan evaporation for the growing season) and site mean dry matter (◆ Experiment 3, ▲ rain-exclusion site Experiment 4, ● rainfed site Experiment 4, and ■ irrigated site Experiment 4). $y = 31.07 + 512.75x$ ($r^2 = 0.93$, $P < 0.05$).

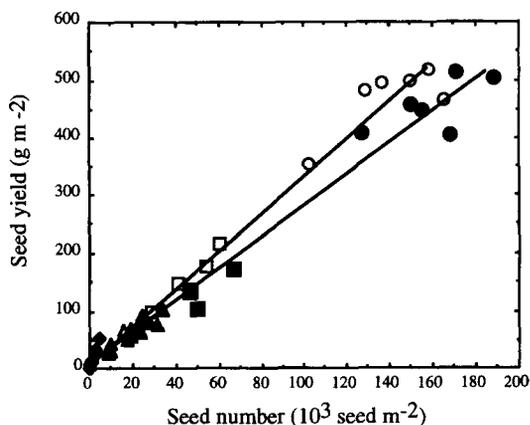


Fig. 3. Relationship between seed number and yield under field conditions across low-deficit (mustard ● and canola ○ at both sites of Experiment 2, mustard ■ and canola □ at the irrigated site of Experiment 4) and high-deficit treatments (mustard ◆ and canola ◇ Experiment 3, mustard ▲ and canola △ at the rain-exclusion site of Experiment 4). Each point represents a cultivar. $y = 7.63 + 0.0033x$ ($r^2 = 0.99$, $P < 0.001$) in canola and $y = 9.49 + 0.0026x$ ($r^2 = 0.98$, $P < 0.001$) in mustard.

group with canola appearing to have an advantage except under severely deficient conditions.

Seed and, ultimately, oil yield are the integrators of all these components and they both reflect an advantage to mustard under high water deficits; this advantage diminishes to a performance similar to that of canola at the lowest deficits tested in these experiments (Fig. 1b and j).

The importance of different components of yield varied. Seed yield is the product of seed number and seed weight. However, as discussed above, there is little change in individual seed weight across sites despite large differences in seed yield. Under field conditions, these large yield differences are almost exclusively explained by differences in seed number, accounting for 99% of the yield variation in canola and 98% in mustard when data were pooled across the three field experiments (Fig. 3).

In the field, yield in both canola and mustard can be related to the amount of dry matter accumulated prior to peak flowering (Fig. 4). Under low-deficit conditions a linear relationship can be fitted to these data with variation in dry matter at peak flowering accounting for 77% of the yield variation in canola ($y = 99.14 + 0.386x$, $P < 0.001$) and 90% in mustard ($y = 40.94 + 0.366x$, $P < 0.001$). However, it is clear that these data are at extremes with no intermediate values of dry matter at peak flowering, hence the extent of variation in yield explained by these differences is likely to be overestimated. It is nonetheless clear that more dry matter at peak flowering is associated with higher yield under low-stress conditions. Under high deficits, the slope of this relationship was lower and no difference could be discerned between the species, with one regression line explaining the response of both species ($y = -0.23 + 0.121x$, $r^2 = 0.35$, $P < 0.05$).

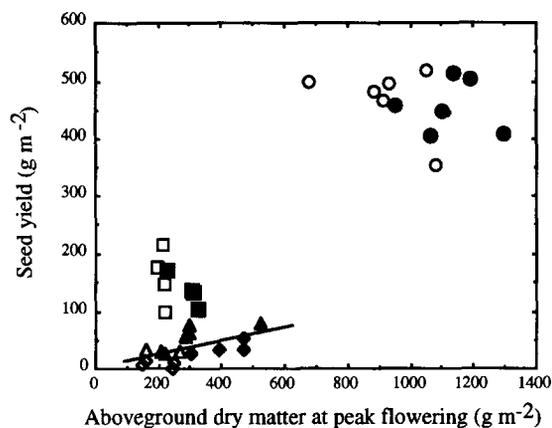


Fig. 4. Relationship between crop dry weight at peak flowering (4.3) and yield for low-deficit treatments (mustard ● and canola ○ at both sites of Experiment 2, mustard ■ and canola □ at the irrigated site of Experiment 4) and high-deficit treatments (mustard ◆ and canola ◇ Experiment 3, mustard ▲ and canola △ at the rain-exclusion site of Experiment 4).

