

CSIRO Publishing

Australian  
Journal of  
Agricultural  
Research

VOLUME 53, 2002  
© CSIRO 2002

A journal for the publication of original contributions  
towards the understanding of an agricultural system

**All enquiries and manuscripts should be directed to:**

*Australian Journal of Agricultural Research*  
CSIRO Publishing  
PO Box 1139 (150 Oxford St)  
Collingwood, Vic. 3066, Australia



**CSIRO**  
PUBLISHING

Telephone: +61 3 9662 7628  
Fax: +61 3 9662 7611  
Email: [publishing.ajar@csiro.au](mailto:publishing.ajar@csiro.au)

Published by CSIRO Publishing  
for CSIRO and the Australian Academy of Science

[www.publish.csiro.au/journals/ajar](http://www.publish.csiro.au/journals/ajar)

## Growth and yield differences between triazine-tolerant and non-triazine-tolerant cultivars of canola

M. J. Robertson<sup>A</sup>, J. F. Holland<sup>B</sup>, S. Cawley<sup>C</sup>, T. D. Potter<sup>D</sup>, W. Burton<sup>E</sup>, G. H. Walton<sup>F</sup>,  
and G. Thomas<sup>G</sup>

<sup>A</sup>CSIRO Sustainable Ecosystems, Agricultural Production Systems Research Unit, 120 Meiers Rd, Indooroopilly, Qld 4068, Australia.

<sup>B</sup>NSW, Tamworth Centre for Crop Improvement, RMB 944, Tamworth, NSW 2340, Australia.

<sup>C</sup>Farming Systems Institute, QDPI, PO Box 308, Roma, Qld 4455, Australia.

<sup>D</sup>SARDI, PO Box 618, Naracoorte, SA 5271, Australia.

<sup>E</sup>Victorian Institute of Dryland Agriculture, Private Bag 260, Horsham, Vic. 3401, Australia.

<sup>F</sup>Agriculture Western Australia, Locked Bag 4, Bentley Delivery Centre, WA 6983, Australia.

<sup>G</sup>QDNR, Leslie Research Centre, Qld 4350, Australia.

**Abstract.** Canola tolerant to the triazine group of herbicides is grown widely in Australian broad-acre cropping systems. Triazine-tolerant (TT) cultivars are known to have a yield and oil content penalty compared with non-TT cultivars. This study was designed to elucidate the crop physiological basis for the yield differences between the two types. Two commercial cultivars, near-isogenic for the TT trait, were compared in a detailed growth analysis in the field, and 22 crops were compared for phenology and crop attributes at maturity. In the growth analysis study, the TT trait was found to lower radiation use efficiency, which carried through to less biomass at maturity. There were minimal effects on leaf area development and harvest index, and no effect on canopy radiation extinction. Across the 22 crops, where yield varied from 240 to 3400 kg/ha in the non-TT cultivar, yield was on average 26% less in the TT cultivar due to less biomass produced, as there was no significant effect on harvest index. The difference in oil content (2–5%) was greater in low oil content environments. Flowering was delayed by 2–10 days with a greater delay being in later flowering environments. Quantification of the physiological attributes of TT canola allows the assessment of the productivity of different cultivar types across environments.

**Additional keywords:** radiation use efficiency, leaf area, harvest index, biomass, herbicide.

### Introduction

Canola (oilseed rape) is the main winter-growing oilseed in Australia, expanding from 50 000 ha in 1988 to 1 700 000 ha in 1999 (Colton and Potter 1999). Cultivars with tolerance to the triazine group of herbicides were first commercialised in 1993 with the release of the cultivar Siren. New cultivars rapidly followed with both early maturity and mid-season maturity. This resulted in the rapid spread of triazine-tolerant (TT) canola across Australia, especially in Western Australia where TT cultivars now comprise more than 90% of the total crop (Colton and Potter 1999). TT cultivars are used particularly in those areas where the weed burden cannot be controlled in standard canola cultivars (Sutherland 1999).

Tolerance to triazine herbicides is associated with low photosynthetic performance resulting from inefficient photochemistry (Arntzen *et al.* 1982; Hart and Stemler 1990a, 1990b; Hart *et al.* 1992). This leads to lower early vigour, reduced growth and yield, and lower grain oil content in the absence of application of triazine herbicides (Colton

and Potter 1999; Lythgoe *et al.* 2001). Although other forms of herbicide resistance with no associated yield penalty are now becoming available to Australian canola growers (e.g. imidazolinone), TT cultivars will continue to be grown in the foreseeable future because of their lower costs of production, the incorporation of the TT trait into well adapted genetic backgrounds, and compatibility with rotations and herbicide use.

Although rules-of-thumb are available for the yield penalty associated with the TT trait (e.g. Colton and Potter 1999), there is little understanding about causal physiological mechanisms at the level of the crop. Some understanding of the crop physiological processes affected by the TT trait will allow the calculation of growth and productivity differences between TT and non-TT canola across diverse environments. Such knowledge, when incorporated into tools such as crop simulation models, can be used to assess the productivity of different cultivar types across environments and aid the design of improved crop management systems.

The aims of this paper are to (1) analyse the crop physiological basis for growth and yield differences between non-triazine-tolerant and triazine-tolerant cultivars of canola through measurement of canopy development, radiation interception, and biomass accumulation and partitioning to yield, and (2) examine variation in the performance of a triazine-tolerant compared with a near-isogenic non-triazine-tolerant cultivar across diverse production environments in Australia.

## Materials and methods

The studies described in this paper compared the performance of a TT cultivar (Surpass600TT) with that of a non-triazine-tolerant cultivar (Surpass600). Surpass600TT and Surpass600 originate from the breeding program of Pacific Seeds and are near-isogenic for the TT trait (A. Easton, Pacific Seeds, Toowoomba, QLD, pers. comm.).

### Growth analysis experiment

A TT cultivar (Surpass600TT) was compared with a non-TT cultivar (Surpass600) in terms of growth, development, and yield under fully irrigated and partly irrigated conditions at Lawes, south-east Queensland (27° 33' S, 152° 34' E) in the 1999 season. The soil at the site is a Black Vertosol (endocalcareous, self-mulching, black, Vertosol, Ug5.15) with a clay content around 60% and organic carbon in the surface layers of 1.5%.

