CHAPTER 5*
YIELD AND YIELD COMPONENTS

* The substance of this Chapter has been published as a paper in Field Crops Research (1995), 42:1-13 a copy is presented in appendix 5.1.

5.1 Introduction

Development of mustard as an Australian crop will depend chiefly on whether it can produce larger oil yields than canola in marginal environments and reach comparable oil quality, an objective that appears to be feasible (Kirk and Oram, 1981; Love et al., 1990). Mustard's adaptation to drought conditions, at least in terms of dry matter production (Chapter 4), does appear to be greater than in canola but it is necessary to establish further that this advantage is reflected in higher seed yields. A yield advantage for mustard has been reported in drought conditions in Australia (Angus and van Herwaarden, 1989) and in India (Kumar et al., 1987; Singh et al., 1990a), but in Sweden the opposite was reported (Ali et al., 1988; Ohlsson et al., 1990). The reports possibly conflict because the maturity of the cultivars used in the comparisons were not matched. Furthermore, seed yield was often the only parameter measured, making it impossible to determine how these differences arose.

A comparison of yield and yield components of mustard and canola, carried out in northern NSW, for a range of soil moisture regimes is reported in this chapter. Results form each experiment are presented followed by an analysis of the response of the two species across all experiments. The mechanisms by which yield components varied between the species are discussed in relation to breeding for higher yields under conditions of water deficit.

5.2 Results

5.2.1. Experiment 1.

Maturity was not matched in this preliminary experiment as discussed in section 4.3.1. Total dry matter production was strongly influenced by days to final maturity (Fig. 4.1) as was yield with 74% ($P<0.001$) of yield variation being explained by the number of days from sowing to maturity (Appendix 4.1). Direct comparison of the results are, therefore, not valid as they are confounded with maturity. Consequently no yield or yield component data are presented in this chapter but for the sake of completeness they are available in appendix 4.1.

5.2.2. Experiment 2.

Yield and yield components are presented in Table 5.1. The crops did not differ significantly in either dry matter production or seed yield. These two components were severely reduced in both crops when water availability was limited with a suggestion ($P<0.1$) that high water deficits reduced canola yield more than that of mustard.

Harvest index increased in mustard at high water deficit and the reverse occurred in canola. There were more pods plant^{-1} in mustard and more pods at the low compared to the high deficits. Seed number per plant was higher for both species at the fully watered site and 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 but there was no such effect in mustard; however, under low deficit conditions the number of seeds pod^{-1} in canola was twice that in mustard.

Table 5.1. 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 2 (glasshouse experiment). n=3

Treatment	AGDM ($g\ plant^{-1}$)	SY‡ ($g\ plant^{-1}$)	HI (%)	PN	SN x1000	SN/PN	SW‡ (mg)
Low deficit							
B. napus	110	34	30.9	576	12.1	20.7	2.58
B. juncea	133	26	19.6	1024	10.4	9.9	2.82
High deficit							
B. napus	42	8	19.4	269	3.0	11.9	2.71
B. juncea	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

‡ Corrected to 8% moisture

5.2.3. Experiment 3.

Mustard produced more dry matter than canola (P<0.1) irrespective of imposed moisture regime, but this did not result in increased seed yield (Table 5.2). 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 2. 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. Mustard had a lower harvest index, average seed weight and oil concentrations at both moisture levels. It had greater protein concentration in the meal at both sites.

Table 5.2 Yield and yield components Experiment 3.

Cultivar	Dry matter ($g\ m^{-2}$)	Seed yield ($g\ m^{-2}$)	Harvest index (%)	Pods per m^{-2}	Seeds per m^{-2}	Seed # per pod	Mean seed weight (mg)	Oil content % dry matter	Protein content (%)	Oil yield ($g\ m^{-2}$)
Irrigated site										
B. napus										
79NO13-364	1434	482	33.5	6776	128576	19.4	3.74	47.6	20.8	229
Maluka	1477	518	35.1	8406	158271	20.0	3.27	47.2	21.1	244
Taparoo	1374	495	37.6	5399	136274	26.0	3.64	47.4	20.5	234
mean	**1408**	**498ns**	**35.4*****	**6860**	**141040**	**21.8ns**	**3.55*****	**47.4†**	**20.8**	**236ns**
B. juncea										
CPI61680	1765	448	25.0	9209	154866	17.3	2.89	45.4	25.8	202
JE8	1744	506	29.0	9369	187518	21.8	2.69	49.3	21.7	250
WA5	1823	458	24.2	10365	149182	15.7	2.98	44.7	23.4	207
mean	**1777†**	**470**	**26.1**	**9648ns**	**163855ns**	**18.3**	**2.85**	**46.4**	**23.6*****	**220**
CV%	23.9	32.2	11.0	46.1	28.9	29.7	7.1	2.3	4.5	31.5
Rainfed site										
B. napus										
79NO13-364	1100	355	32.0	4499	102190	22.7	3.49	45.6	22.0	160
Maluka	1405	466	33.6	6607	164929	25.9	2.81	45.8	20.7	214
Taparoo	1374	500	35.9	5995	149516	25.2	3.30	47.0	20.6	235
mean	**1293**	**440**	**33.8*****	**5700**	**138878**	**24.6ns**	**3.20*****	**46.1***	**21.1**	**203ns**
B. juncea										
CPI61680	2090	514	24.8	9674	170330	19.0	3.02	45.7	26.0	233
JE8	1586	406	25.5	8073	167516	21.4	2.43	46.1	21.7	187
WA5	1538	411	26.6	5210	126392	24.2	3.25	42.5	23.4	174
mean	**1738†**	**444ns**	**25.6**	**7652ns**	**154746ns**	**21.5**	**2.90**	**44.8**	**23.9*****	**198**
CV%	31.9	30.4	6.4	36.3	28.3	21.4	5.5	2.5	2.9	34.7

Symbols († or *) referer to significance level of the orthogonal contrast comparing mustard and canola cultivars († $P<0.1$, * $P<0.05$, ** $P<0.01$, *** $P<0.005$) within each site.

Table 5.3 Yield and yield components Experiment 4

Cultivar	Dry matter ($g\ m^{-2}$)	Seed yield ($g\ m^{-2}$)	Harvest index (%)	Pods per m^{-2}	Seeds per m^{-2}	Seed # per pod	Mean seed weight (mg)	Oil content % dry matter	Protein content (%)	Oil yield ($g\ m^{-2}$)
B. napus										
79NO13-364	149	9.2	5.0	264	529	9.54	2.44	39.1	60.1	6.6
82N128N9x36	141	1.4	0.8	319	91	1.44	1.41	-	-	-
Maluka	183	5.0	2.7	199	270	6.86	2.18	38.2	56.7	2.2
Taparoo	199	13.5	5.7	277	686	14.17	3.04	39.3	56.2	6.9
mean	**168**	**7.3**	**3.6**	**265**	**394**	**8.00**	**2.27**	**38.9**[A]	**57.7**[A]	**5.2**[A]
B. juncea										
CPI61680	321	53.5	13.7	1780	4238	13.43	1.91	38.2	55.7	21.4
JE8	179	26.2	14.0	1651	2362	7.87	1.93	37.5	52.3	10.1
WA5	199	31.6	15.0	1376	2217	9.96	2.25	34.3	60.0	11.5
ZE Sporospelka	217	33.9	16.0	1106	2483	12.87	2.40	40.3	56.0	13.8
mean	**229***	**36.3*****	**14.7*****	**1478*****	**2825*****	**11.03†**	**2.12ns**	**37.6**	**56.0**	**14.2**
CV%	38.3	83.0	52.8	52.3	64.1	47.5	43.7	8.7	11.9	98.9

Symbols († or *) referer to significance level of the orthogonal contrast comparing mustard and canola cultivars († $P<0.1$, * $P<0.05$, ** $P<0.01$, *** $P<0.005$)

[A] Insufficent canola seed was avalaible to preform oil determinations on all replicates of each cultivar, this may cause these values to be over estimated, as the samples measured were the best preforming while the missing samples were the worst. A more accurate estimate of average oil yield for canola may be 2.8 $g\ m^{-2}$ calculated from the average yield and oil contents of the canolas.

5.2.4. Experiment 4

Mustard produced more dry matter than canola in Experiment 4 (Table 5.3). It also yielded more seed, had a larger harvest index and produced more pods m^{-2} and seeds m^{-2}. There were no significant difference between the species in seed weight and a suggestion ($P<0.1$) that the number of seeds pod^{-1} was greater in mustard. No differences in oil or protein concentration were evident but mustard produced more oil per unit area. 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 values presented for canola may be overestimates because they represent an average for the best replicates only, 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.

5.2.5. Experiment 5.

Mustard produced 17% more dry matter than canola at the irrigated site but this was not reflected in seed yield because of mustard's lower harvest index (Table 5.4). Mustard bore more pods m^{-2} but had fewer seeds pod^{-1}, with the net result that there was no difference in the number of seeds produced by either species at this site. Seed weights were less in mustard than in canola while oil concentrations were greater. Protein concentration in the meal did not differ between the species.

At the rainfed site, mustard produced 51% more dry matter than canola but again this difference did not translate into a significant difference in seed or oil yield, because of mustard's lower harvest index. As for the irrigated site, mustard produced more pods m^{-2} but fewer seeds pod^{-1}. It also produced a greater number of seeds than canola but these were lighter than canola seeds. Protein concentration in the mustard meal was greater than in canola but the effect was small.

