Water Stress Effects on Winter Canola Growth and Yield

Eyob H. Tesfamariam,* John G. Annandale, and Joachim M. Steyn

ABSTRACT

Canola (*Brassica napus* L.) is seen as a dryland crop in many parts of the world. In South Africa, there is growing interest in producing canola under irrigation because of its profitability and beneficial disease control characteristics in a rotation system. The objectives of this study were to identify the growth stage most sensitive to water stress and to determine the effect of water stress on crop growth, phenology, seed and oil yield, water use, and seed oil content. A well watered control was compared with treatments stressed during one of the following stages: vegetative, flowering, or seed filling in replicated field studies during 2002 and 2003 at Pretoria, South Africa. Water stress imposed during flowering delayed maturity by 114 growing degree days. In contrast, water stress imposed during seed fill resulted in 127 growing degree days earlier maturity. The well watered control gave the highest value for leaf area index of 8, water use of 709 mm, seed yield of 3831 kg ha^{-1}, and seed oil content of 398 g kg^{-1}. Canola stressed at flowering gave the lowest values for seed yield of 1361 kg ha^{-1}, seed oil content of 340 g kg^{-1}, and water use of 332 mm. Dry matter production per unit water use at seed filling was only a third of its value during the vegetative and flowering stages. Canola seed and oil yield are most sensitive to water stress at flowering and less sensitive during the vegetative and seed-filling stages.

Canola is the third most important source of plant oil in the world after soybean (*Glycine max* (L.) Merr.) and palm oil (*Elaeis guineensis* L.) (Reyes, 2007). Canola is also an excellent rotation crop to control crop pests and soil diseases and has a good stable yield (Booth and Gunstone, 2004). It grows in areas that receive more than 300 mm rain on well drained soils with a good potential for growing wheat (*Triticum aestivum* L.) (Sovero, 1993).

Since its introduction to the country in the early 1990s, canola production in South Africa had expanded to 32,000 ha by 2007 (FAO, 2008). Growing wheat under irrigation in the interior summer rainfall areas is an economic risk because of root diseases or poor seed quality. This has led farmers and researchers to take a serious look at canola as an alternative crop. The successful production of canola has the potential to save more than $10 million annually that is currently invested to import around 782,000 Mg of oilcake for animal feed (Nel et al., 2007).

Canola seed yield and seed oil content generally increase with the amount of water received (Al-Jaloud et al., 1996; Canola Council of Canada, 2008a). Although canola is commonly grown in most parts of the world under rain-fed farming systems, production of canola under irrigation has been a common practice in some parts of the world, such as Australia since 1970 (McCaffery, 2004) and the cooler, drier parts of Montana (Bauder, 2006). Similarly, in the winter rainfall areas of South Africa, farmers supplement rainfall with irrigation to ensure good harvests. However, in the summer rainfall areas of South Africa, canola is grown under season-long irrigation (A.A. Nel, personal communication, 2002). The availability of water for irrigation in many regions is becoming scarce due to an increase in water demand for industrial, domestic, and environmental requirements. Sound irrigation water management practices are required to ensure efficient use of water for optimal yields.

In spite of the rapid expansion of canola cultivation in South Africa, little work has been done to improve seed and oil yield through good irrigation management practices. Studies were conducted by Nielsen (1997) in Akron, Colorado to determine the sensitivity of yield components, seed oil content, and leaf area development to water stress at various growth stages of canola. The irrigation treatments in his study were designed to simulate dryland conditions, and the total amount of water applied for the whole season was similar for all treatments. The only difference between treatments was the distribution of the total irrigation amount, which was divided equally into 15 irrigation events of 15.7 mm throughout the season for the non-stressed treatment and into 10 irrigation events of 23.4 mm for three stress treatments. This resulted in water-limited conditions during the critical stages of crop growth for the stressed and non-stressed (irrigated 15.7 mm weekly) treatments. Nielsen's studies show that water stress at any stage did not significantly affect canola yield. Pot experiments were also conducted by

E.H. Tesfamariam, J.G. Annandale, and J.M. Steyn, Dep. of Plant Production and Soil Science, Univ. of Pretoria, Pretoria, Gauteng 0002, South Africa. Received 20 Aug. 2008. *Corresponding author (tesfamariam@tuks.co.za, eyob.tesfamariam@up.ac.za).

Published in Agron. J. 102:658–666 (2010)
Published online 25 Jan. 2010
doi:10.2134/agronj2008.0043

Abbreviations: GDD, growing degree days; LAD, leaf area duration; LAI, leaf area index; NNN, irrigated throughout the season; NSN, water stress during flowering stage; NNS, water stress during the seed-filling stage; SNN, water stress during the vegetative stage; TWU, total water use; WUE, water use efficiency.

Champolivier and Merrien (1996) to determine the effect of water stress at different growth stages on canola yield and yield components; however, pot experiment findings cannot be easily compared with field trials. Our study was designed to compare major growth stages for sensitivity to water stress and to determine the effects of water stress at major growth stages on crop growth, phenology, seed yield, seed oil content, oil yield, and water use efficiency under South African field conditions.

MATERIALS AND METHODS

Field experiments were conducted at the University of Pretoria Hatfield, Experimental Farm, Pretoria, South Africa (25°45′S, 28°16′E, elevation 1327 m). The soil was a Hutton sandy clay loam (Soil Classification Working Group, 1991) (loamy, kaolinitic, mesic, Typic Eutrustox) with a pH (2.5:1 soil/water ratio) of 6.2. For both years, the study was conducted on fields where commercial dryland maize (*Zea mays* L.) was grown the previous season. Before planting, the field was plowed and disked to create a level seedbed. Weed control was performed by hand. No pests or diseases occurred during either season.