### Design, treatments, and crop management

Experimental design was a randomised complete block, replicated 3 times, with 2 water supply regimes: fully irrigated and partly irrigated. Individual plots were 10 m by 1.5 m to provide for six 1-m<sup>2</sup> quadrat cuts during the growing season. The experiment was sown on 31 May 1999. Row spacing was 20 cm and sowing depth 30 mm. Plots were thinned to the target density of 40 plants/m<sup>2</sup> at 21 days after sowing (DAS). Nitram (NH<sub>4</sub>NO<sub>3</sub>) was applied at a rate of 180 kg N/ha at 32 DAS. Weeds were managed with pre-sowing knockdown herbicides and then mechanically during crop growth. Both the partly and fully irrigated treatments received a total of 115 mm of spray irrigation on 4 dates between sowing and harvest, with fully irrigated treatments receiving 2 extra irrigations totalling 58 mm between the late vegetative stage and mid grain-fill.

### Measurements

Plots were sampled for biomass (1-m<sup>2</sup> quadrats) at intervals during crop growth, with the fully irrigated plots sampled 8 times and the partly irrigated 6 times. On each occasion, a subsample of 5 plants was partitioned into leaf, stem, dead leaf, and, when appropriate, podwall and grain. The plant parts were dried at 80°C and weighed. Prior to drying, the area of the green leaf subsample was measured using an automatic leaf area meter (Delta-T Devices Ltd). At 3 early samplings, leaves attached to the main stem were further partitioned according to node position for measurement of leaf size for each node. Ten tagged plants from each plot were non-destructively sampled on a weekly basis to measure the number of fully expanded leaves on the main stem. These data were used for calculation of the rate of node appearance.

The dates at which the crop reached major phenological stages were recorded. The buds visible stage was defined as 50% of plants with buds visible above the leaf whorl, flowering as when 50% of plants had at least one open flower, and maturity as 95% of pods turned brown.

Solar radiation intercepted by the canopy was recorded daily using Delta-T tube solarimeters. On 2 July (32 DAS), a tube solarimeter (Type TSL, Delta-T Devices, Cambridge, Great Britain) was placed at ground level perpendicular to the crop rows in each replicate plot. A reference tube solarimeter was placed above the crop. Fallen dead leaf was

periodically removed where it had fallen on the solarimeters. The tube solarimeters were used to record the incident and transmitted short-wave radiation (0.35–2.5 µm) at 2-min intervals. Daily totals and individual tube-calibration factors were used to calculate the fraction of the incident radiation intercepted by the crop ( $f$ ). The amount of radiation intercepted was calculated as the product of the daily fraction intercepted and incident radiation.

At maturity, 2 m<sup>2</sup> was sampled for grain yield and biomass determination. All plants from the quadrat were threshed by hand. A subsample was retained for determination of grain oil content using near infrared reflectance.

Meteorological data including rainfall, maximum and minimum temperature, and total solar radiation (LI-COR LI200sz Pyranometer) were recorded on a daily basis.

### Data analysis

Data were analysed in terms of the key determinants of biomass accumulation: the interception of solar radiation by the crop leaf canopy and the use of this intercepted radiation to grow biomass. The radiation extinction coefficient ( $k$ ) quantifies the effectiveness with which a crop canopy, of a given leaf area index, intercepts radiation.

Light interception fraction ( $f$ ) was related to leaf area index (LAI) using Beer's Law:

$$f = 1 - \ln^{-k} \text{LAI}$$

where  $k$  is the extinction coefficient.

Radiation use efficiency (RUE) describes how efficiently intercepted radiation is converted to biomass. Cumulative intercepted radiation was calculated by multiplying the daily incoming solar radiation by  $f$  for each day after emergence. Values of  $f$  between emergence and the installation of tube solarimeters were estimated by interpolation. RUE was calculated as the slope of the linear regression of accumulated biomass on cumulative intercepted radiation, with a non-zero intercept allowed. The regression was fitted using a step-wise regression procedure where, starting at crop maturity, data were dropped from the regression until no further improvement was gained in the proportion of variance accounted for by the regression.

Analysis of variance was used to test for treatment effects at individual sampling times.

### Comparison of cultivars across diverse environments

Surpass600 and Surpass600TT were sown in a total of 22 environments, comprising different locations, sowing dates, rates of N fertiliser, and water supply (Table 1). Seed in each experiment originated from the same source to minimise variation in response due to seed lot.

At each location, except those at Lawes, crops were grown under dryland conditions. Standard agronomy was used for growing canola in each region. Triazine herbicides were not used, so that cultivar differences were not due to responses to herbicide application. Measurements were made on phenology and above-ground biomass. Grain yield and grain oil content were determined at maturity. Not all measurements were conducted in all crops. In all but one crop, yield was measured. Of the harvested crops, 12 were sampled by hand, which enabled an estimate of above-ground biomass and harvest index to be made, whereas in the remainder, yield was determined with a machine harvester. Grain oil content was determined in 16 crops. In 17 crops, measurements were made of the date of start of flowering.

Regression analysis was performed to determine the relative performance of the TT and non-TT cultivar in terms of grain yield, biomass, harvest index, and oil content.

In both studies in this paper, crop biomass and grain yield are expressed on an oven-dry basis and oil content at 8.5% moisture content.

**Table 1. Details of locations and sowing dates for the comparison of cultivars across environments**

Location	Latitude (S) and longitude (E)	Sowing dates
Hodgson, Qld	26.55, 148.78	17 May 1999
Nindigully, Qld <sup>A</sup>	28.36, 148.82	22 June 1999
Roma, Qld	26.55, 148.78	26 April, 26 May, 12 July 1999
Rocky Crossing, Qld	28.63, 148.86	18 June 1999
St George, Qld	28.04, 148.58	14 May 1999
Lawes, Qld <sup>B</sup>	27.55, 152.34	31 May 1999
Talwood, Qld	28.52, 150.33	11 May 2000
Muckadilla, Qld	26.55, 148.78	12 May 2000
Tara, Qld	27.17, 150.27	5 June 2000
Horsham, Vic.	36.67, 142.30	26 June 1999
Moree, NSW	29.48, 149.84	17 June 1999
Tamworth, NSW	31.09, 150.85	14 April, 17 May, 18 June, 20 August 1999
Mingenew, WA	29.19, 115.44	31 May 1999
Newdegate, WA	33.09, 119.02	24 June 1999
Kybybolite, SA	36.88, 140.93	23 June 1999

<sup>A</sup> With and without N fertiliser.