At the rain-exclusion site, mustard produced at least twice as much dry matter, seed and oil as canola. It also had over four times as many pods m^{-2} and just under three times the number of seeds m^{-2}. Oil concentration in the mustard seed was also greater. No significant differences existed in the harvest indices of the two species. Canola had more seeds pod^{-1} and heavier individual seed weights. No difference in protein concentration occurred.

Table 5.4 Yield and yield components, Experiment 5.

Cultivar	Dry matter (g m^{-2})	Seed yield (g m^{-2})	Harvest index (%)	Pods per m^{-2}	Seeds per m^{-2}	Seed # per pod	Mean seed weight (mg)	Oil content % dry matter	Protein content (%)	Oil yield (g m^{-2})
Irrigated site										
B. napus										
79NO13-364	482	147	30.4	3064	40858	13.44	3.58	46.6	38.8	68.9
82N128N9x36	345	97	28.0	2722	29036	10.72	3.35	46.1	38.3	44.7
Maluka	580	178	31.1	3781	54351	14.44	3.24	47.3	39.1	84.1
Taparoo	673	216	32.1	3956	60145	15.53	3.58	45.8	40.8	98.9
mean	**520**	**160**	**30.4*** **	**3381**	**46098**	**13.53*** **	**3.44*** **	**46.5**	**39.2**	**74.0ns**
B. juncea										
CPI61680	590	134	22.7	5543	46179	8.42	2.89	48.8	38.7	65.4
JE8	445	106	23.8	5991	50139	8.31	2.10	48.3	41.1	51.7
WA5	575	138	23.4	6246	46636	7.29	2.96	43.2	40.1	59.7
ZE Sporospelka	832	173	20.7	6001	66608	11.19	2.58	50.2	40.6	87.0
mean	**610***	**138ns**	**22.7**	**5945*** **	**52391ns**	**8.80**	**2.63**	**47.6***	**40.1ns**	**66.0**
CV%	23.4	27.2	8.1	21.3	24.2	9.3	5.6	2.7	6.2	27.9
Rainfed site										
B. napus										
79NO13-364	231	64	27.7	1238	15880	12.39	4.00	45.1	47.7	28.9
82N128N9x36	327	91	27.8	2359	24178	10.25	3.77	44.0	46.2	40.0
Maluka	229	68	28.6	1378	19020	12.84	3.65	44.4	46.6	30.6
Taparoo	141	41	25.9	993	9700	9.20	4.06	42.4	47.6	17.3
mean	**232**	**66**	**27.5*** **	**1492**	**17195**	**11.17*** **	**3.87*** **	**44.0**	**47.0**	**29.2**
B. juncea										
CPI61680	357	78	21.6	3525	27824	7.87	2.80	46.2	51.8	36.1
JE8	258	50	19.1	2986	17898	6.05	2.77	42.7	51.0	21.2
WA5	370	86	22.9	3817	24907	6.42	3.46	41.1	52.8	35.5
ZE Sporospelka	414	102	24.4	3462	34461	9.88	2.96	47.9	46.2	48.6
mean	**350*** **	**79ns**	**22.0**	**3448*** **	**26273** **	**7.56**	**3.00**	**44.5ns**	**50.5***	**35.4ns**
CV%	35.2	40.4	8.1	34.2	38.2	13.4	5.9	4.1	7.5	40.2
Rain exclusion site										
B. napus										
79NO13-364	180	29	15.1	787	9542	11.46	3.01	39.7	55.0	11.8
82N128N9x36	166	29	16.5	929	8468	8.75	3.49	38.5	52.4	11.5
Maluka	152	26	16.9	648	8300	12.34	3.16	40.6	54.8	10.6
Taparoo	161	34	18.3	909	9078	9.13	3.60	41.5	49.3	14.0
mean	**165**	**30**	**16.7**	**818**	**8847**	**10.42*** **	**3.31*** **	**40.1**	**52.9ns**	**12.0**
B. juncea										
CPI61680	336	62	18.3	2964	23857	8.18	2.61	43.3	54.2	26.9
JE8	350	76	21.8	3326	31721	9.81	2.40	43.0	53.5	32.7
WA5	435	78	17.9	4509	27094	6.28	2.85	40.9	45.2	31.6
ZE Sporospelka	335	55	15.9	2163	19302	8.53	2.90	43.0	51.4	24.2
mean	**364*** **	**68*** **	**18.5ns**	**3241*** **	**25494*** **	**8.20**	**2.69**	**42.5*** **	**51.1**	**28.9*** **
CV%	25.5	45.8	35.0	37.1	44.2	21.4	9.4	4.1	10.4	46.2

Asterisk referer to significance level of the orthogonal contrast comparing mustard and canola cultivars (* $P<0.05$, ** $P<0.01$, *** $P<0.005$) within each site.

5.2.6. Relationships across experiments

The performance of mustard and canola has been compared across sites and experiments (Fig. 5.1) using the "site mean total dry matter production" as an index of the stress conditions at a particular site (Finlay and Wilkinson, 1963). A small site mean dry matter production indicates water limiting conditions and a greater site mean dry matter production indicates less limiting conditions. Using this approach the field sites are ranked from the smallest soil water deficit to the largest as follows; irrigated site Experiment 3, rainfed site Experiment 3, irrigated site Experiment 5, rainfed site Experiment 5, rain exclusion site Experiment 5 and Experiment 4. Data from the glasshouse experiment, converted to a per unit area basis, are also included in Figure 5.1. The high level of productivity in the glasshouse experiment suggests that edge effects were present; however, trends in the data are similar to those in the other experiments and are included to allow a general comparision across all experiments. The comparison 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 throughout to limit such extraneous influences. The extent to which this was achieved can be gauged by 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 5.2) in those experiments where relevant data were available (Experiments 4 and 5).

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) components 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 5.1a). Similarly, pod number (Fig. 5.1d) and total seed number per unit area (Fig. 5.1e) 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 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 4, Fig. 5.1f) and individual seed weight (except under glasshouse conditions, Fig. 5.1g). Components of yield that fall into the second group, showing no comparative advantage to either species regardless of the moisture regieme, were seed oil (Fig. 5.1h) and meal protein (Fig. 5.1i). Harvest index (Fig. 5.1c) was the only component that fell into the third group with canola appearing to have an advantage except under severe water deficits.

Seed and, ultimately, oil yield are the integrators of all these components and both reflected an advantage to mustard under high water deficits; this advantage diminished to a similar performance at the lowest deficits tested in these experiments (Fig. 5.1. b & j).

The importance of the different components of yield varied. Seed yield is the function of seed number and seed weight. As discussed above, there was little change in individual seed weight across sites despite large differences in seed yield. Under field conditions, those differences can be almost exclusively explained by differences in seed number, which accounted for 99% and 98% of the yield variation in canola and mustard respectively, when data were pooled across the three field experiments (Fig. 5.3).

In the field both canola and mustard yields can be related to the amount of dry matter accumulated prior to peak flowering (Fig. 5.4). 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 ($y=-0.23+0.121x$, $r^2 = 0.35$ $P<0.05$).

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. 5.5). 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) in both species, with the exception of three canola genotypes under the severest water deficits experienced (Experiment 4).

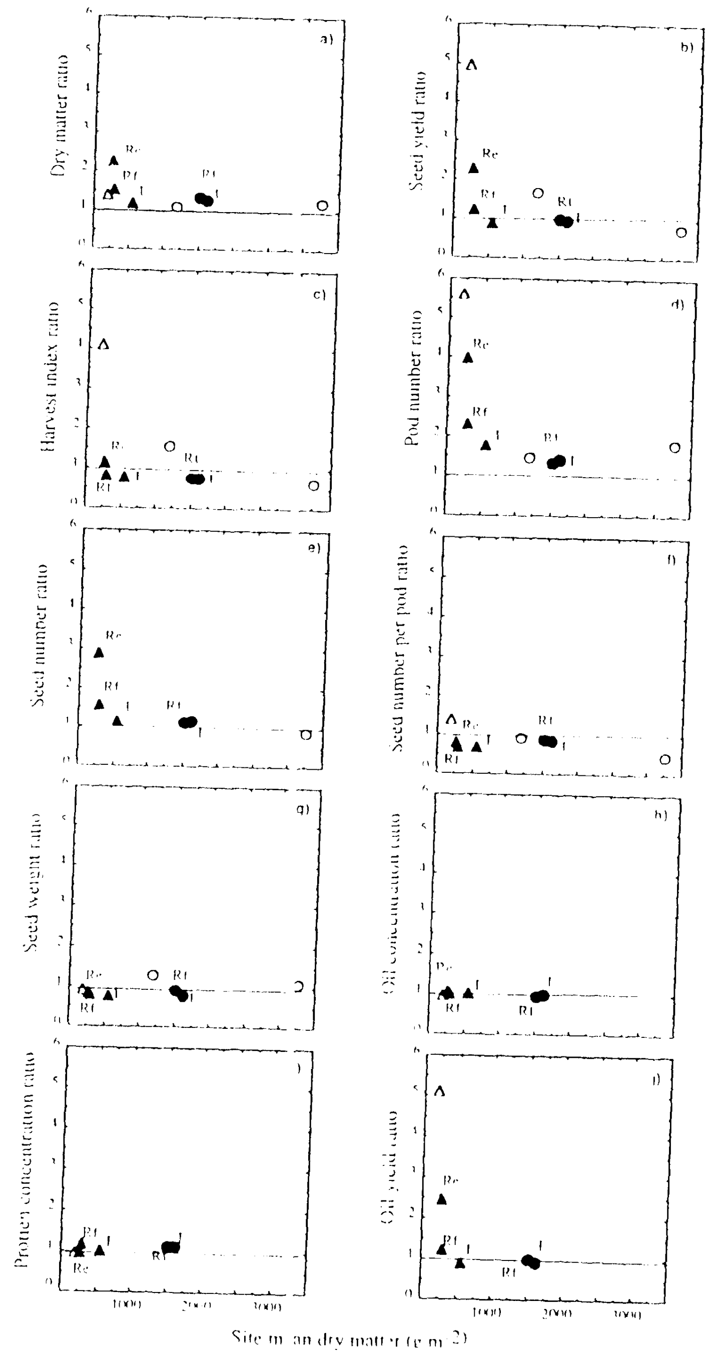

Figure 5.1. Relative performance of mustard compared to canola (mustard/canola) for different Experiments (○ Experiment 2, ● Experiment 3, Δ Experiment 4, ▲ Experiment 5, Re = Rainexclusion, Rf = Rainfed and I = Irrigated) and components of yield (a) dry matter, (b) seed yield, (c) harvest index, (d) pod number, (e) seed number, (f) seed number per pod, (g) seed weight, (h) oil concentration, (i) protein concentration and (j) oil yield.