Being in the Southern Hemisphere, a hybrid winter canola (Hyola 60, developed by Pacific seeds [Zeneca], Toowoomba, Queensland, Australia and released in 2001) was planted in rows on 23 May 2002 and on 21 May 2003 at a rate of 5.3 kg ha^{-1} using a seed planter with double disk openers. This cultivar was selected because it is the best performer in this area, with a target seed yield of 4 t ha^{-1} (A.A. Nel, personal communication, 2002). Plots consisted of 17 rows in 2002 and 47 rows in 2003, spaced 0.15 m apart and 4 m (2002) or 7 m (2003) in length, with two border rows on either side. At harvest, a 0.56 m length of the three middle rows in 2002 and the six middle rows in 2003, were used for seed and oil yield determination. An automated rainout shelter was used to cover the plots for possible precipitation events in 2002. However, in 2003, the study was conducted in an open field. The experimental site is in a summer rainfall area and therefore no rainfall was recorded during these winter months, except once after harvest time in 2003. Temperature and rainfall data recorded during the study period are presented in Table 1.

The growing season was divided into three developmental stages: vegetative (28 June to 8 August), flowering (8 August to 12 September), and seed filling (12 September to 25 October). According to the standardized growth scale (Biologische Bundesanstalt, Bundessortenamt and Chemical industry decimal system) (Canola Council of Canada, 2008b), these three developmental stages could be categorized as follows: vegetative stage was from GS14 (rosette stage growth, fourth leaf) to GS59 (first petal visible, but flowers buds still closed); flowering stage was from GS59 to GS69 (end of flowering); and seed filling was from GS69 to GS89 (fully ripe). The crop emerged 8 d after planting. The seedlings grew vigorously until the implementation of the first water stress treatment (stress during the vegetative stage, SNN), which commenced directly after the unfolding of the fourth leaf. There was no visible dormancy in growth and development after stand establishment and before the implementation of the first water stress treatment.

There were four water stress–timing treatments: irrigated throughout the season (NNN), water stress during the vegetative stage (SNN), water stress during the flowering stage (NSN), and water stress during the seed-filling stage (NNS). These treatments were organized in a randomized block design with four replicate blocks in 2002 and a completely randomized design with three replicates in 2003. In 2002, each plot received 33 kg N ha^{-1}, 50 kg P ha^{-1}, and 67 kg K ha^{-1} at planting, but no N was top dressed. This was because soil analysis showed the presence of adequate N, P, and K reserves carried over from the previous crop (121 mg kg^{-1} NO_3^-, 80 mg kg^{-1} Bray1-P, and 180 mg kg^{-1} K in the top 0.3 m soil layer). In 2003, fertilizer was applied at rates of 60 kg N ha^{-1}, 45 kg P ha^{-1}, and 60 kg K ha^{-1} in the form of NPK (3:2:1) and KCl at planting. Five weeks later, a top dressing of 40 kg N ha^{-1}, 40 kg P ha^{-1}, and 40 kg K ha^{-1} was applied. Additional N was applied at the beginning of the flowering stage in the form of limestone ammonium nitrate at a rate of 100 kg N ha^{-1}, adding up to a total of 200 kg N ha^{-1} for the whole season.

A sprinkler irrigation system was used to apply 5 mm irrigation every third day for 5 wk until the crop was well established. After establishment, drip irrigation was used to irrigate individual non-stressed plots back to field capacity once a week. Water was withheld completely on plots undergoing stress treatments. The lateral spacing of the dripper lines was 0.6 m. Pressure-compensated drip emitters were spaced 0.30 m apart in-line and had a flow rate of 2.3 L h^{-1} at a working pressure in the range of 100 to 150 kPa. Total water use (TWU) during the season was determined as the difference in soil profile water content between physiological maturity (GS87) and crop emergence (GS09) plus the amount of irrigation water applied during the season. Runoff was assumed to be negligible because the application rate of the dripper lines was too low to trigger runoff. Similarly, the amount of irrigation applied was according to the profile deficit to bring it back to field capacity; thus, drainage was negligible.

Table 1. Mean maximum temperature, mean minimum temperature, mean average temperature, and total precipitation recorded for 2-wk periods during the 2002 and 2003 growing seasons, University of Pretoria, Hatfield experimental farm, Pretoria, South Africa.

		May	June		July		Aug.		Sept.		Oct.	
Year	Parameter†	Week 4	Weeks 1–2	Weeks 3–4	Weeks 1–2	Weeks 3–4	Weeks 1–2	Weeks 3–4	Weeks 1–2	Weeks 3–4	Weeks 1–2	Weeks 3–4
2002	T_{max}, °C	22.8	18.3	19.1	18.6	20.3	22.4	22.8	22.1	27.5	26.6	31.4
	T_{min}, °C	9.1	6.2	5.7	3.2	4.6	7.6	11.9	9.0	12.2	11.8	15.1
	T_{ave}, °C	16.0	12.3	12.4	10.9	12.5	15.0	17.4	15.6	19.9	19.2	23.3
	Rain, mm	0	0	0	0	0	0	0	0	0	0	0
2003	T_{max}, °C	21.5	19.9	19.2	17.8	22.1	19.9	19.5	25.9	26.7	31.8	23.3
	T_{min}, °C	6.0	6.8	5.8	3.5	5.7	7.8	6.9	10.8	12.9	16.7	11.9
	T_{ave}, °C	13.8	13.4	12.5	10.7	13.9	13.9	13.2	18.4	19.8	24.3	17.6
	Rain, mm	0	0	0	0	0	0	0	0	0	0	26‡

† $T_{avg.}$, mean average temperature; T_{max}, mean maximum temperature; T_{min}, mean minimum temperature.

‡ Rain occurred after harvesting (evening of harvesting date).