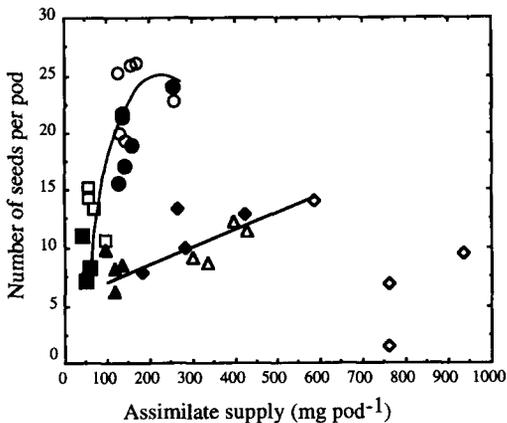


Fig. 5. Relationship between assimilate supply (crop dry weight at peak flowering divided by pod number at maturity) and number of seeds per pod for low-deficit treatments (mustard ● and canola ○ at both sites of Experiment 2, mustard ■ and canola □ at the irrigated site of Experiment 4) and high-deficit treatments (mustard ◆ and canola ◇ Experiment 3, mustard ▲ and canola △ at the rain-exclusion site of Experiment 4). Three canola cultivars from Experiment 3 have been excluded from the regression, see text for explanation.

The capacity to support seeds and pods was measured by the amount of dry matter per pod (crop dry matter at peak flowering divided by the number of pods assessed at maturity). Variation in crop dry matter per pod explained 73% ($P < 0.001$) of the variation in seed number per pod in both species under low-deficit conditions using a curvilinear fit (Fig. 5). There was no evidence of a difference between the species in this relationship. Under high-deficit conditions seed numbers per pod were still positively associated with crop dry matter per pod ($y = 6.597 + 0.0128x$, $r^2 = 0.61$, $P < 0.001$, linear regression) for both species, with the exception of three canola genotypes under the severest water deficits experienced (Experiment 3).

4. Discussion

The results show that under high soil water deficits (rain exclusion site, Experiment 4) seed yields in mustard were more than double those of canola. These results agree with the reputed drought tolerance of mustard and studies both in Australia (Angus and van Herwaarden, 1989) and India (Kumar et al., 1987; Singh et al., 1990). However, they differ from Swedish studies (Ali et al., 1988; Ohlsson et al., 1990) which found no evidence of differences between the species. These

later studies were carried out under relatively non-limiting conditions with mean monthly temperatures not exceeding 16°C and a water table present at 1.2 m depth, suggesting that these crops experienced relatively low water deficits. More seriously, the genotypes used were not matched for maturity thus limiting the validity of the species comparison.

Surprisingly, under low soil water deficits the species have the same yield (glasshouse experiment and the irrigated site of Experiment 2 and 4). It would be expected that yield potential in canola would be higher than in mustard under non-limiting conditions since a substantial canola breeding program has been in place in Australia for the last 20 years while mustard has only recently received attention. This is an important finding as the data show that under close to ideal conditions (seed yields of 5 t/ha) yields in mustard were as high as in canola. We know of no published comparative studies carried out under low stress where maturity was matched. However, studies where maturity was not matched do provide some general support for the existence of a high yield potential in mustard (Woods et al., 1991; Woods, 1992). The present findings suggest that the breeding effort involved in producing high-yielding well-adapted mustard cultivars may be less than might have been initially expected.

Oil concentration in seed did vary with stress level but both species responded in a similar manner; hence the oil yield per hectare mirrors that of seed yield with oil yield in mustard more than double that of canola at the high-deficit sites and similar to that of canola at the low-deficit sites. Again this is a surprising result as low oil yield could well be expected from a crop that has been subjected to less intensive breeding for Australian conditions. Protein concentration in the meal appeared to be similar in both species though there was a slight tendency for mustard to have a higher concentration. Given the strong association between oil yield and seed yield the rest of this discussion is based on seed yield.