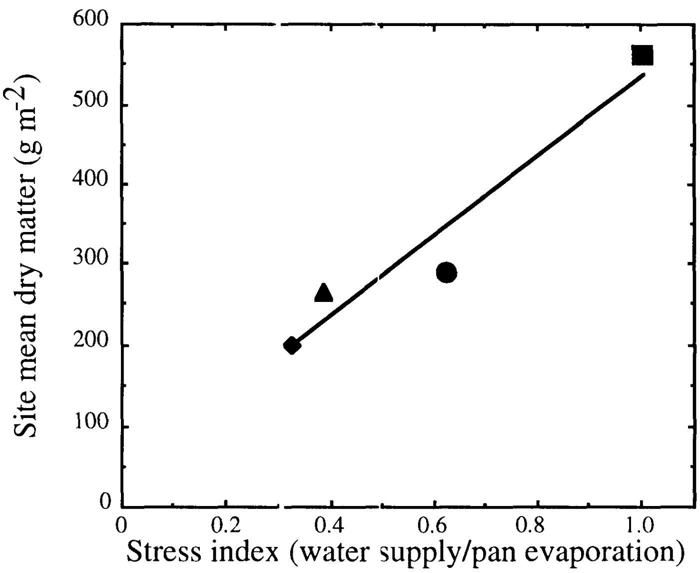

Figure 5.2. Relationship between a stress index (soil water plus rainfall divided by class A pan evaporation for the growing season) and site mean dry matter (◆ Experiment 4, ▲ rain-exclusion site Experiment 5, ● rainfed site Experiment 5, and ■ irrigated site Experiment 5). y=31.07+512.75x (r^2=0.93, P<0.05).

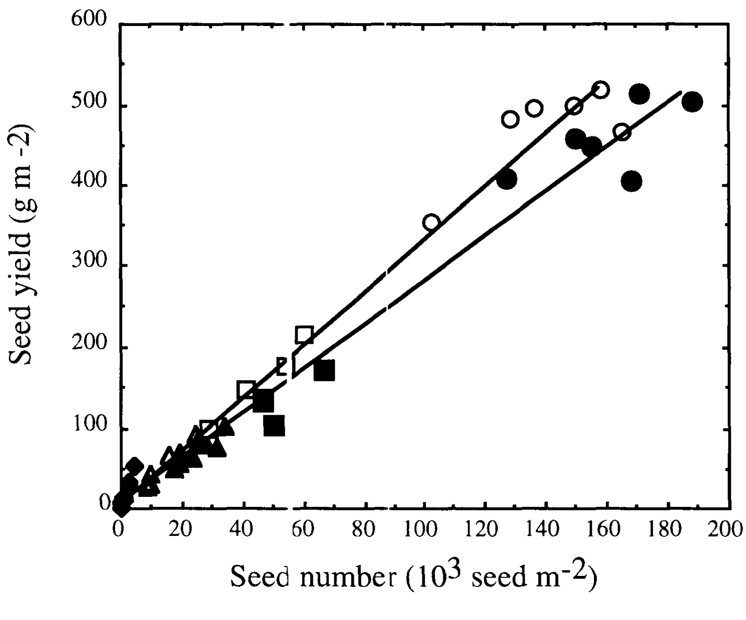

Figure 5.3. Relationship between seed number and yield under field conditions across low-deficit (● mustard and ○ canola at both sites of Experiment 3, ■ mustard and □ canola at the irrigated site of Experiment 5) and high deficit treatments (◆ mustard and ◊ canola Experiment 4, ▲ mustard and Δ canola at the rain-exclusion site of Experiment 5). 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.

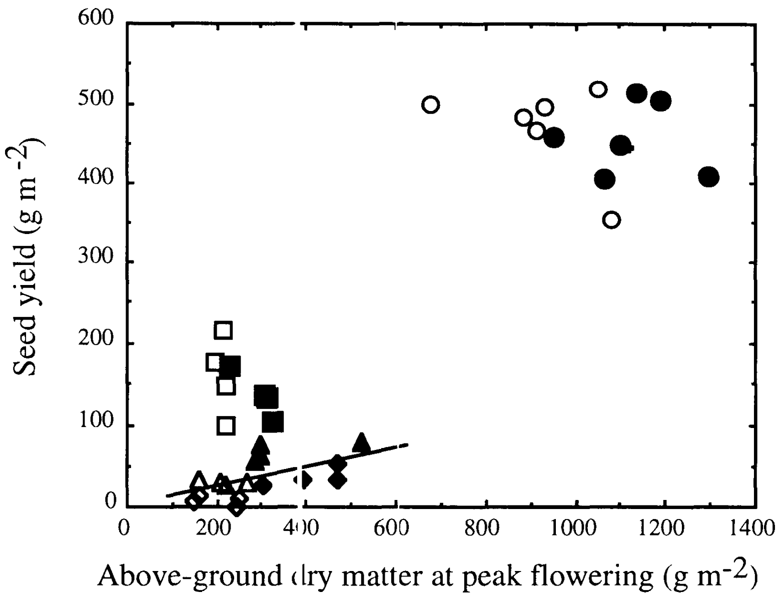

Figure 5.4. Relationship between crop dry weight at peak flowering (4.3) and yield for low deficit treatments (● mustard and ○ canola at both sites of Experiment 3, ■ mustard and ❑ canola at the irrigated site of Experiment 5) and high deficit treatments (◆ mustard and ◊ canola Experiment 4, ▲ mustard and Δ canola at the rain-exclusion site of Experiment 5)

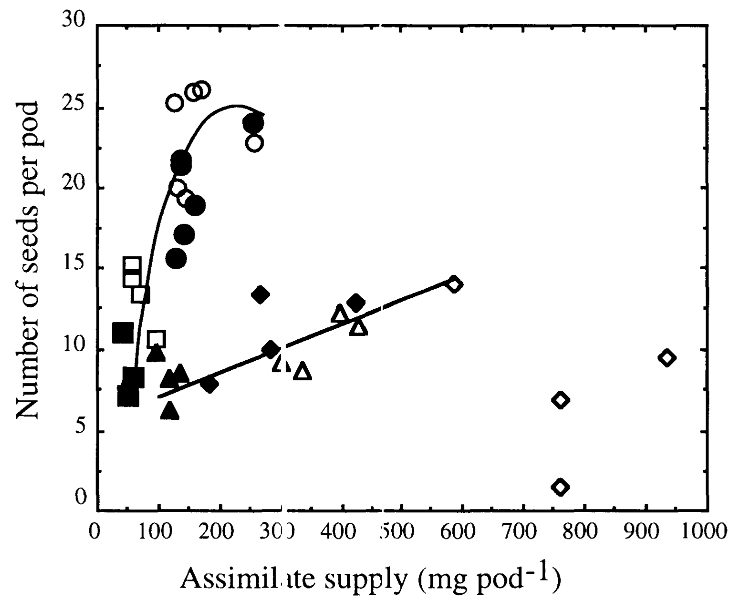

Figure 5.5. Relationship between assimilate supply (crop dry weight at peak flowering divided by pod number at maturity) and number of seeds per pod for low deficit treatments (● mustard and ○ canola at both sites of Experiment 3, ■ mustard and ❑ canola at the irrigated site of Experiment 5) and high deficit treatments (◆ mustard and ◊ canola Experiment 4, ▲ mustard and Δ canola at the rain-exclusion site of Experiment 5). Three canola cultivars from Experiment 4 have been excluded from the regression, see text for explanation.

5.3 Discussion

The results show that under high soil water deficits (rain exclusion site, Experiment 5) 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., 1990a). 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 impairing 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 3 and 5). 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 tonnes per ha) yields in mustard were as high as in canola. I 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 presence of a high yield potential in mustard (Woods et al., 1991; Woods, 1992). The present findings suggest that the breeding effort required to produce high yielding and well-adapted mustard cultivars may be less than might have been initially expected.

Oil concentration in the seed varied with stress level but both species responded in a similar manner; hence the oil yield per hectare mirrored that of seed yield with mustard's oil production more than double that of canola at the high deficit sites and at a similar level at the low deficit sites. Again this is a surprising result as lower 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 5.3). The trend for smaller seed weights in mustard 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 respectively). Earlier studies of canola have reported similarly close associations between seed yield and seed number (Mendham et al., 1981). This does not imply that variation in seed weight is unimportant. However, given the relative stability of the differences between the species in seed weight over a wide range of water deficits, factors that influence seed number are likely to be more important in adaptation to high deficits.