Crop water use was estimated from soil water measurements conducted once a week to a depth of 1 m in 2002 and 1.5 m in 2003, using a site-calibrated neutron soil probe (Model 503 DR CPN Hydroprobe; Campbell Pacific Nuclear, CA). In 2002, soil water measurement to a depth of 1 m underestimated water use by canola, consequently affecting the yield. Therefore, we opted for a depth of 1.5 m the following year to match the expected rooting depth of canola (Canola Council of Canada, 2008b). The soil profile had a field capacity of 381 mm per 1.5 m soil depth, determined according to Marshall and Holmes (1988).

In 2003, three replications of whole plant (aboveground) samples were taken approximately every 2 wk for growth analysis from an area of 0.5 m^2 (typically 26 plants per sample). In 2002, however, plant samples were taken from only one plot per treatment, with a sampling area of 0.25 m^2 (typically 13 plants per sample) because of small experimental plots. The sampling dates for both years were 52 (GS33), 67 (GS50), 78 (GS59), 94 (GS63), 108 (GS67), 125 (GS75), 152 (GS84), and 160 (GS87) days after planting (DAP). The samples were partitioned into leaves, stems, and pods. One-sided leaf area was measured with an LI-3100 belt driven leaf area meter (LI-COR, Lincoln, NE). The components were then dried in a forced-draft oven at 70°C for 48 h to determine aboveground biomass. Aboveground biomass was calculated as the sum of leaf, stem, and pod dry matter. Leaf area index (LAI) was computed from the measured one-sided leaf area divided by the ground sampling area. Leaf area duration (LAD), which quantifies the size and duration of the canopy, was computed from the area under the LAI over time curve after Richards (1969) using Eq. [1].

$$LAD = [(LAI_2 + LAI_1)/2](t_2 - t_1)(m^2\ m^{-2}\ d^{-1}) \quad [1]$$

According to Evans (1972), LAD is the integral of leaf area index with respect to time and therefore takes into account the duration and extent of photosynthetic tissue but not the rate of photosynthesis per unit leaf area.

Thermal time requirement of canola in growing degree days (GDD) was computed from average daily air temperature (T_{avg}) using Eq. 2 (Monteith, 1977).

$$GDD = (T_{avg} - T_b)\Delta t \quad [2]$$

where T_b is the base temperature, and Δt is the time interval (1 d). Thermal time requirements for canola were recorded in GDD using 5°C as the base temperature (Canola Council of Canada, 2005).

Crop physiological maturity was determined by randomly taking one whole plant sample from each replication of a treatment and shelling pods to estimate the percentage of brown seeds. The crop for a given treatment was considered physiologically mature once 65 to 70% of the seed color was dark brown to black. At physiological maturity, whole aboveground samples were harvested by hand-sickle-cutting from a 2-m^2 area (2002) and a 6-m^2 area (2003) for seed and oil yield determination. The samples were placed in woven bags and hung in a well ventilated shed for 6 d until pod color was yellow to light brown and the seed moisture content near 100 g kg^{-1}. Once the seeds reached an average moisture content of 100 g kg^{-1}, they were threshed by hand-rubbing the pods.

Representative seed samples were taken for seed oil content determination by the Perishable Products Export Control Board, Silverton, Pretoria, South Africa. Seed oil content was determined using the hexane extraction method and expressed at an 85 g kg^{-1} seed moisture content. Oil yield was calculated as the product of seed yield and seed oil content.

The 2002 experiment was a randomized complete-block design with four replicates, and the 2003 experiment was a completely randomized design with three replicates. Combined ANOVA over years was applied to seed yield, seed oil content, oil yield, water use by growth stage, TWU, and water use efficiency (WUE). Aboveground biomass, LAI, and LAD measurements were not replicated in 2002 and therefore could not be analyzed across years. To be able to apply ANOVA on the combined data to test for differences between the four water stress treatments, as well as the treatment × year interaction, the combined data were analyzed as unblocked. Bartlett's chi-square and Levene's F tests were used for homogeneity of treatment and year variance tests, and the data were found to be acceptably normal. Replications within years were considered random effects in the combined ANOVA, and year and water stress treatments were considered fixed effects in the ANOVA. Treatment and treatment × year interaction means were separated using Fisher's protected t test least significant difference at the 5% level of significance (Snedecor and Cochran, 1980). Data were analyzed using the statistical program GenStat (Payne et al., 2007). Graphic representations of Tables 3 and 5 are included to better illustrate the effect of each treatment on LAI and aboveground biomass during the growing season. Standard error bars on figures indicate standard deviation at $P \leq 0.05$.

Linear weighted regression analysis was used to determine the relationship between seed yield and LAD, using mean values per treatment per season because in 2003 LAD was replicated. Linear least-squared regression analysis was used to determine the relationship between seed yield and seasonal water use for the well watered treatment.

RESULTS AND DISCUSSION

Growth, Development, and Yield

Leaf Area Index

During 2003, foliage of NNN grew vigorously, and LAI reached a maximum of 8 $m^2\ m^{-2}$ (Fig. 1). The implementation of water stress during the vegetative period (38–78 DAP) reduced LAI of the SNN treatment below all other treatments at 67 and 94 DAP (Fig. 1; Tables 2 and 3). Some leaves, however, recovered with the resumption of irrigation later in the season. Results from the 2002 study period also appeared to hold the same trend, even though statistics could not be performed. Water stress during the flowering stage (NSN) significantly reduced LAI of the crop at 125 DAP (Fig. 1). Late stress (NNS) resulted in rapid leaf senescence (152 DAP).

The presence of sufficient plant-available soil water throughout the growing season (NNN) helped the crop maintain a larger leaf area. It also increased the period over which the canopy remained functional (highest leaf area duration). Leaf area duration was highest for NNN (524 d $m^2\ m^{-2}$) (Table 3).