<sup>B</sup> Full and part irrigation.

## Results

### Growth analysis experiment

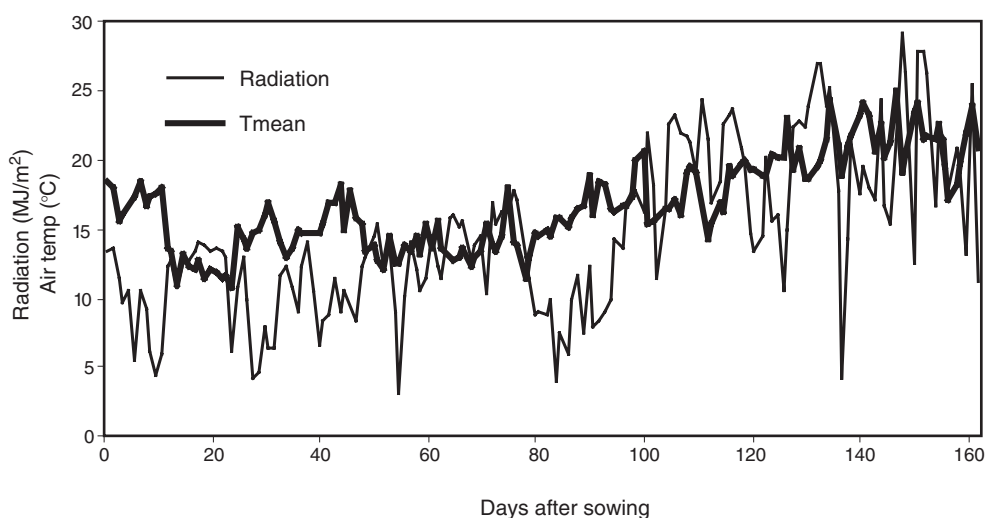
Daily climatic conditions for the experiment are presented in Fig. 1. Mean daily temperature varied between 11 and 18°C for the first 80 days of the season (approximately until first flowering); thereafter it exceeded 18°C until maturity. Mean daily temperature for the sowing to harvest period was 16.0°C. Solar radiation varied between 3 and 29 MJ/m<sup>2</sup>, with an overall mean for sowing to harvest of 14.3 MJ/m<sup>2</sup>. The extra irrigations received by the fully irrigated treatment

resulted in slightly better soil water status than in the partly irrigated treatment from 67 days after sowing until maturity.

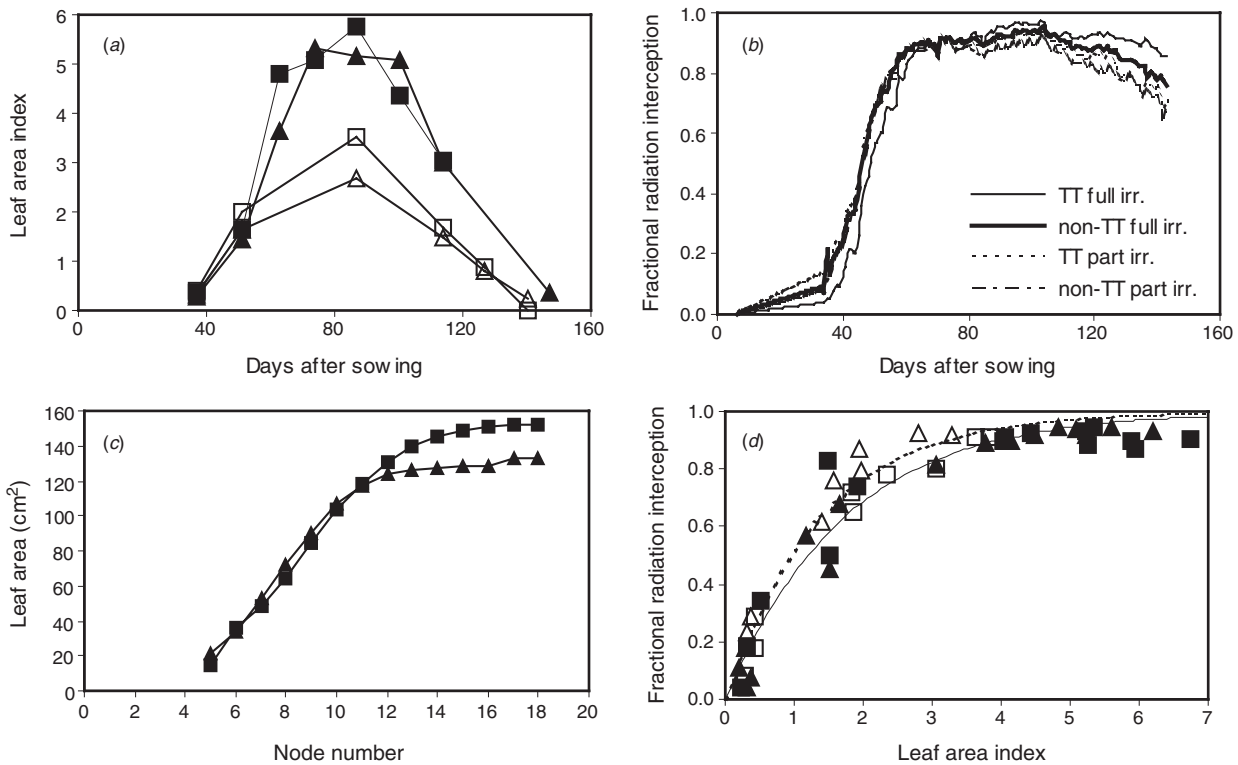
The TT trait delayed phenology in both treatments. Surpass600TT reached buds visible 8 days later than Surpass600 (66 v. 74 DAS), and this difference propagated through to the start of flowering (81 v. 88 DAS) and physiological maturity (116 v. 122 DAS).