In Brassicas seed number is clearly a function of the number of pods per unit area and the number of seeds per pod. The yield structure of the two species differed in that canola had fewer pods and more seeds per pod than mustard. These field results were supported by the glasshouse study. In a comparison of yield structure in mustard and *B. campestris*, *B. napus* and *B. carinata* the same association was noted with mustard having the highest pod numbers per unit area but the fewest seeds per pod (Bhargava and Tomar, 1990). The same structural difference was also noted in a narrower comparison between *B. campestris* and mustard (Chauhan and Bhargava, 1986).

In canola, Mendham et al. (1984) have argued that breeders should be aiming to produce plants with fewer pods but with a higher potential number of seeds per pod as this would maximise seed survival and thereby increase seed number per unit area. A similar ideotype has been suggested for both canola and mustard in India (Bhargava and Tomar, 1990). It might appear that the data presented in this chapter argue against such an ideotype as mustard, with more pods and fewer seeds per pod, produced higher yields than canola under drought and similar yields under low deficit conditions. However, before reaching this conclusion it is necessary to establish if the differences found in seed number (and hence in yield) arose from differences in yield structure or from other factors particularly differences in dry matter production.

The relative importance of dry matter accumulation and yield structure is examined in Figure 5.6. Pod number, number of seeds per pod and total seed number are plotted against the dry matter present at maturity with these relationships being broken up into three phases. Phase one (I) contains plants with final dry matter between 0 and 400 g m^{-2}, corresponding approximately to those sites with high soil moisture deficits (Experiment 4 and the rain exclusion and rainfed sites of Experiment 5); phase two (II) contains plants with final dry matter between 400 and 1250 g m^{-2} corresponding to the moderate yields of the irrigated site in Experiment 5, and phase three (III) corresponds to plants with high yields (Experiment 3).

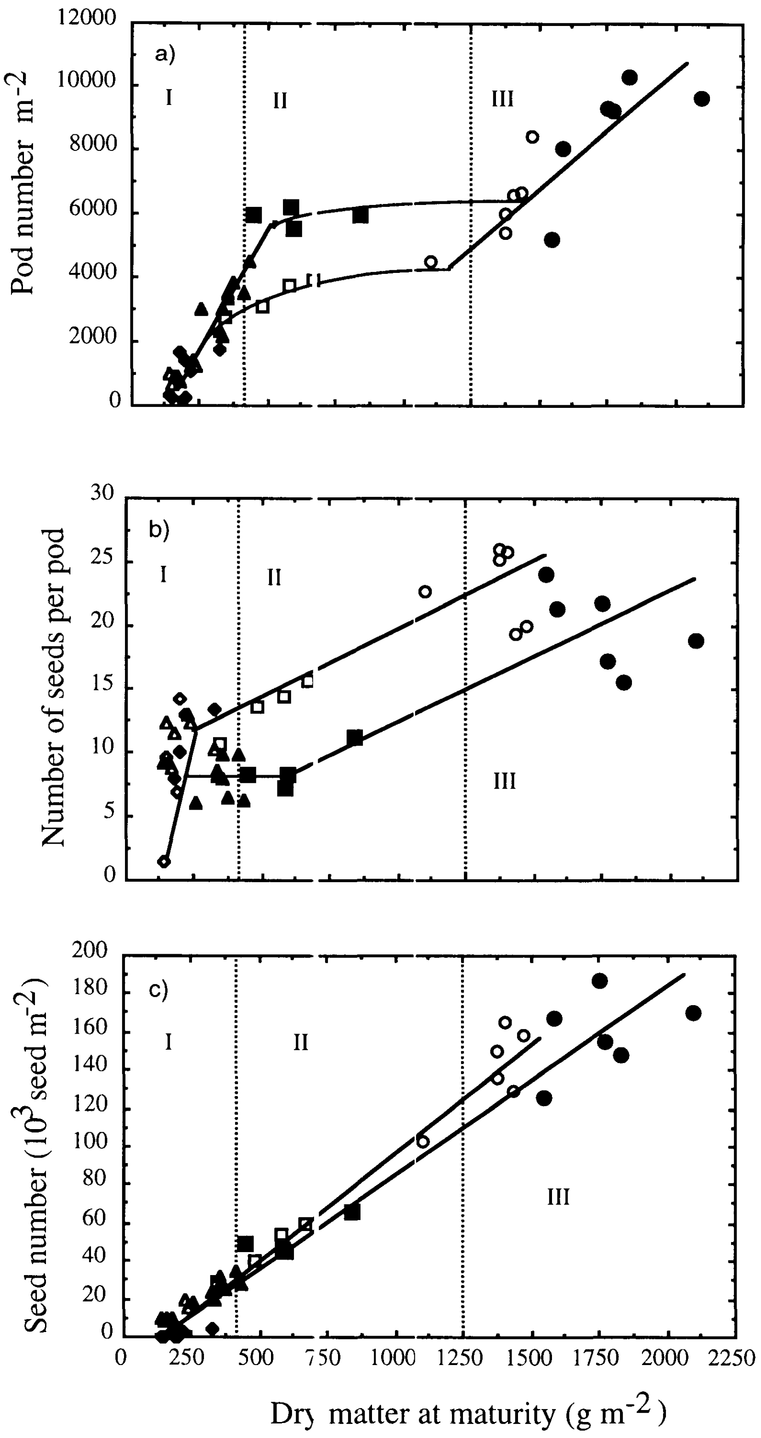

Figure 5.6. Relationship between dry matter at final harvest and a) pod number, b) number of seeds per pod and c) seed number. Symbols as for Fig. 5.3. Each point represents a cultivar. Lines in (a) and (b) are fitted by eye and in (c) by linear regression, canola y=-12367+112.1x (r^2=0.98, $P<0.001$) and mustard y=-10250+96.0x, (r^2=0.96, $P<0.001$).

The relationship between pod number and final dry matter indicates that, under low soil water deficits (Fig 5.6 a, phase III), canola and mustard plants producing the same final dry matter carry the same number of pods. However, under high or moderate water deficits (Fig. 5.6 a, phases I and II) mustard plants with a similar final dry matter as canola plants carry more pods. There is a different relationship between number of seeds per pod and final dry matter. Under high deficits (Fig 5.6 b, phase I) the number of canola seeds per pod increases (1 to 15) with increasing dry matter while the number of mustard seeds per pod remains relatively stable (approximately 8); in the second and third phase mustard plants of the same weight have 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 final dry matter producing similar seed numbers (Fig. 5.6 c). Under low deficits, canola does have a slight advantage in seed numbers because of its higher numbers of seeds per pod and its similar pod numbers. 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 chapter though sparsely distributed across a full range of dry matter production under low deficit conditions, do fit this model (Fig. 5.4). 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 numbers per pod and total numbers 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 deficits (Fig. 5.5). 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 deficits there is still a clear relationship between assimilate supply and ability to maintain seeds per pod. The only exception occured in canola at the very high deficits in Experiment 4. Crop dry weights per pod were quite high but the numbers of seeds per pod were low in three out of four canola genotypes, indicating seed abortion for reasons other than assimilate shortage (Fig. 5.5). Canola lost turgor more readily than mustard (Chapter 7) and 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, 1983; Morgan and King, 1984). The similar efficiencies of using assimilate to support seed numbers 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 (i.e. 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 indices is reflected in the individual site and treatment data. However, despite this inefficiency, mustard yields more seed 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 (1994a) 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 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.

5.4 Conclusion

Surprisingly, mustard seed and oil yields, at least in northern NSW are equal to those of canola under non drought conditions. Under drought conditions mustard has a seed yield advantage which increases with increasing severity of drought, with a fivefold advantage found under the severest conditions tested. Oil yields followed a similar pattern though the magnitude of the advantage was less being just short of a threefold advantage under the severest conditions tested. Mustard's seed protein concentration was found to be at least equal to that of canola and slightly higher under low stress conditions.

It is concluded that the large differences in yield structure (mustard having a greater number of pods but fewer seeds per pod) is not the primary cause of mustard's yield advantage under drought. The advantage is attributed, in terms of growth, to mustard's greater dry matter (assimilate) production which more than compensates for mustard's lower individual seed weights and poorer harvest indices.

The mechanism(s) underlying mustard's greater dry matter production under water stress require further study. Despite lacking a clear understanding of these mechanisms evidently mustard is comparatively well adapted to dry conditions and as such is worthy of further development in Australia.

CHAPTER 6
WATER USE AND WATER USE EFFICIENCY

6.1. Introduction

Adaptation to drought conditions is clearly influenced by the efficiency with which plants exchange water for carbon. In separate reviews, Fischer and Turner (1978) and Sinclair et al. (1983) suggested that variation in this efficiency is unlikely within species and variation between species will occur only when the species differ in their biochemical pathway (e.g. C_3 versus C_4). However, more recent studies have shown within species variation in wheat (Condon et al., 1993), barley (Hubick and Farquhar, 1989) and peanuts (Hubick et al., 1988; Wright et al., 1988a). There are few available studies on the variation in this efficiency in Brassicaceae. I am aware of only one comparing mustard and canola (Lewis, 1992). In that study, conducted under field conditions, no differences were found in their water use efficiency, assessed as total dry matter production divided by total water use. However, this assessment was based on only one cultivar of mustard and two of canola. In contrast, under glasshouse conditions, Lewis (1992) did find mustard to be more efficient than canola. In the current experiments large differences in growth (Chapter 4) and yield (Chapter 5) occurred between these species under high water deficits. In this chapter differences between the two species in water use efficiency are discussed in relation to the observed differences in growth and yield as are other factors that may influence the efficiency.