Total Aboveground Biomass

An increase in aboveground biomass over time was observed for all treatments (Fig. 2). In 2003, treatment NNN had a

Table 2. Degrees of freedom, mean squares, and *F* probabilities for the analysis of variance of leaf area index sampled at 52, 67, 78, 94, 108, 125, and 152 d after planting at University of Pretoria, Hatfield experimental farm, South Africa, in 2003.

Source of variation	df	Mean squares							
		Vegetative			Flowering		Seed filling		LAD‡
		52 DAP†	67 DAP	78 DAP	94 DAP	108 DAP	125	152	
Treatment	3	0.035**	0.884**	0.746**	0.470**	0.244ns§	3.617**	3.129**	2689**
Error	8	0.0001	0.045	0.055	0.053	0.070	0.137	0.010	123.8

** Significant at the 0.01 level of probability.

† DAP, days after planting.

‡ LAD, leaf area duration.

§ ns, nonsignificant at the 0.05 probability level.

Table 3. Mean leaf area index for samples taken at 52, 67, 78, 94, 108, 125, and 152 d after planting and leaf area duration of canola for the 2003 growing season, University of Pretoria, Hatfield experimental farm, Pretoria, South Africa.

Treatment†	Leaf area index							LAD§
	Vegetative			Flowering		Seed filling		
	52 DAP‡	67 DAP	78 DAP	94 DAP	108 DAP	125 DAP	152DAP	
	m^2 leaf m^{-2} ground							d m^2 m^{-2}
NNN	0.97	2.50	2.98	5.55	7.45	8.01	2.36	524
SNN	0.97	1.71	2.92	4.78	7.22	7.43	1.84	468
NSN	0.96	3.01	3.93	5.44	6.80	5.60	1.16	455
NNS	0.75	2.24	3.65	5.66	7.36	7.77	0	483
$LSD_{0.05}$	0.02	0.40	0.44	0.43	ns¶	0.76	0.19	21
CV, %	1	9	7	4	4	5	8	2

† NNN, no water stress; NNS, stress during the seed-filling stage; NSN, stress during flowering; SNN, stress during the vegetative stage.

‡ DAP, days after planting.

§ LAD, leaf area duration.

¶ ns, nonsignificant at the 0.05 probability level.

higher LAD (Table 3) than the water-stressed treatments and was able to accumulate a higher final total aboveground biomass (Fig. 2). This supports the strong relationship between radiation interception and production of a crop under non-limiting water supply conditions (Sinclair, 1984).

The rate of aboveground biomass production during the vegetative stage was least when the crop was stressed during this stage (SNN) but slowly recovered with the resumption of irrigation (Fig. 2). Similarly, when the crop was stressed during the flowering stage (NSN), the rate of aboveground biomass production for NSN was least of all treatments (Fig. 2). Results from the 2002 study also showed similar trends, although statistics could not be performed on the data. Water stress during the flowering stage resulted in a significant decline of LAI at 125 DAP (as a result of wilting and senescing of leaves) (Fig. 1). Water stress during the flowering stage (treatment NSN) also resulted in the abortion and abscission of pods (Fig. 3), both contributing to lower aboveground biomass compared with NNN, SNN, and NNS throughout the seed-filling stage (125, 152, and 160 DAP, respectively) (Fig. 2; Tables 4).

Crop Development

According to Daniel et al. (1986), phenological development of winter oilseed rape is an important aspect of the yield formation process because the time of flowering depends on the combined effect of photoperiod and temperature. The GDD requirement of NNN for emergence was 77. The GDD recorded from planting date to the flowering and maturity stages for the same treatment were 997 and 1742 (Table 5), respectively. This was higher than the GDD required for flowering (759–832) and maturity (1326–1445) by spring canola at Ontario, Canada (Hall, 2006).

Plants stressed during the vegetative stage (SNN) were observed to produce new leaves after the resumption of irrigation following the stress period and reached maturity at about the same time as NNN. This shows that canola is an indeterminate crop that is capable of producing new large leaves after resumption of irrigation to compensate for the few small leaves that developed because of water stress during the vegetative stage. The resumption of irrigation after water stress during the flowering stage (NSN) also triggered the initiation of new flowers and delayed leaf senescence. Consequently, the crop

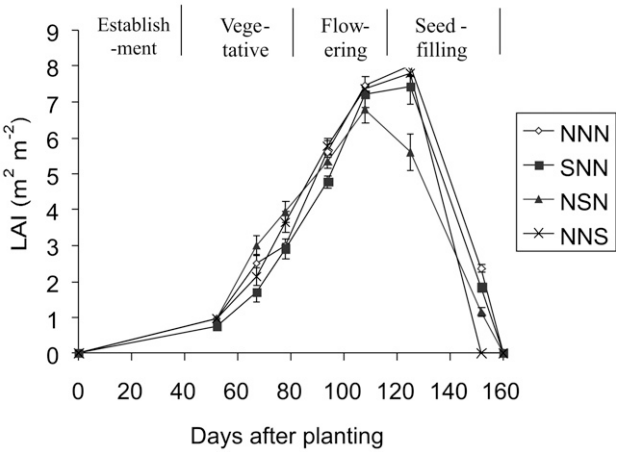

Fig. 1. Leaf area index (LAI) of canola subjected to different water stress treatments during the 2003 winter growing season. Error bars indicate the standard deviation from means of LAI at $P \leq 0.05$. NNN, no water stress; NNS, stress during the seed-filling stage (115–152 d after planting [DAP]); NSN, stress during the flowering stage (80–115 DAP); SNN, stress during the vegetative stage (38–80 DAP).

matured physiologically 114 GDD (9 d) later than NNN. The treatment stressed during the seed-filling stage (NNS) reached maturity 127 GDD earlier than NNN and SNN, which was not expected. This could be due to a combination of factors, including a higher leaf temperature compared with air temperature as a result of water stress (Patel et al., 2001).