There was no effect of the TT trait on early leaf area development in either treatment, as shown by similar values of LAI for the 2 cultivars at 37 and 51 DAS (Fig. 2a). However, at 87 DAS the non-TT crop had a tendency to have a higher LAI ( $P < 0.1$ ) than the TT crop in both the full-irrigation (5.8 v. 5.2) and part-irrigation (3.5 v. 2.7) treatments. These differences did not persist during grain-fill as leaves senesced and were shed. The development of leaf area differences between the cultivars can be seen to be due, in part at least, to larger leaves in the non-TT cultivar at nodes 12–18 (Fig. 2c). Mean leaf size was 140 cm<sup>2</sup> in the non-TT type v. 130 cm<sup>2</sup> in the TT for nodes 12–18. The rate of main stem node production was also greater in the non-TT cultivar, as demonstrated by more main stem nodes at all stages of crop development. For example, at 51 DAS in the fully irrigated treatment the non-TT cultivar had 9.4 fully expanded main stem leaves, whereas the TT cultivar had 8.5; a significant difference ( $P < 0.01$ ). In the partly irrigated treatment, the difference was also apparent, with 10.3 and 8.2 nodes in the non-TT and TT cultivars, respectively. Using a base temperature of 0°C and accumulating thermal time from 10 days after sowing (the approximate emergence date) gives an average node appearance interval at 51 DAS of 63 and 70 degree-days per node for the non-TT and TT cultivars, respectively.

Differences in LAI did not translate into obvious differences in radiation interception (Fig. 2b). All crops reached full cover (90% interception) at around 60 DAS.



**Fig. 1.** Daily mean temperature and incident solar radiation for the duration of the experiment.



**Fig. 2.** (a) Green leaf area index, (b) fractional radiation interception, (c) individual leaf area as a function of node number, and (d) fractional radiation interception as a function of leaf area index. TT (triangles) and non-TT (squares) cultivars in fully irrigated (closed symbols) and partly irrigated (open symbols) treatments. Fitted regressions in (d) are for part irrigation (dotted line),  $Y = 1 - \exp(-0.72 * LAI)$ ; and full irrigation (solid line),  $Y = 1 - \exp(-0.58 * LAI)$ .

Interception declined slightly during pod-filling to 70–90% at maturity due to leaf senescence and shedding. There was some indication that the TT cultivar in the fully irrigated treatment had lower interception leading up to canopy closure, but this was not significant.

The radiation extinction coefficient ( $k$ ) quantifies the effectiveness with which a crop canopy of a given leaf area index intercepts radiation. The value of  $k$  was determined by the regression fit for the hyperbolic relationship between LAI and  $f$ . No difference was found between the 2 cultivars (Fig. 2d), nor was there a significant effect of water regime on  $k$  (0.72 in partly irrigated *v.* 0.58 in fully irrigated). This indicates that the TT trait does not affect the effectiveness with which the canopy intercepts radiation.

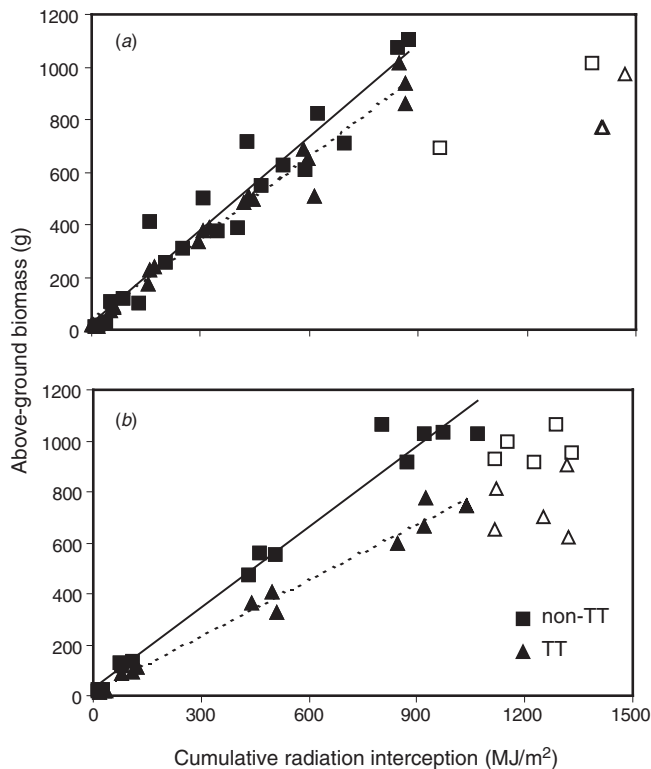
Radiation use efficiency (RUE) describes how efficiently intercepted radiation is converted to biomass. Piece-wise linear regression of above-ground biomass on cumulative intercepted radiation to determine maximum RUE accounted for more than 93% of the variance in all 4 treatments. Although there was no effect of cultivar on the amount of radiation intercepted, there was a strong effect on RUE (Fig. 3). RUE was significantly lower for the TT *v.* non-TT in both the fully irrigated (1.18 *v.* 1.05 g/MJ) (Fig. 3a) and

partly irrigated treatments (1.06 *v.* 0.74 g/MJ) (Fig. 3b), which is equivalent to 11 and 30% reduction in the fully and partly irrigated treatments, respectively. The effect of water deficit on RUE between the partly and fully irrigated treatments was greater for the non-TT cultivar than for the TT cultivar, suggesting a greater sensitivity to water deficit for RUE in the TT cultivar.

At physiological maturity, the non-TT cultivar out-yielded the TT cultivar by 29 and 39% in the fully irrigated and partly irrigated treatments, respectively (Table 2). The reduction in grain yield due to the TT trait came about due to almost equal effects of reduced biomass and reduced harvest index. Oil content was reduced by 12 and 5% in the fully and partly irrigated treatments, respectively. The effect of water deficit was statistically significant only for harvest index.