Some comment on terminology is required. Water use efficiency, as assessed by total dry matter production divided by total water use, is referred to as water use efficiency of dry matter production (W_d). Similarly total seed yield divided by total water use is referred to as water use efficiency of seed production (W_s). Transpiration efficiency is used to refer to (1) gas exchange measurements on a leaf level (T_l), (2) the amount of dry matter accumulated over the season divided by total water use, when water loss through soil evaporation has been minimised (T_d) and (3) the seed yield divided by water use, again when soil water loss has been minimised (T_s).

6.2. Results

6.2.1. Water use

In the glasshouse experiment (Experiment 2) mustard exceeded canola in the total amount of water used under low deficits (Table 6.1) while no difference was found under high deficits, where both crops used less water.

Water use data were not collected from Experiment 3. No significant differences were found between the species in Experiment 4 (Table 6.2). In Experiment 5, at the low deficit site, there was again no significant difference (Table 6.2) but at the high deficit site mustard used 57 mm less water than canola

($P<0.005$). No water use measurements were taken at the rain-fed site of Experiment 5. Most water was used at the irrigated site of Experiment 5 followed by the rain-exclusion site with about half the water use of the irrigated site and lastly by water use in Experiment 4 amounting to less than a quarter of that of the irrigated site of Experiment 5.

Water use from emergence to growth stage 3.1 (vegetative growth) and from 3.1 to 5.5 (reproductive growth) are presented for Experiment 5 in Table 6.3. No differences were found for the vegetative growth phase at the high deficit site. However, mustard used 55 mm less water than canola during the reproductive phase. There were no differences in water use between the species at the low deficit site for either growth phase.

6.2.2. Transpiration efficiency of dry matter production (T_d)

Because soil evaporation was minimised in Experiment 2 the data presented approximate to those for canopy transpiration efficiency (Table 6.4). There was some weak evidence for mustard having a greater T_d than canola ($P=0.26$), with a 12% advantage at low deficits and a 16% advantage under high deficits.

6.2.3. Water use efficiency of dry matter production (W_d)

In Experiment 4, mustard had a greater ($P<0.1$) W_d than canola (Table 6.5). This was also the case at both sites in Experiment 5 (Table 6.5), where the advantage increased from 1.2 to 2.8 times at the low and high deficit sites respectively. The values of W_d reported here are of a similar order to those reported elsewere though they tend to be slightly lowerer eg. Taylor et al. (1991) has reported W_d of canola ranging between 16 and 29 kg ha^{-1} mm^{-1} while values between 31 and 44 kg ha^{-1} mm^{-1}have been reported for mustard by Ramakrishna (1990).

W_d was partitioned for different phases of growth in Experiment 5 (Table 6.6). At the low deficit site there were no differences in W_d for either phase of growth. At the high deficit site, W_d in mustard's vegatative phase was 1.4 times that of canola ($P<0.01$). The advantage increased in the reproductive phase with mustard being more than five times as efficient as canola ($P<0.005$). At the low deficit site W_d for vegative growth appeared to be less than for reproductive growth, whereas, at the high deficit site, W_d for the reproductive phase was greater than for the vegetative phase for both species.

6.2.4. Transpiration efficiency of seed production (T_s)

In Experiment 2, under low deficit conditions there were no differences between the species in T_s (Table 6.7). At the high deficit site, mustard had 1.9 times larger T_s than canola ($P<0.01$) and was more efficient there than at the low deficit site ($P<0.01$). There was no difference between the mustard's T_s at the high deficit site and canola's at the low deficit site.

Table 6.1. Total water use (mm) for glasshouse experiment (Experiment 2).

Treatment	Total water use (mm)
Low deficit, *B. napus*	561 b
Low deficit, *B. juncea*	839 a
High deficit, *B. napus*	264 c
High deficit, *B. juncea*	252 c
Water	***
Species	*
Water x Species interaction	*
CV%	20.2

Means followed by the same letter are not significantly different (P=0.05)

Table 6.2. Total water use (mm) for field experiments.

	Experiment 4	Experiment 5 rain exclusion	Experiment 5 irrigated
B. napus			
79NO13-364	85	246	514
82N128N9x36	98	261	462
Maluka	73	243	483
Taparoo	78	226	485
mean	**84**	**244**	**486**
B. juncea			
CPI61680	86	183	486
JE8	103	207	491
WA5	66	187	486
ZE Skorospelka	119	172	486
mean	**94 ns**	**187 *****	**487 ns**
CV%	38.2	19.2	6.1

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

Table 6.3. Water use (mm) for different periods of growth in Experiment 5.

	Rain exclusion site		Irrigated site	
	0 to 3.1	3.1 to 5.5	0 to 3.1	3.1 5.5
B. napus				
79NO13-364	67	179	167	346
82N128N9x36	62	199	171	291
Maluka	64	179	166	317
Taparoo	60	166	161	324
mean	**63**	**181**	**166**	**320**
B. juncea				
CPI61680	53	130	169	317
JE8	58	149	170	322
WA5	69	118	165	321
ZE Skorospelka	66	106	172	314
mean	**62 ns**	**126 *****	**169 ns**	**318 ns**
CV%	18.3	27.5	5.5	9.0

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

Table 6.4. Transpiration efficiency of dry matter production (kg ha^{-1} mm^{-1}) for glasshouse experiment (Experiment 2).

Treatment	Transpiration efficiency (kg ha^{-1} mm^{-1})
Low deficit, *B. napus*	40.8 a
Low deficit, *B. juncea*	45.7 a
High deficit, *B. napus*	42.6 a
High deficit, *B. juncea*	49.7 a
Water	ns
Species	ns
Water x Species interaction	ns
CV%	19.5

Means followed by the same letter are not significantly different (P=0.05)

Table 6.5. Water use efficiency (kg ha^{-1} mm^{-1}) for field experiments.

	Experiment 4	Experiment 5 rain exclusion	Experiment 5 irrigated
B. napus			
79NO13-364	20.8	7.9	9.5
82N128N9x36	17.7	6.8	7.5
Maluka	27.1	6.7	12.0
Taparoo	24.1	7.2	13.9
mean	**22.4**	**7.1**	**10.7**
B. juncea			
CPI61680	39.1	18.2	12.2
JE8	23.6	17.2	9.2
WA5	33.1	23.7	11.9
ZE Skorospelka	22.7	19.5	17.1
mean	**29.6** †	**19.7** ***	**12.6** †
CV%	45.6	28.8	24.2

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

Table 6.6. Water use efficiency (kg ha^{-1} mm^{-1}) for different periods of growth in Experiment 5.

	Rain exclusion site		Irrigated site	
	0 to 3.1	3.1 to 5.5	0 to 3.1	3.1 to 5.5
B. napus				
79NO13-364	27.3	0.1	5.5	11.5
82N128N9x36	19.2	3.2	5.0	9.0
Maluka	18.1	2.9	7.8	14.4
Taparoo	14.9	4.7	7.4	17.2
mean	**19.9**	**2.7**	**6.4**	**13.0**
B. juncea				
CPI61680	23.8	15.9	9.9	13.4
JE8	25.8	14.0	7.8	9.9
WA5	32.3	18.2	9.7	13.0
ZE Skorospelka	32.5	13.8	8.1	22.2
mean	**28.6** **	**15.5** ***	**8.9 ns**	**14.6 ns**
CV%	36.3	85.8	47.3	32.5

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

Table 6.7. Transpiration efficiency of seed production (kg ha^{-1} mm^{-1}) for the glasshouse experiment.

Treatment	Transpiration efficiency (kg ha^{-1} mm^{-1})
Low deficit, *B. napus*	12.7 ab
Low deficit, *B. juncea*	9.1 a
High deficit, *B. napus*	8.0 a
High deficit, *B. juncea*	14.8 b
Water	ns
Species	ns
Water x Species interaction	**
CV%	23.4

Means followed by the same letter are not significantly different (P=0.05)

Table 6.8. Water use efficiency of seed production (kg ha^{-1} mm^{-1}) for field experiments.

	Experiment 4	Experiment 5 rain exclusion	Experiment 5 irrigated
B. napus			
79NO13-364	1.3	1.3	2.9
82N128N9x36	0.2	1.2	2.1
Maluka	0.8	1.2	3.7
Taparoo	1.5	1.5	4.5
mean	**0.9**	**1.3**	**3.2**
B. juncea			
CPI61680	5.3	3.4	2.8
JE8	3.1	3.7	2.2
WA5	5.0	4.1	2.8
ZE Skorospelka	3.5	3.3	3.6
mean	**4.2 *** **	**3.6 *** **	**2.8 ns**
CV%	77.3	48.5	27.6

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

6.2.5. Water use efficiency of seed production (W_s)

In Experiment 4, W_s of mustard was 4.7 times greater (P<0.005) than that of canola (Table 6.8). At the rain-exclusion site of Experiment 5, mustard's W_s was 2.8 times greater (P<0.005), while at the irrigated site there was no statistical difference between the species. Water use efficiency of seed production found in these experiments falls within the range of those reported elsewhere, such as 5.6 to 9.5 for canola (Bernardi and Banks, 1991; Taylor et al., 1991) and 2.4 to 9.6 for mustard (Upasani and Sharma, 1986; Singh et al., 1991).

6.2.6. Relationships across experiments.

The relative efficiency of water use in dry matter or seed production has been plotted against site mean dry matter production (5.3.2) in Figure 6.1. The efficiency of dry matter production increased as water deficit increased in Experiment 5.