Seed Yield

When data were combined for both years, there was a significant ($P < 0.01$) year × water stress interaction for seed yield (Table 6). The year × water stress treatment interaction shows a generally similar yield ranking of water stress treatments for each year. This shows that the interaction

Table 4. Degrees of freedom, mean squares, and *F* probabilities for the analysis of variance of aboveground biomass sampled at 52, 67, 78, 94, 108, 125, 152, and 160 d after planting and growing degree days to physiological maturity of four water stress treatments at University of Pretoria, Hatfield experimental farm, South Africa, in 2003.

Source of variation	df	Mean squares								
		Vegetative			Flowering		Seed filling			
		52 DAP†	67 DAP	78 DAP	94 DAP	108 DAP	125 DAP	152 DAP	160 DAP	GDD to PM‡
Treatment	3	2595 ns§	49,612*	1,550,000**	5,423,667**	6,350,000**	5,407,500**	2,409,507**	2,409,507**	29,359**
Error	8	1736	5566	29,242	117,188	52,220	208,517	101,065	101,065	226

* Significant at the 0.05 level of probability.

** Significant at the 0.01 level of probability.

† DAP, days after planting.

‡ GDD, growing degree days; PM, physiological maturity.

§ ns, nonsignificant at the 0.05 probability level.

Table 5. Mean aboveground biomass of canola for samples taken at 52, 67, 78, 94, 108, 125, 152, and 160 d after planting and growing degree days to physiological maturity for the 2003 growing season, University of Pretoria, Hatfield experimental farm, Pretoria, South Africa.

Treatment†	Aboveground biomass								GDD§ to PM
	Vegetative			Flowering		Seed filling			
	52 DAP‡	67 DAP	78 DAP	94 DAP	108 DAP	125 DAP	152 DAP	160 DAP	
	kg ha^{-1}								°C
NNN	746	1600	3200	5580	10,200	15,800	18,550	18,550	1742
SNN	722	1400	1800	3000	6,800	13,900	17,654	17,654	1758
NSN	788	1700	3400	5970	8,600	12,800	16,370	16,370	1856
NNS	730	1504	3000	5384	9,400	15,200	17,420	17,420	1615
$LSD_{0.05}$	ns¶	141	322	645	430	860	599	599	28
CV, %	5	6	5	7	3	3	1	2	1

† NNN, no water stress; NNS, stress during the seed-filling stage; NSN, stress during flowering; SNN, stress during the vegetative stage.

‡ DAP, days after planting.

§ GDD, growing degree days; PM, physiological maturity.

¶ ns, nonsignificant at the 0.05 probability level.

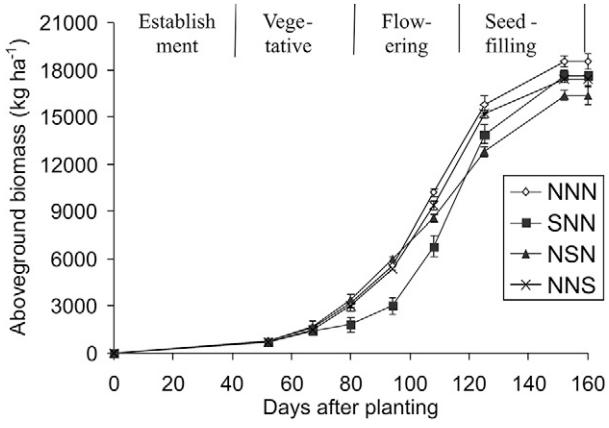

Fig. 2. Aboveground biomass over time of canola for four water regimes during the 2003 winter growing season. Error bars indicate the standard deviation from means of aboveground biomass over time at $P \leq 0.05$. NNN, no water stress; NNS stress during the seed-filling stage (115–152 days after planting [DAP]); NSN, stress during the flowering stage (80–115 DAP); SNN, stress during the vegetative stage (38–80 DAP).

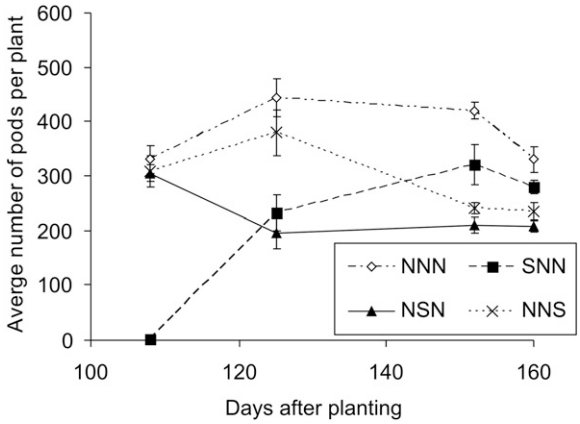

Fig. 3. Canola pod quantity as affected by water stress imposed at different growth stages during the 2003 growing season in Pretoria, South Africa. NNN, no water stress treatment; NNS, stress during the seed-filling stage; NSN, stress during the flowering stage; SNN, stress during the vegetative stage.

was primarily caused by magnitude yield differences between the years. This interaction occurred because of a combination of factors, including water stress. Although irrigation was applied according to profile deficit to field capacity, the profile was monitored only to a depth of 1 m in 2002 but was extended to 1.5 m in 2003. Soil water deficit readings for the 2003 growing season show that 20% of the water was extracted below a depth of 1 m, mainly during the critical stages of growth (data not shown). In addition, no nitrogen top dressing was applied during 2002, which could have contributed to the lower yield during this year.