#### Comparison of cultivars across diverse environments

The environments sampled in this study provided a wide range of days to flowering, biomass production, and grain yield over which to compare the TT and non-TT cultivars (Figs 4, 5). For example, in the non-TT cultivar, days to flowering varied from 64 to 104, biomass at maturity from 2643 to 10 904 kg/ha, grain yield from 240 to 3400 kg/ha,



**Fig. 3.** Relationship between above-ground biomass and cumulative radiation interception in the (a) full irrigation, and (b) part irrigation treatments. Fitted regressions (to closed symbols) are: non-TT full irrigation,  $y = 1.18x + 26.5$ ,  $R^2 = 0.93$ ; TT full irrigation,  $y = 1.05x + 26.5$ ,  $R^2 = 0.97$ ; non-TT part irrigation,  $y = 1.06x + 29.0$ ,  $R^2 = 0.98$ ; TT part irrigation,  $y = 0.74x + 8.94$ ,  $R^2 = 0.98$ .

and grain oil content from 34.3 to 46.1%. Linear regression analysis was used to examine the relationship between the 2 cultivar types across environments in terms of phenology and crop attributes at maturity.

Across the environments sampled, the TT cultivar was consistently later in the start of flowering. In early flowering environments (*c.* 60–70 days), flowering was delayed relative to the non-TT cultivar by 2–4 days, whereas in later flowering environments (*c.* 100 days) the delay was 10 days. Days to flowering in the TT cultivar could be predicted from

that in the non-TT cultivar using a linear relationship with an  $R^2$  of 0.97 (Fig. 4).

In all environments the non-TT cultivar out-yielded the TT cultivar, with average yields of 1603 v. 1206 kg/ha; a 24.7% difference. The absolute difference in yield between the cultivars was greater in higher yielding environments. Linear regression between the 2 cultivars for grain yield gave a fitted equation with an intercept not significantly different from zero and a slope of 0.74 (Fig. 5a). The high  $R^2$  value (0.93) for this regression suggests that the yield of the non-TT cultivar could be predicted to be on average 74% of the non-TT across a wide range of grain yield. Regression plots for biomass at maturity and harvest index show that the source of the lower yield in the TT cultivar is primarily reduced biomass production (Fig. 5b). The regression between the 2 cultivars for HI was not significantly different from the 1 : 1 line, although there was a trend for HI to be lower in the TT cultivar in low-yielding environments (Fig. 5d). Grain oil content in the TT cultivar could also be related linearly to that in the non-TT cultivar (Fig. 5c). The absolute difference in oil content tended to be larger at lower oil contents. At oil contents of around 45% in the non-TT cultivar, that in the TT cultivar was only about 2 oil percentage points less, whereas at oil contents less than 40% in the non-TT the difference was 4–5%.

Across cultivar types and environments, grain yield could be related linearly to biomass at maturity (Fig. 6a), implying that biomass accounts for a moderate to high degree of the variation ( $R^2 = 0.83$ ) in grain yield across environments and cultivar types.

Although the TT trait resulted in lower yield and lower oil content than the non-TT cultivar in any given environment, there was not a universal relationship between oil content and grain yield across cultivar types. Within a cultivar there was a positive correlation between oil content and yield; however, at a given yield level, particularly at yields less than 2000 kg/ha, the non-TT cultivar still had a higher oil content (Fig. 6b).

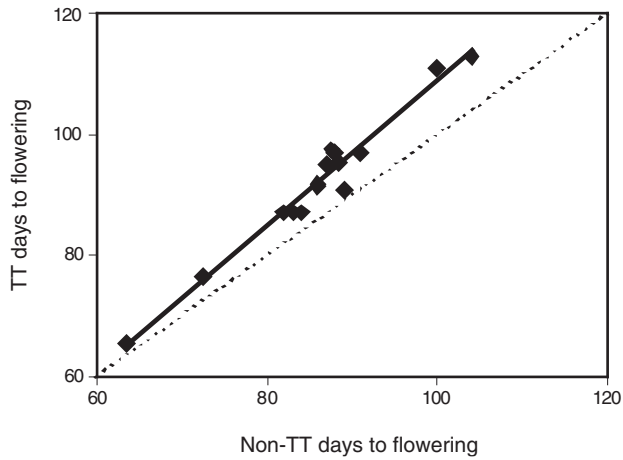
## Discussion

Although the yield penalty associated with the triazine tolerance trait has been known for about 25 years now (e.g. Beversdorf and Hume 1984), there has never been a

**Table 2.** Crop attributes at physiological maturity and the percentage reduction due to the effects of triazine tolerance (TT) and water deficit (W)

Significant effects ( $P < 0.05$ ) of TT and W on crop attributes are also indicated

	Full irrigation		Part irrigation		Reduction due to TT (%)		Reduction due to W (%)		Significance
	TT	Non-TT	TT	Non-TT	Full irrigation	Part irrigation	TT	Non-TT	
Grain yield (g/m <sup>2</sup> )	227	319	179	292	29	39	21	8	TT, W
Total biomass (g/m <sup>2</sup> )	878	1012	838	1090	13	23	5	-8	TT
Harvest index	0.269	0.318	0.217	0.271	15	20	19	15	TT, W
Oil content (%)	40.5	46.1	42.3	44.5	12	5	-4	4	TT