However, under the greater deficits of Experiment 4, the relative advantage diminished. In contrast, the efficiency of mustard seed production showed an unambiguous adaptive response to stress with its W_s increasing with increasing water deficit. Supporting evidence for this response can be seen in the data of Experiment 2, where mustard's T_s increased with increasing deficit (Table 6.7).

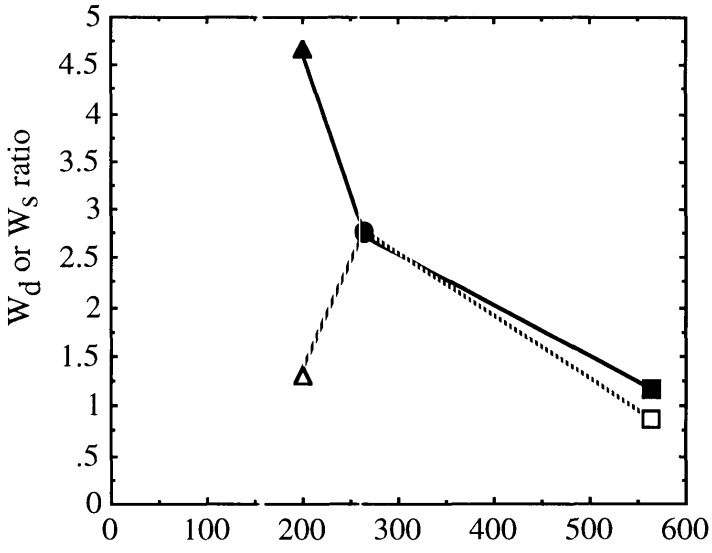

Figure 6.1. Relative water use efficiency (mustard/canola) of dry matter production (W_d, open symbols) and seed production (W_s, closed symbols) for different experiments (triangles for Experiment 4, circles for rain exclusion site Experiment 5 and squares for irrigated site Experiment 5).

6.2.7. Transpiration efficiency on a gas exchange basis (T_l)

Field measurements of transpiration efficiency on an instantaneous basis are presented in Table 6.9. In Experiment 3, these measurements were made prior to the imposition of water treatments hence the data have been pooled across the sites. Mustard was found to use water more efficiently than canola on the selected day ($P<0.005$). This was due to a comparatively higher ($P<0.1$) photosynthetic rate combined with lower ($P<0.005$) stomatal conductance. There were no differences between the species in sub stomatal CO_2 concentration. In Experiment 4, T_l of mustard was greater ($P<0.1$) than that of canola. Photosynthetic rates were higher ($P<0.05$), while there was no difference between the species in either stomatal conductance or substomatal CO_2 concentration. In Experiment 5, data were collected only from the irrigated site. For that site, on the selected day, no differences in T_l, Pn, g_s or C_i were found.

Table 6.9. Field measurements of transpiration efficiency (T_l) on a gas exchange basis, photosynthesis (Pn), stomatal conductance (g_s) and sub stomatal CO_2 concentration (C_i).

	T_l µmol CO_2 mol^{-1} H_2O	Pn µmol m^{-2} s^{-1}	g_s mol m^{-2} s^{-1}	C_i ppm
Experiment 3^A				
B. napus				
79NO13-364	8.8	15.5	1.793	294
Maluka	6.9	14.4	2.373	329
Taparoo	6.2	13.2	2.077	366
mean	**7.3**	**14.4**	**2.081**	**330**
B. juncea				
CPI61680	11.9	18.2	1.587	255
JE8	11.1	18.2	1.626	310
WA5	10.5	14.7	1.383	316
mean	**11.2 *****	**17.02 †**	**1.532 *****	**294 ns**
CV%	29.2	29.1	22.3	24.8
Experiment 4^B				
B. napus				
79NO13-364	23.6	12.9	0.608	173.2
Maluka	17.9	15.7	0.867	200.8
mean	**20.8**	**14.3**	**0.738**	**187.0**
B. juncea				
CPI61680	25.1	21.7	0.982	218.4
WA5	33.3	18.4	0.615	201.8
mean	**29.2 †**	**20.1 ***	**0.799 ns**	**210.1 ns**
CV%	45.2	30.3	35.5	15.0
Experiment 5^C				
Irrigated site				
B. napus				
79NO13-364	40.5	14.5	0.399	230
Maluka	32.6	16.9	0.546	260
mean	**36.6**	**15.7**	**0.473**	**245**
B. juncea				
CPI61680	34.0	24.9	0.774	233
WA5	48.7	14.2	0.312	238
mean	**41.4 ns**	**19.6 ns**	**0.543 ns**	**235 ns**
CV%	24.8	29.1	40.2	7.8

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

^A 26/9/90, 110 days after sowing, measurements taken between 11.00 am and 1.30 pm. Uniformly overcast day with an average PAR of 434± 5 mmol m^{-2} s^{-1} (n=72) for the measurement period.

^B 31/10/90, 57 days after sowing, measurements taken between 10.30 am and 1.00 pm. Clear day with an average PAR of 1832±55 mmol m^{-2} s^{-1} (n=34) for the measurement period.

^C 9/10/91, 133 days after sowing, measurements taken between 11.30 am and 1.30 pm. Clear day with occasional clouds and an average PAR of 1466±86 mmol m^{-2} s^{-1} (n=30) for the measurement period.

6.2.8. Leaf conductance

In Experiment 5, leaf conductance was measured on three occasions using porometry (Fig. 6.2). No significant differences were found between the species at either site regardless of the leaf surface measured. It is clear, however, from these data that conductances of both leaf surfaces, at 118 days after sowing, were substantially less in the high than in the low deficit treatments.

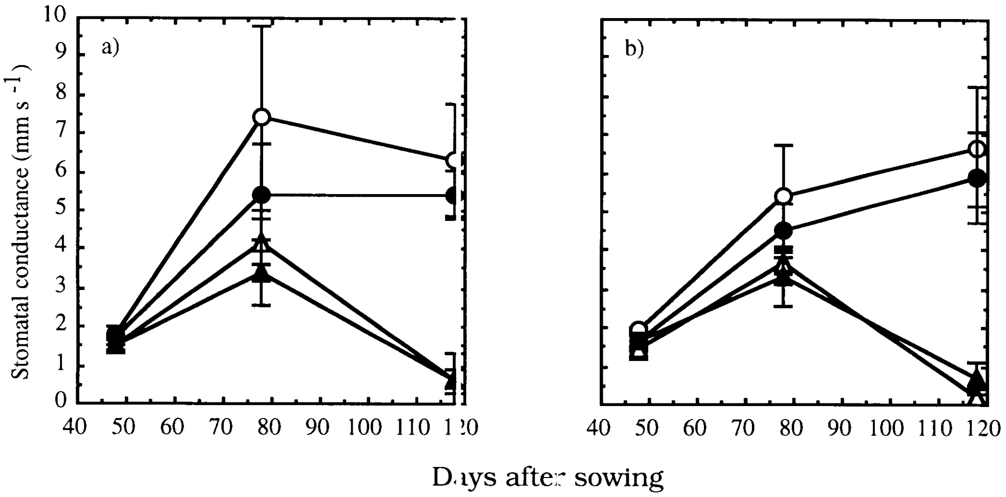

Figure 6.2. Change in stomatal conductance with time for a) adaxial and b) abaxial leaf surfaces (○ canola low deficit, ● mustard low deficit, Δ canola high deficit, ▲ mustard high deficit). Bars indicated standard errors.

6.2.9. Epidermal conductance

Data from Experiment 2 (Table 6.10) show that the species does not influence epidermal conductance (g_e) while water deficit does ($P<0.005$). Plants from the low water deficit treatments had an average g_e of 0.242 mm s^{-1} compared to 0.130 mm s^{-1} for the high deficit treatments (CV% = 59.4).

Table 6.10. Epidermal conductance (g_e, mm s^{-1}) of canola and mustard plants grown at different levels of water deficit under the glasshouse conditions of Experiment 2 (± s.e.)

Species	Low deficit	High deficit
Canola	0.28±0.05	0.12±0.02
Mustard	0.26±0.05	0.14±0.02

The influence of water deficit on g_e was further examined by plotting g_e against the amount of available water in the profile (Fig. 6.3.). The data are quite variable but nonetheless the general pattern is clear with g_e increasing from less than 0.1 mm s^{-1} under high water deficits (TAW<50%) to approximately 0.4 mm s^{-1} under low water (TAW> 75%).

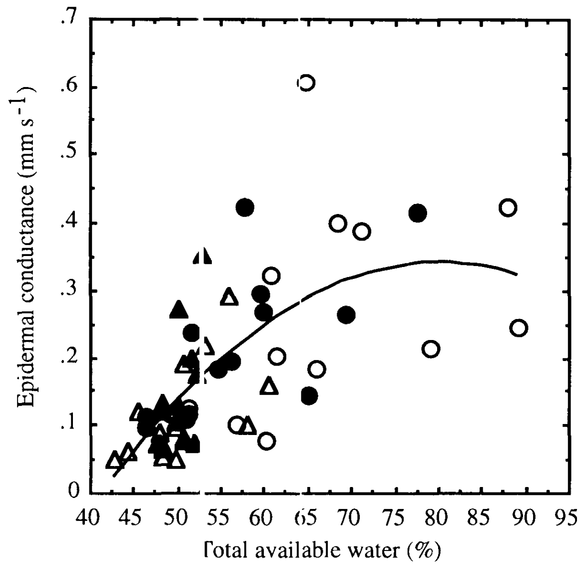

Figure 6.3. Effect of water deficit on epidermal conductance (O canola low deficit, ● mustard low deficit, Δ canola high deficit, ▲ mustard high deficit). This relationship is described by a curvilinear relationship, y=-1.121+0.36x-0.00023x^2, (r^2=0.466, P<0.001).