Generally, seed yield was low during the 2002 growing season compared with the 2003 season (Table 7). Among treatments, treatment NSN produced the lowest yield in each year; the yields for treatment NSN were 49 and 70% of the control in 2002 and 2003, respectively. In 2002, treatments SNN and NNS produced 90 and 86% of the control yield, respectively. In 2003, treatments SNN and NNS produced 84 and 78%, respectively, of the control yield. The SNN and NNS treatments responded similarly compared with the control in each year, but the NSN treatment reduced yield more in 2002 than in 2003. This is related to greater water stress for the treatments in 2002 than in 2003.

The highest seed yield harvested from NNN during the 2003 growing season is attributed to the highest LAD observed during the season (Table 3). Evans et al. (1975) and Annandale et al. (1984) reported similar findings for wheat (*Triticum aestivum* L.). The larger photosynthetic source developed during the growing season (Fig. 1) was able to supply enough assimilates to support prolific flowering and the highest number of pods (Fig. 3). The lowest seed yield was harvested from NSN, probably because of low LAD and aboveground biomass (Tables 3 and 5) and the subsequent abortion of flowers, resulting in a lower number of seed-bearing pods (Fig. 3).

Although treatment NNS experienced rapid leaf senescence, the pods could have served as a photosynthetic source for seed development. The number of pods per plant from treatments NNN and SNN were within the ranges reported by Afridi et al. (2002) and Tanveer et al. (2005) (274–352 pods per plant) in Pakistan. Although the pod numbers per plant for treatments NNS and NSN were below the ranges mentioned by these authors, it was within the ranges reported from studies conducted at Lethbridge and Outlook in Canada (Canola Council of Canada, 2008a).

A linear relationship with an adjusted r^2 value of 0.89 was observed between seed yield and LAD for the period from the beginning of flowering until harvest (GS59 to GS87) (Fig. 4). This is in agreement with the work done by Evans et al. (1975), who observed that in most situations 90 to 95% of the carbohydrates in the seed were being derived from photosynthesis during the seed-filling stage. These authors expect a close correlation between LAD after anthesis and yield under conditions where LAI reaches its peak before anthesis and progressively declines with stress, which is also true without stress. Therefore, it is of ultimate importance to support the crop with optimum water and nutrient supply, especially during the flowering and seed-filling stages to ensure high seed yield by maintaining a high LAD (source) to support seed development (sink).

Table 6. Degrees of freedom, mean squares, and *F* probabilities for the combined analysis of variance for seed yield, seed oil content, and oil yield of four water stress treatments at University of Pretoria, Hatfield experimental farm, South Africa, in 2002 and 2003.

Source of variation	df†	Mean squares		
		Seed yield	Seed oil content	Oil yield
Year	1	5,840,217**	5352**	1,169,970**
Error (a)	5	12,260	2.8	1,786
Water stress	3	2,080,561**	1007.6**	360,581**
Year × water stress	3	170,423**	17.6*	22,973**
Error (b)	15	24,051	5.0	3,280

* Significant at the 0.05 level of probability.

** Significant at the 0.01 level of probability.

† df, degrees of freedom.

Table 7. Mean seed yield, seed oil content, and oil yield of canola grown at the University of Pretoria, Hatfield experimental farm, Pretoria, South Africa in 2002 and 2003 under four water stress treatments. Analysis represents for the interaction between water stress treatment and year.

Treatment†	Mean seed yield	Seed oil content	Oil yield
	kg ha^{-1}	g kg^{-1}	kg ha^{-1}
2002-NNN	2775	365	1013
2002-SNN	2488	351	874
2002-NSN	1361	340	462
2002-NNS	2382	346	825
2003-NNN	3831	398	1523
2003-SNN	3218	378	1217
2003-NSN	2662	366	974
2003-NNS	2987	372	1111
CV, %	6	1	6
$LSD_{0.05}$	270	3.7	100

† NNN, no water stress; NNS, stress during the seed-filling stage; NSN, stress during flowering; SNN, stress during the vegetative stage.

Seed Oil Content and Oil Yield

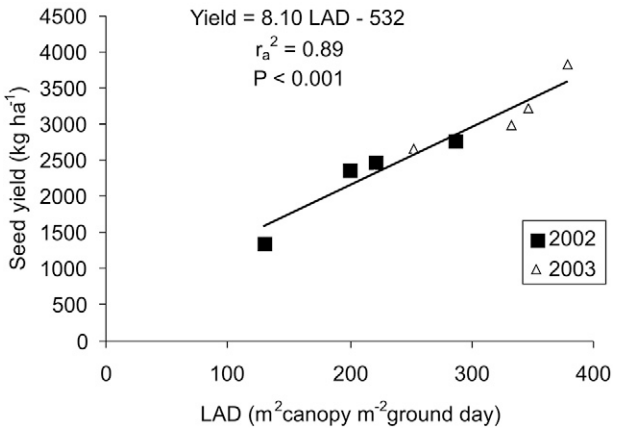

Fig. 4. Linear weighed regression function of canola seed yield vs. leaf area duration (LAD) for the period from beginning of flowering (GS59) until harvest (GS87) for the 2002 and 2003 growing seasons in Pretoria, South Africa (combined data of all water stress treatments).

When data were combined for both years, there was a significant year × water stress interaction for seed oil content ($P < 0.05$) and seed oil yield ($P < 0.01$) (Table 6). The year × water stress treatment interaction shows similar treatment seed oil content rankings for each year. This shows that the interaction was primarily caused by magnitude seed oil content differences between the years. The highest seed oil content and seed oil yield were obtained from NNN during the 2003 growing season, and lowest was obtained from NSN in 2002; both were significantly ($P < 0.05$) different from all other seed oil contents and oil yields (Table 7). Generally, seed oil content and oil yield were low during the 2002 growing season relative to the 2003 season.