In both species over 98% of the variation in seed yield across the range of soil moisture regimes tested could be accounted for by variation in seed number (Fig. 3). The trend for smaller seed weight in mustard compared to canola is reflected in the separate regression lines relating seed yield to seed number for the two species with the slope of the relationship reflecting the overall mean seed weight across experiments and treatments (3.3 and 2.6 mg for canola and mustard

final dry matter as canola plants will have a higher number of pods. The relationship between number of seeds per pod and final dry matter is of a different nature. Under high deficits (Fig. 6b, phase I) the number of seeds per pod in canola increased (1 to 15) with increasing dry matter while the number of seeds per pod in mustard remained relatively stable (approximately 8); in the second and third phase, mustard plants of the same weight had fewer seeds per pod than canola.

These differences in yield structure almost entirely cancel each other out under conditions of high or moderate water deficits resulting in canola and mustard plants with the same dry matter producing similar seed numbers (Fig. 6c). Under low deficits canola does have a slight advantage in seed number due to its higher number of seeds per pod and similar pod number. Hence, the adaptation of mustard to drought conditions does not appear to be primarily due to its different yield structure.

Fischer (1979) presented a framework for understanding yield and yield components in wheat. The essence of this model is that seed number which sets yield potential, is largely determined by the end of anthesis and post-anthesis conditions subsequently determine to what extent the crop reaches that potential. Despite the large differences in growth between canola and cereals, e.g. determinate versus indeterminate plants, a similar understanding can be applied. Mendham et al. (1981, 1984) showed that canola yield potential is set by the amount of dry matter accumulated before peak flowering (growth stage 4.3). The results for mustard presented in this paper, though sparsely distributed across a full range of dry matter production under low-deficit conditions, do fit this model (Fig. 4). Under high-deficit conditions this relationship is clearly present with both species behaving in a similar manner.

Mendham et al. (1984) further showed that seed survival in canola is linked to assimilate supply, with the capacity of the crop to maintain both seed number per pod and total number of pods being related to the dry weight of the crop at peak flowering per pod (e.g. dry weight at peak flowering divided by pod number at maturity). Similar relationships were found in the experiments reported here under low-deficit conditions (Fig. 5). The curvilinear relationship averaged across the species was $y = 1.53 + 0.194x - 0.0004x^2$ which is very similar to that reported by Mendham et al. (1984)

for a range of canola cultivars. This indicates that there is little difference between canola and mustard in their ability to support seeds or pods under low-deficit conditions. While the slope of the relationship is lower under high-deficit conditions there is still a clear relationship between assimilate supply and ability to maintain seeds per pod. The only exception was for canola at the very high deficits in Experiment 3. Crop dry weights per pod were quite high but the number of seeds per pod was low in three out of four canola genotypes, indicating seed abortion for reasons other than assimilate shortage (Fig. 5). Canola lost turgor more readily than mustard in these studies (unpublished data). This may have led to increased levels of abscisic acid which in turn increased seed abortion, as is the case in wheat (Saini and Aspinall, 1982; Morgan and King, 1984). The similar efficiencies of using assimilate to support seed number found here, except under very severe water deficits, shows that the different yield structure in mustard does not adversely affect this crop's ability to support seeds.

The importance of dry matter (ie total assimilate) as a principal determinant of yield is illustrated by the fact that across sites and treatments over 99% of the variation in seed yield could be explained in terms of dry matter accumulated at maturity in both canola ($y = -35.63 + 0.37x$) and mustard ($y = -24.15 + 0.27x$). Differences in slope between the two species reflect the lower overall mean harvest index of mustard (27%) compared to canola (37%). This overall comparative inefficiency in mustard in regard to harvest index is reflected in the individual site and treatments data. However, despite this inefficiency, mustard yields more seed than canola under high-deficit conditions as the total assimilate accumulated in mustard is larger.

In a study comparing the adaptation of a range of temperate cereals to rainfed environments Lopez-Castaneda and Richards (1994) found that barley was the most suited to high-deficit conditions. They concluded that the most important factor in barley's adaptive advantage to water deficits compared to other crops was its consistently higher dry matter production across environments. Similarly, it would appear that the adaptive advantage of mustard to high deficits is primarily due to greater dry matter production rather than to differences in yield structure.

The mechanism(s) underlying mustard's greater dry matter production under water stress require further study. Despite our lack of clear understanding of the mechanisms, mustard is evidently comparatively well adapted to dry conditions. As such it is worthy of further development in Australia.

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