6.2.10. Stomatal frequency

The data from Experiment 2 were analysed using a split-plot design with the species and water treatments as whole plots, leaf surface as subplot and sample position from the leaf as the sub-sub plot. No effect of water deficit was found in these data, nor did position on the leaf have a large effect, hence the data presented have been pooled across deficit and sampling position (the full analysis is presented in Appendix 6.1). Both species had a similar number of stomata on the adaxial leaf surface and both had a higher (P<0 05) number of stomata on the abaxial compared to the adaxial surface (Table 6.11) However, mustard was found to have a higher (P<0.05) number of stomata than canola on the abaxial surface.

The frequency of stomata proved to be slightly higher than those reported by Major (1975) in *B. napus*, 92.3 and 124.8 per mm^2 for the adaxial and abaxial surfaces respectively. However, the ratio for adaxial to abaxial stomatal numbers of 0.74 calculated from Major (1975) is in close agreement with the ratio of 0.72 found in the current work. The difference in absolute numbers probably reflects differences in the size of leaves sampled. The ratio was 0.61 in mustard reflecting that crops higher number of stomata on the abaxial surface.

Table 6.11. Stomatal frequency (number mm^{-2}) sampled for adaxial and abaxial leaf surfaces of mustard and canola in Experiment 2 (n=54)

Leaf surface	Mustard	Canola
Adaxial	180.6 a	167.7 a
Abaxial	298.0 c	232.6 b

Means with the same letter are not significantly different (P=0.05).

6.3. Discussion

A comparatively high W_d arises from either lower water use or greater dry matter production or a combination of these. In the present field experiments, mustard's water use was either lower than that of canola as at the rain-exclusion site of Experiment 5 or was at a similar level as in Experiment 4, and also at the irrigated site of Experiment 5. This actuality, combined with its consistently greater dry matter production (Chapter 4) resulted in mustard's W_d being always greater than that of canola under the conditions of these experiments. In Experiment 5, this advantage in W_d was relatively greater at the high deficit site suggesting an adaptive response in mustard. However, in Experiment 4, at even greater levels of water deficit (5.2.6), the advantage was not as great as at the rain-exclusion site of Experiment 5. This may have resulted from late season insect damage affecting the dry matter weights (5.2.4.). The evidence for an adaptive response in W_d is thus weakened lacking positive support from Experiment 4 data.

Lewis (1992) in the only published comparison of W_d in mustard and canola that I am aware of, did not find significant differences with levels of 22.7 and 25.2 kg ha^{-1} mm^{-1} for canola and mustard respectively. However, this finding was based on only one cultivar of mustard and two of canola. He did report a significantly higher W_d for mustard under glasshouse conditions. Hence, while the published data are limited, it appears that the W_d of mustard is at least equal to that of canola and often greater.

Better water use efficiency of seed production was unambiguously adaptive in nature with mustard's advantage in W_s increasing with increasing water deficit. Clearly this arises from the interaction of dry matter production and harvest index and reflects the fact that there are adaptive differences in these parameters with the relative advantage of mustard in dry matter production increasing with increasing water deficits and its disadvantage in HI decreasing (Chapter 5). Similarly, under glasshouse conditions, mustard had a higher transpiration efficiency of seed production at the crop level under high deficits with no differences apparent under low deficits.

A higher W_d does not necessarily imply a higher transpiration efficiency. It may simply be the product of lower evaporation from the soil (Es) under a close canopy with the result that more of the total water is available for transpiration. Though Es was not measured directly in these experiments it would be reasonable to expect that it would be lower under a mustard canopy early in the season as this species had a higher LAI (Chapter 4). Furthermore, when W_d for the vegetative phase was plotted against leaf area index in Experiment 5 (Fig. 6.4) a positive relationship was found.

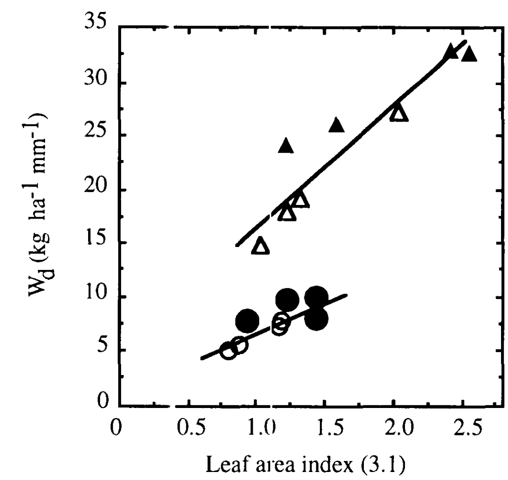

Figure. 6.4. Relationship between water use efficiency on a dry matter basis for the vegetative phase with the leaf area index at the end of the phase. (O canola low deficit, ● mustard low deficit, Δ canola high deficit, ▲ mustard high deficit). Under low deficit conditions y=7.00+10.19x, (r^2=0.88, P<0.005) and under high deficit conditions y=0.98+5 90x, (r^2=0.68, P<0.005).

However, there are two reasons why it is unlikely that Es more than partly explains the differences in W_d found in these studies. First, integrated estimates of transpiration efficiency over the season show a trend, albeit a weak one, for a higher T_d in mustard. Second, in rain-exclusion work, as the soil surface dries and is not rewet Es will normally be only a small proportion of ET. Consequently a major proportion of the water used in Experiment 4 and at the rain-exclusion site of Experiment 5 will have been by transpiration rather than from Es. At both sites mustard had a better W_d than canola, suggesting that, at least in part, the differences arose from differences in T_d.

Transpiration efficiencies at a leaf level were measured only once in each field experiment. As the measurements were taken at different stages of phenology it is not possible to gauge to what extent the differences in T_l were adaptive in nature. There is a further complication with the leaf transpiration data in that differences at leaf level are not always expressed at a canopy level (e.g. Frank et al., 1987 in wheatgrass). Nonetheless, in the current experiments the T_l of mustard was either equal to or higher than that of canola, a fact that is likely to explain the greater T_d of mustard.

When the W_d data for different phases of growth are examined against water deficits, as assessed by site mean dry matter production, it is clear that there is no adaptive response expressed for the vegetative phase (Fig. 6.5) with mustard having a similar advantage in W_d at both high and low deficit sites. This is not surprising since there was little difference in water deficit between the sites at this early stage in the experiment (Chapter 7). However, in the reproductive phase there is strong evidence for an adaptive response (Fig. 6.5). This can be taken as evidence supporting adaptive differences in the T_d of the crops as the Es would have been small in this phase. These differences may be influenced by the disparate yield structure of the species. Singh et al. (1986) showed that the pods made a contribution of 61.1% towards canopy photosynthesis relative to the 35.2% contribution by the leaves during late pod filling. Hence, pods are important sites for water and carbon exchange late in the season and they must influence T_d and W_d. The canopy structure of mustard, with a relatively high number of small pods, may give this crop an advantage in T_d under high deficit conditions.

Dark respiration is another factor that can influence whole plant T_d. Singh et al. (1990b) reported it to be as high as 39% of the carbon gain by the canopy of mustard under drought conditions. A variation in this rate between the species would be reflected in T_d. However, I am not aware of any published comparisons of the species for this factor. Nonetheless, the above comments remain valid as these processes are integrated in the final T_d and W_d measurements. In general the current work suggests that real differences in transpiration efficiency exist, both at a leaf and canopy level.

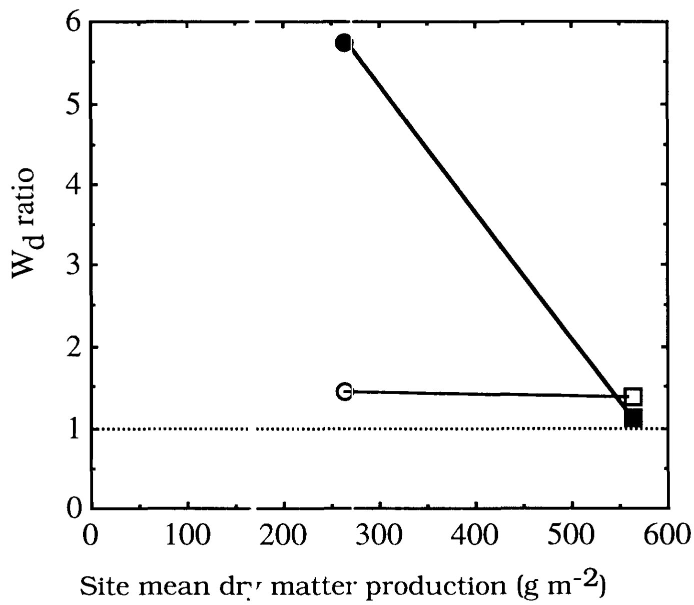

Figure 6.5. Relative water use efficiency (mustard/canola) of dry matter production for vegetative growth, open symbols and reproductive growth, closed symbols, for different sites of Experiment 5 (circles for rain exclusion site and squares for irrigated site).

Differences in instantaneous T_l can arise through differences in conductance or photosynthetic rates or a combination of these. The gas exchange data (Table 6.9) show that on one occasion out of three there were differences in conductance, mustard having a lower conductance than canola. When g_s was measured by porometery no differences were found between the species nor could differences in epidermal conductance be shown. It would appear that the differences in T_l are predominantly a function of the higher assimilation rate of mustard. In work with peanut cultivars, it was similarly concluded that the differences found in T_l were predominantly caused by variation in the assimilation capacity of the cultivars (Wright et al., 1988a; Hubick et al., 1988). It does need to be stressed, however, that T_l is a ratio and, as such, the lower g_s observed in Experiment 3 contributed to the increased T_l.