The high seed oil content and oil yield from NNN could be attributed to the availability of sufficient soil water throughout the growing season, which maintained a large source size that contributed to high seed yield and oil content. This is in agreement with the work done by Gunasekera et al. (2006), Nielsen (1997), the Manitoba Agriculture Food and Rural Initiatives (1999), and Szumigalski and Van Acker (2006). The latter authors point out that in oil seed crops, seed oil content decreases under low soil water conditions.

This study further showed that the presence of sufficient soil water during the reproductive growth stages, ultimately the flowering stage, plays the biggest role in improving seed oil content and oil yield.

Water Use and Water Use Efficiency

When data were combined for both years, there was a significant ($P < 0.01$) year × water stress interaction for TWU (Table 8). The year × water stress treatment interaction for TWU means shows similar treatment rankings for each year (Table 9). This shows that the interaction was primarily caused by water use magnitude differences between the years.

Generally, water use was lower during 2002 than in 2003 (Table 9) because the crop was under-irrigated during 2002. The 2003 well watered treatment (NNN) used more water than the other water stress treatments. This can most likely be attributed to the combination of a continuous water supply according to crop demand and larger leaf area developed during the season, contributing to maximum possible evapotranspiration. In contrast, the treatment that was water stressed during the flowering stage (NSN) used the lowest amount of water.

Table 8. Degrees of freedom, mean squares, and *F* probabilities for the combined analysis of variance for water use at three growth stages (vegetative, flowering, and seed filling), total water use, and water use efficiency of four water stress treatments at University of Pretoria, Hatfield experimental farm, South Africa, in 2002 and 2003.

Source of variation	df†	Mean squares				
		Vegetative stage	Flowering stage	Seed-filling stage	TWU‡	WUE§
Year	1	10,698.86**	25,725.00**	18,945.03**	161,175**	0.69**
Error (a)	5	61.60	460.50	132.94	991.6	0.03
Water stress	3	5,875.14**	33,947.00**	26,337.24**	48,487**	1.12**
Year × water stress	3	473.36**	100.70ns¶	1,325.24**	3,772**	0.19ns
Error (b)	15	38.83	75.60	71.24	506	0.11

** Significant at the 0.01 level of probability.

† df, degrees of freedom.

‡ TWU, total water use.

§ WUE, water use efficiency.

¶ ns, nonsignificant at the 0.05 probability level.

Table 9. Mean water use of canola per growth stage (establishment, vegetative, flowering, and seed filling), total water use, and water use efficiency for four water stress treatments, 2003, University of Pretoria, Pretoria, South Africa.

Treatment†	Mean water use by growth stages				TWU‡	WUE§
	Establishment	Vegetative	Flowering	Seed filling		
	mm					kg mm^{-1}
2002-NNN	80	101	213	165	559	5.00
2002-SNN	80	54	203	161	498	5.00
2002-NSN	80	91	64	97	332	4.10
2002-NNS	80	108	213	47	448	5.30
2003-NNN	80	140	273	216	709	5.41
2003-SNN	80	74	257	215	626	5.14
2003-NSN	80	152	136	185	553	4.80
2003-NNS	80	146	270	67	563	5.31
CV, %		5.9	6.7	6.0	4.3	6.5
$LSD_{0.05}$		11	ns¶	16	43	ns

† NNN, no water stress; NNS, stress during the seed filling stage; NSN, stress during flowering; SNN, stress during the vegetative stage.

‡ TWU, total water use.

§ WUE, water use efficiency.

¶ ns, nonsignificant at the 0.05 probability level.

When data were combined for both years, there was a significant ($P < 0.01$) year × water stress treatment interaction for water use during the vegetative and seed-filling stages (Table 8). The highest water use was recorded for water stress treatments NSN and NNN during the vegetative and seed-filling stages, respectively, in 2003 (Table 9). The lowest water use was recorded for water stress treatments SNN and NNS during the vegetative and seed-filling stages, respectively, in 2002. There was no significant year × water stress interaction for water use during the flowering stage, indicating that the water use response across treatments was similar each year. Highest water use during the flowering stage was recorded for water stress treatments NNN and NNS in both years. The lowest water use was recorded for water stress treatment NSN during the flowering stage of each year. Generally, crop water use was highest during the flowering stage of canola for all the treatments except NSN (Table 9). This is attributed to the maximum leaf area growth observed at this stage (Fig. 1), which contributed to maximum possible evapotranspiration.

Total water use showed stressing canola during the vegetative stage (SNN) saved 61 mm (2002) and 83 mm (2003) of water at the expense of 287 and 613 kg ha^{-1} seed yield, respectively (Tables 7 and 9). Water stress during the seed-filling stage (NNS) resulted in 111 and 146 mm less water use in 2002 and 2003, respectively, for treatment NNS compared with the non-stressed water treatment NNN. Lower water use by the treatment stressed during the flowering stage (NSN) than NNN resulted in yield reductions of 1414 and 1169 kg ha^{-1} in 2002 and 2003, respectively, for treatment NSN compared with NNN (Table 7).

Canola water use efficiency ranged from 5.41 kg mm^{-1} for treatment NNN in 2003 to 4.1 kg mm^{-1} for treatment NSN in 2002 (Table 9). When data were combined for both years, there was no significant ($P > 0.05$) year × water stress interaction for WUE (Table 8). However, the water stress treatment main effect was significant ($P < 0.01$) for WUE (Table 8). The highest water use efficiency was recorded for water stress treatment NNS (5.31 kg mm^{-1}), and lowest was recorded for water stress treatment NSN (4.45 kg mm^{-1}). This is in contrast to the findings of Nielsen (1997), who reported the lowest WUE from treatments stressed during the seed-filling stage (NNS).