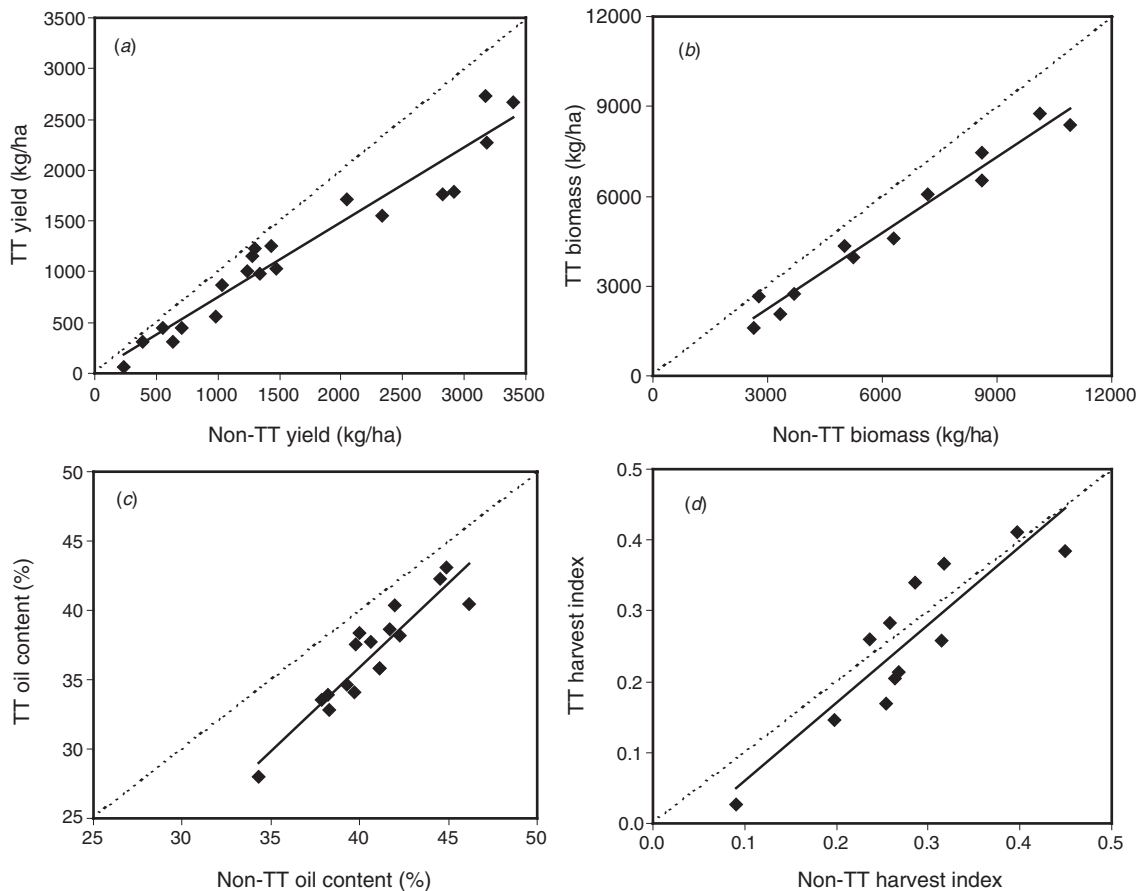


**Fig. 4.** Relationship between TT and non-TT cultivars for days from sowing to flowering. Fitted regression is  $y = 1.20x - 11.4$ ,  $R^2 = 0.97$ ,  $n = 15$ ; 1 : 1 line is shown.

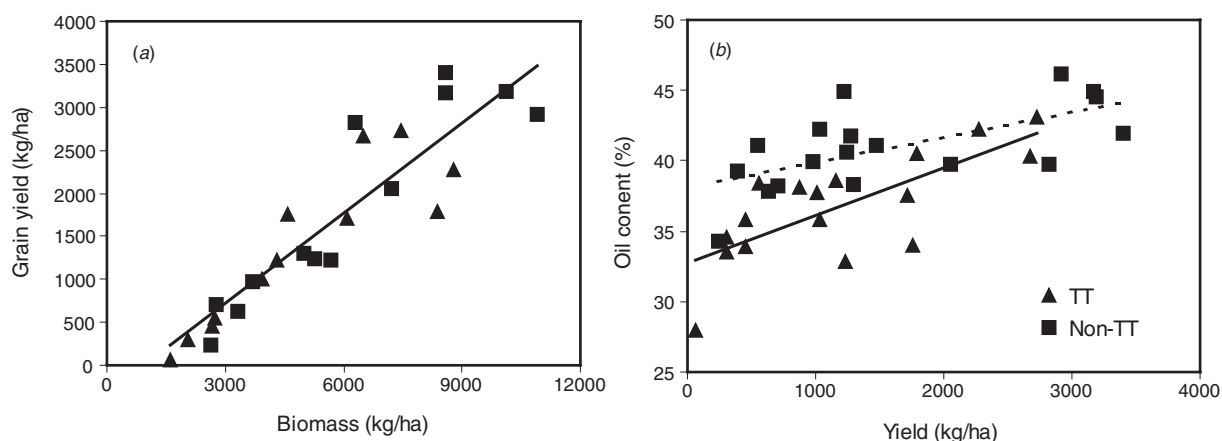
crop physiological analysis of the causal mechanisms for reduced productivity. Such an analysis has application in the configuration of simulation models for analysing causes in

yield variation. Although a number of crop physiological frameworks are available, we chose to use that employing concepts of canopy leaf area expansion, interception of solar radiation, conversion of intercepted radiation to biomass, and partitioning of biomass to grain yield. Such an approach is used in most current simulation models, including those for canola and rapeseed (Gabrielle *et al.* 1998; Robertson *et al.* 1999).

In the growth analysis study, grain yield in TT crops relative to non-TT was reduced by 29 and 39% in the fully and partly irrigated treatments, respectively. This was in-line with the results of the multi-environment comparison where grain yield was on average 26% less in the TT crops, across a yield range of 240–3400 kg/ha. Rules of thumb in the Australian industry state that ‘yields for triazine-tolerant cultivars are some 15–20% lower than with standard cultivars’ (Colton *et al.* 1997); slightly lower than our findings. In Canada, Beversdorf and Hume (1984) found that the TT cultivar Tower yielded 80% of the non-TT cultivar Regent. In a study of TT and non-TT reciprocal hybrids, yield was 21–25% less in the tolerant hybrids (Beversdorf *et al.* 1988). The study of Potter and Salisbury (1993) gave a



**Fig. 5.** Relationship between TT and non-TT cultivars for (a) grain yield, fitted regression is  $y = 0.74x + 10.7$ ,  $R^2 = 0.93$ ,  $n = 21$ ; (b) total biomass at maturity, fitted regression is  $y = 0.85x - 320$ ,  $R^2 = 0.97$ ,  $n = 12$ ; (c) oil content,  $y = 1.22x - 12.7$ ,  $R^2 = 0.85$ ,  $n = 17$ ; (d) harvest index,  $y = 1.10x - 0.05$ ,  $R^2 = 0.80$ ,  $n = 12$ . In all cases 1 : 1 line is shown.