An association between high transpiration efficiency, as measured by low carbon isotope discrimination, and poor early canopy growth has been reported in wheat (Condon et al., 1993). This does not appear to be the case with mustard as high W_d is associated with vigorous early canopy growth (Fig. 6.4). Some of this difference arises from differences in Es and hence is unrelated to T_d. However, there is some evidence, as discussed earlier, to suggest a greater T_d in mustard, giving at least a circumstantial indication that a negative association between T_d and canopy growth is unlikely to exist in mustard or canola.

Wright et al. (1988a) found a negative relationship between carbon isotope discrimination and specific leaf weight (SLW) in peanuts indicating a positive relationship between T_l and SLW. Measurements of specific leaf weight made the present experiments represent a mean SLW of the canopy as opposed to the SLW of the individual leaf used for the gas exchange measurements. In Figure 6.6, T_l has been plotted against specific leaf weight. No relationship was apparent in Experiment 4 (Fig. 6.6. a) but in Experiment 5 there was some evidence of a positive relationship between T_l and specific leaf weight for SLWs between 45 and 65 g m^{-2} (Fig 6.6b). For SLW exceeding 65 g m^{-2} the relationship breaks down. A relationship between T_l and SLW is to be expected as thicker leaves have more photosynthetic machinery per unit leaf area than have thinner leaves, assuming a constant nitrogen to carbon ratio. The evidence for such a relationship, under the field conditions prevalent in these experiments, is tenuous. This may reflect difficulties in using a bulk mean of specific leaf weight for the whole canopy rather than to suggest that no such relationship exists on an individual leaf basis.

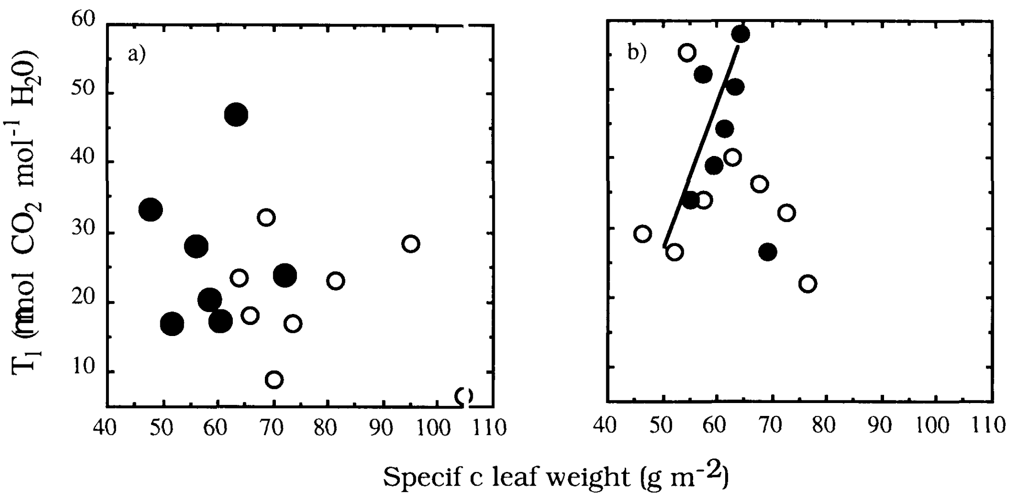

Figure 6.6. Relationship between transpiration efficiency on a gas exchange basis and specific leaf weight a) 57 days after sowing in Experiment 4 and b) 110 days after sowing for the irrigated sight of Experiment 5. (○ canola, ● mustard). For specific leaf weights between 45 and 65 in b y=-29.19+1.24*x*, (r^2=0.40, P<0.05).

Leaf conductance values tended to be greater for the adaxial compared to the abaxial leaf surface under irrigated conditions. Singh et al. (1982b) have reported a similar finding for mustard and there are reports of corresponding findings in other species, for example in wheat (Morgan, 1977b). Stomatal frequency on the adaxial leaf surface was found to be similar for mustard and canola. Both species had more stomata on the abaxial than on the adaxial surface, a common feature in most plant species (Blackmore and Tootill, 1988). Mustard differed from canola in having more abaxial stomata. These differences in the number and distribution of stomata do not appear to influence g_s (or g_e) which shows little variation between the species. When some variation does occur, g_s is lower in mustard than canola, opposite to what would be expected if there was a positive relationship between g_s and stomatal number (over the range measured here). Hence differences in stomatal number are unlikely to contribute to the adaptive advantage of mustard under water deficit conditions.

Epidermal conductance represents the lowest water loss that a leaf can sustain while still functional. Muchow and Sinclair (1989) showed that g_e was positively related to stomatal density in *Sorghum bicolor*, indicating that it is made up of losses through incompletely sealed stomata as well as through the cuticle. The values reported here are within a similar range to those reported by others elsewhere, such as 0.03 to 0.17 mm s^{-1} for four grain legumes (Sinclair and Ludlow, 1986). There was no evidence of differences between mustard and canola in this trait with parallel reductions in g_e in the presence of increasing water deficits (Fig 6.3). Therefore, this trait does not appear to contribute to mustard's adaptive advantage under water deficits. It should, however, be noted that this conclusion is based on work with only one cultivar of each species. The finding of declining g_e with increasing water deficit in mustard and canola concurs with findings in other species e.g. *Prunus laurocerasus* (Meidner, 1986).

There is an interesting negative relationship between W_d and harvest index in the data, at least for mustard (Fig. 6.7). In peanut a negative association between harvest index and transpiration efficiency has been noted (Wright et al., 1988a) but it was absent in some cultivars suggesting that the relationship may be associative rather than causal.

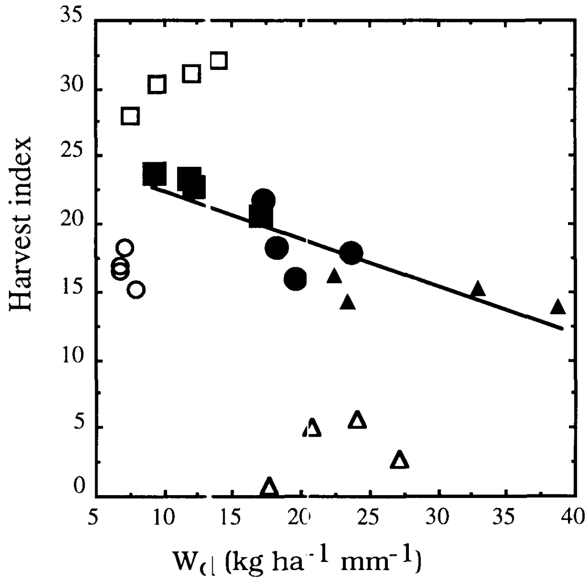

Figure 6.7. Association between water use efficiency of dry matter production and harvest index across three different sites. Open symbols represent canola and closed mustard, triangles for Experiment 4, circles for rain exclusion site Experiment 5 and squares for irrigated site Experiment 5. y=26.25-0.37x, (r^2=0.74, P<0.005).

Differences in W_d, as discussed, probably arise from two main factors. First, the greater early vigour of mustard reduces the amount of soil evaporation, thus increasing the proportion of soil water available for transpiration. Second, mustard uses the water transpired with greater efficiency than canola both at a leaf and a canopy level. Mustard is able to maintain a greater leaf area duration and thereby produce more dry matter than canola under stress conditions (Chapter 4). The greater efficiency of water use in mustard is a factor in these differences. At a more mechanistic level the differences in transpiration efficiency may arise from a greater assimilation efficiency in mustard. To explain the large adaptive differences between the species in growth and yield requires that this difference in assimilation efficiency also be adaptive in nature. The data are not sufficient to indicate if this is the case but it may well be so. How mustard could maintain assimilation efficiency under stress levels that reduce the efficiency in canola is of interest and one possible explanation is examined in Chapters 7 and 8.

6.4. Conclusion

Mustard has a water use efficiency of dry matter production equal to or greater than that of canola when their phenology is matched. Its water use efficiency of seed production is equal to that of canola under low deficit conditions and is greater under high deficits. This is also likely to be the case for W_d, but, the evidence for an increasing advantage with increasing water deficit is less conclusive. As water use efficiency is a highly integrated character many factors play a part in its determination. Some of the factors that were found to vary between mustard and canola and are likely to influence their water use efficiency are as follows:-

1) Vigorous early canopy development in mustard which is likely to reduce soil water evaporation as a proportion of total water use and thereby allowing more of the available water to be transpired

2) Higher leaf level transpiration efficiency in mustard. In large part this is probably due to mustard's greater assimilation capacity rather than a difference in stomatal conductance.

3) Higher leaf level transpiration efficiency of mustard expressed in a higher canopy level T_d on some occasions.

4) Differences in pod transpiration efficiency may strongly influence water use efficiency. This may be related to difference in pod characteristics in the species.

Neither stomatal density nor epidermal conductance are likely to explain the differences between mustard and canola in water use efficiency. The negative relationship found between harvest index and water use efficiency of dry matter production indicates that care needs to be taken to determine that this is not a causal relationship if W_d were to be considered as a breeding criterion.

Mustard's ability to maintain leaf function under deficit conditions is likely to be linked to its ability to maintain assimilation rates over the season and it may also help to maintain a higher assimilation efficiency.