**Fig. 6.** Relationship between (a) grain yield and total biomass at maturity, fitted regression is  $y = 0.35x - 337$ ,  $R^2 = 0.83$ ,  $n = 24$ ; (b) oil content and grain yield, fitted regressions are  $y = 0.0034x + 33$ ,  $R^2 = 0.55$ ,  $n = 17$  for the TT cultivar, and  $y = 0.0018x + 38$ ,  $R^2 = 0.40$ ,  $n = 17$  for the non-TT cultivar.

seed yield of TT lines 26% lower than of a non-TT canola. The current study suggests that the yield reduction of 25% applies across a wide yield range, with the implication that absolute yield differences will not be as great in low-yielding environments in comparison with high-yielding environments.

Of the above physiological processes contributing to the formation of grain yield that were studied in the growth analysis experiment, by far the dominant effect of the TT trait was on RUE. Given that the TT trait is known to interfere with the effective operation of the leaf photosynthetic apparatus (Arntzen *et al.* 1982; Hart and Stemler 1990a, 1990b; Hart *et al.* 1992), it was anticipated that the TT cultivar would have a lower RUE. RUE was reduced by 11 and 30% in the fully and partly irrigated treatments, respectively. The maximum value of RUE of 1.18 g/MJ attained by the non-TT cultivar in the fully irrigated treatment is close to values measured by Mendham *et al.* (1981), Wright *et al.* (1988), and Morrison and Stewart (1995). The reduced RUE in the TT cultivar translated into 13 and 23% less biomass at physiological maturity in the non-TT crops in the fully and partly irrigated treatments, respectively. In the multi-environment comparison, biomass at maturity was reduced on average by 15%. In a controlled environment study, Donnelly and Hume (1984) found that TT plants exhibited a 0–21% decrease in dry matter production, depending upon the growth temperature.

Water limitation reduced RUE more in the TT than in the non-TT cultivar. The measurements made in the growth analysis experiment do not permit an analysis of why this occurred. It suggests, however, that the processes of net photosynthesis are more sensitive to water stress in the TT cultivar. This result requires further experimentation to elucidate the physiological mechanisms involved. One possibility is that TT cultivars have lower transpiration

efficiency, as suggested by carbon isotope discrimination studies (Matus *et al.* 1995), and hence less ability to fix carbon under water-limiting conditions.

Although reduced RUE and consequently less biomass at maturity accounted for most of the grain yield reduction in the TT cultivar, effects on harvest index were less clear. In the growth analysis experiment, HI was reduced in the TT cultivar by 15 and 20% in the fully and partly irrigated treatments. However, in the multi-environment study there was no consistent effect on HI for values in the non-TT crop varying from 0.09 to 0.45. There was a trend for lower HI in the TT cultivar when the non-TT cultivar HI was less than *c.* 0.25. Harvest index measured at maturity is a consequence of the balances between biomass accumulation before and during grain-filling, as well as the extent of translocation of stored dry matter from vegetative organs to grain. These processes will be affected by the timing and severity of stresses with respect to the stage of crop development. Hence it is probably not surprising that there is no clear difference in HI, except at low HI levels where stress patterns may be severe enough to differentiate between the 2 types. Under severe stress the later phenology of the TT type may be instrumental in producing a lower HI.

An unexpected result in this study was the lack of an effect of the TT trait on early leaf area development. TT cultivars are usually regarded as having lower early canopy vigour than non-TT types. For example, Lythgoe *et al.* (2001) compared a TT cultivar (Pinnacle) with a non-TT cultivar (Dunkeld) and found the LAI at the 4–5 leaf stage was 0.26 *v.* 0.53, respectively. In the growth analysis experiment, significant differences in LAI did not become apparent until flowering, by which time LAI values were above those required for 90% radiation interception and so LAI differences had no effect on the amount of radiation intercepted. The lack of an effect on early-season LAI



occurred despite a faster rate of leaf appearance in the non-TT cultivar from emergence onwards. It was not until later, when leaves appearing on the main stem were larger in area in the non-TT cultivar, as well as appearing more quickly, that a difference in LAI occurred. The lack of an effect of the TT trait on radiation interception may be related to the climatic conditions in which this experiment was conducted: considerably warmer than traditional canola-growing areas in southern Australia. In the current experiment, canopy closure occurred at around 60 days, which is considerably earlier than the 90 days required to reach an LAI of 3 (approximating 90% interception) measured by Wright *et al.* (1988) for an irrigated crop in Victoria. In conditions of rapid canopy development, small initial differences in leaf area expansion do not have time to amplify into larger differences in LAI and the amount of radiation intercepted before canopy closure occurs. In cooler environments, such differences may have more time to develop and influence radiation interception.

A notable effect of the TT trait was to delay phenology, and this was seen in the stages leading up to maturity in the growth analysis experiment, as well as the multi-environment study where sowing to flowering varied from 64 to 104 days. Beversdorf *et al.* (1988) reported a delay of 2 days in flowering for a TT *v.* a non-TT reciprocal hybrid. In stressful environments, particularly those with a terminal water deficit, it is likely that the later phenology on the TT type will have an additional detrimental effect upon productivity on top of the depressive effect on RUE, by delaying grain filling to a time of the season where water is more limiting and high temperatures are likely to reduce oil contents.

There was evidence that for a given yield level below *c.* 2000 kg/ha, the TT cultivar had a lower oil content than the non-TT type and it is possible that this is, in part at least, related to the later flowering and maturity dates of the TT cultivar. A later grain-filling period in the TT cultivar would mean, on average, higher temperatures and greater water deficit, meaning less favourable conditions for oil accumulation (Hocking *et al.* 1997; Hocking and Stapper 2001). Other studies have also shown lower oil contents in TT types (Beversdorf *et al.* 1988); however, the present study highlights that the difference is not constant across the range of oil contents, but rather is up to 6% at low oil contents and 2% at high oil contents. Given that the absolute difference in yield is less in low yielding, and therefore low oil content, environments, this will tend to mitigate the effect of the large difference in oil content in the TT cultivar on crop profitability.

This study highlighted the strong relationship between grain yield and biomass across environments and cultivars. The existence of a positive intercept in this relationship has 2 implications: firstly, that harvest index is not constant but increases with grain yield; and secondly, that a minimum

amount of biomass is required to produce any grain yield, and in this case this threshold is about 1000 kg/ha. Similar relationships have been found for maize, soybean, and sunflower (Vega *et al.* 2000).

## Conclusions

This study has confirmed the industry rule-of-thumb that TT canola yields, on average, about 25% less than non-TT canola. We have shown that the yield reduction applies across the full yield range and is primarily due to less biomass production via lower radiation-use efficiency. Differences between the TT and non-TT cultivars in terms of phenology and oil content could be related through consistent relationships. Knowledge of the causal mechanisms for reduced productivity can be incorporated into simulation models, which could be used in different environments to assess the trade-off between the yield and oil penalty associated with TT canola and benefits in weed control.

## Acknowledgments

Expert assistance with field sampling was provided by Natalie Hillcoat, Shayne Cawthray, and Brian Gilmartin at Lawes, by Tony King and Christine Holmes at Nindigully, by Brett Cocks at other Queensland field sites, and by Rodney Bambach at Tamworth. This work was funded, in part, by the Grains Research and Development Corporation.

## References

- Arntzen CJ, Pfister K, Steinbeck KE (1982) The mechanism of chloroplast triazine resistance: alterations in the site of herbicide action. In 'Herbicide resistance in plants'. (Eds HM LeBaron, J Gressel) pp. 185–214. (John Wiley: New York)
- Beversdorf WD, Hume DJ (1984) OAC Triton spring rapeseed. *Canadian Journal of Plant Science* **64**, 4.
- Beversdorf WD, Hume DJ, Donnelly-Vanderloo MJ (1988) Agronomic performance of triazine-resistant and susceptible reciprocal spring canola hybrids. *Crop Science* **28**, 932–934.
- Colton B, Butler B, Milne BR (1997) Using triazine herbicides in canola. AgNote, NSW Agriculture, No. DPI/183.
- Colton B, Potter TD (1999) History. In 'Canola in Australia: the first thirty years'. (Eds PA Salisbury, TD Potter, G McDonald, AG Green) pp. 1–4. (Organising Committee of the 10th International Rapeseed Congress)
- Donnelly MJ, Hume DJ (1984) Photosynthetic rates and growth analysis of triazine-tolerant and normal rapeseed. *Canadian Journal of Plant Science* **64**, 2.
- Gabrielle B, Denoroy P, Gosse G, Justes E, Andersen MN (1998) Development and evaluation of a CERES-type model for winter oilseed rape. *Field Crops Research* **57**, 95–111.
- Hart JJ, Radosevich SR, Stemler A (1992) Influence of light intensity on growth of triazine-resistant rapeseed (*Brassica napus*). *Weed Research* **32**, 349–356.
- Hart JJ, Stemler A (1990a) Similar photosynthetic performance in low light-grown isonuclear triazine-resistant and triazine-susceptible *Brassica napus* L. *Plant Physiology* **94**, 1295–1300.
- Hart JJ, Stemler A (1990b) High light-induced reduction and low light-enhanced recovery of photon yield in triazine-resistant *Brassica napus* L. *Plant Physiology* **94**, 1301–1307.

- Hocking PJ, Kirkegaard JA, Angus JF, Gibson AH, Koetz EA (1997) Comparison of canola, Indian mustard and Linola in two contrasting environments. I. Effects of nitrogen fertilizer on dry-matter production, seed yield and seed quality. *Field Crops Research* **49**, 107–125.
- Hocking PJ, Stapper M (2001) Effects of sowing time and nitrogen fertiliser on canola and wheat, and nitrogen fertiliser on Indian mustard. I. Dry matter production, grain yield, and yield components. *Australian Journal of Agricultural Research* **52**, 623–634.
- Lythgoe B, Norton RM, Nicholas ME, Connor DJ (2001) Compensatory and competitive ability of two canola cultivars. In 'Proceedings of the 10th Australian Agronomy Conference, Hobart, 2001'. (Eds The Regional Institute) (CD-ROM)
- Matus A, Slinkard A, Kessel C van (1995) Carbon isotope discrimination: potential for indirect selection for seed yield in canola. *Crop Science* **35**, 1267–1271.
- Mendham NJ, Shipway PA, Scott RK (1981) The effect of delayed sowing and weather on growth, development and yield of winter oil-seed rape (*Brassica napus*). *Journal Agricultural Science, Cambridge* **96**, 389–416.
- Morrison MJ, Stewart DW (1995) Radiation-use efficiency in summer rape. *Agronomy Journal* **87**, 1139–1142.
- Potter TD, Salisbury PA (1993) Triazine resistant canola in southern Australia. In 'Proceedings of the 7th Australian Agronomy Conference, Adelaide, 1993'. pp. 80–82.
- Robertson MJ, Holland JF, Kirkegaard JA, Smith CJ (1999) Simulating growth and development of canola in Australia. In 'Proceedings 10th International Rapeseed Congress, 1999'. (Eds N Wratten, PA Salisbury) (CD-Rom)
- Sutherland S (1999) Weed management. In 'Canola in Australia: the first thirty years'. (Eds PA Salisbury, TD Potter, G McDonald, AG Green) pp. 59–65. (Organising Committee of the 10th International Rapeseed Congress)
- Vega CRC, Sadras VO, Andrade FH, Uhart SA (2000) Reproductive allometry in soybean, maize and sunflower. *Annals of Botany* **85**, 461–468.
- Wright GC, Smith CJ, Woodroffe MR (1988) The effect of irrigation and nitrogen fertilizer on rapeseed (*Brassica napus*) production in south-eastern Australia. I. Growth and seed yield. *Irrigation Science* **9**, 1–13.

Manuscript received 10 September 2001, accepted 21 January 2002