A linear regression function was fit to the water use and yield data of the non-water stress treatment (NNN) of the two seasons per replicate (Fig. 5). According to this function, canola produced 7.09 kg ha^{-1} of seed for every mm of water consumed, which is within the ranges reported by Johnston et al. (2002) for the semiarid region of the Canadian prairies.

CONCLUSIONS

Based on our results, canola is most sensitive to water stress during the flowering stage and less sensitive during the vegetative and seed-filling stages. Irrigation resumption after water stress during the flowering stage (NSN) delayed leaf senescence, enhanced the formation of new flowers, and delayed pod ripening by 114 GDD compared with the NNN and SNN treatments. Stressing canola during the seed-filling stage (NNS) caused the crop to mature 127 GDD earlier than the NNN and SNN treatments. There was a very strong seed yield response to the amount of water used. Water use efficiency, seed yield and oil content, and oil yield were highest for water stress treatment NNN and lowest for NSN. Canola production is source limited under well watered conditions; however, it becomes sink limited when stress occurs in the flowering stage.

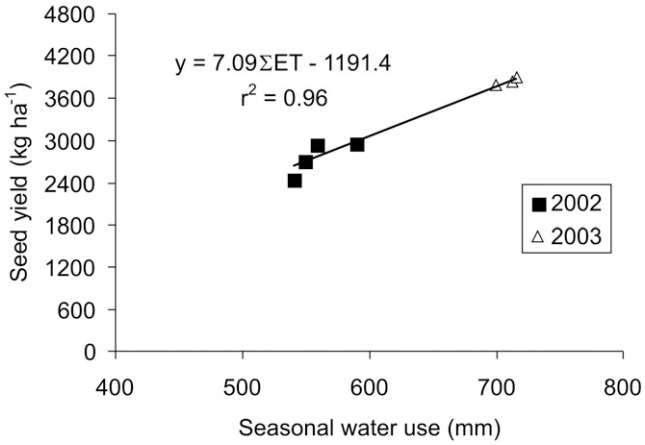

Fig. 5. Water production function of well watered canola (NNN) (dry mass seed vs. seasonal water use per replicate) grown in Pretoria, South Africa, during 2002 and 2003.

From an irrigation management and biophysical production perspective, in areas with a sufficient water supply it would be advisable to irrigate canola according to crop demand throughout the growing season to ensure highest seed yield, oil content, and oil yield. In contrast, in areas where water scarcity is a crucial issue, high WUE at the expense of some seed and oil yield can be achieved by stressing the crop during the vegetative or grain-filling stages. Nonetheless, the choice of strategy needs to consider a long-term cost–benefit analysis, which takes into account the initial irrigation system capital cost and the running cost (water, labor, and electricity) as opposed to the additional yield gained by additional irrigation.

ACKNOWLEDGMENTS

This study was supported by the Human Resource Development of Eritrea, Water Research Commision of South Africa. The authors thank Dr. Andre A. Nel, ARC-Grain crops Institute, for his professional advise and Marie Smith, ARC-biometry unit, for her assistance in statistical analyses and interpretation.

REFERENCES

Afridi, M.Z., M.T. Jan, I. Ahmed, and M.A. Khan. 2002. Yielding components of canola response to NPK nutrition. Pakistan J. Agron. 1:133–135.

Al-Jaloud, A.A., G. Hussian, S. Karimula, and A.H. Ali-Hamidi. 1996. Effect of irrigation and nitrogen on yield and yield components of two rapeseed cultivars. Agric. Water Manage. 30:57–68.

Annandale, J.G., P.S. Hammes, and P.C. Nel. 1984. Effect of soil fertility on the vegetative growth, yield and water use of wheat (*Triticum aestivum* L.). S. Afr. J. Plant Soil 1:96–97.

Bauder, J.W. 2006. The right strategy for irrigating your canola crop. Available at http://waterquality.montana.edu/docs/irrigation/canolastrategy.shtml (verified 15 Jan. 2010). The Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT.

Booth, E.J., and F.D. Gunstone. 2004. Rapeseeds and rapeseed oil: Agronomy, production, and trade. p. 1–16. *In* F.D. Gunstone (ed.) Rapeseed and canola oil production, processing, properties and uses. Blackwell Publishers, Oxford, UK.

Canola Council of Canada. 2005. Temperature, frost and hail. Available at http://www.canola-council.org/chapter5.aspx#ch5_sec1a (verified 13 Jan. 2010). Canola Council of Canada, Winnipeg, MB.

Canola Council of Canada. 2008a. Effects of moisture on canola growth. http://www.canola-council.org/chapter4.aspx#ch4_tab2 (verified 13 Jan. 2010). Canola Council of Canada, Winnipeg, MB.

Canola Council of Canada. 2008b. Growth stages of the canola plant. http://www.canola-council.org/chapter3.aspx (verified 13 Jan. 2010). Canola Council of Canada, Winnipeg, MB.

Champolivier, L., and M. Merrien. 1996. Effects of water stress applied at different growth stages to *Brassica napus* L. var. *oleifera* on yield, yield components and seed quality. Eur. J. Agron. 5:153–160.

Daniel, R.W., D.H. Scarisbrick, and L.G. Smith. 1986. Oilseed rape physiology. p. 83–126. *In* D.H. Scarisbrick and R.W. Daniels (ed.) Oilseed rape. Collins, London UK.

Evans, G.C. 1972. The quantitative analysis of plant growth. Blackwell Sci. Publ., Oxford, UK.

Evans, L.T., I.F. Wardlaw, and R.A. Fischer. 1975. Wheat. p. 101–150. *In* L.T. Evans (ed.) Crop physiology. Cambridge Univ. Press, London, UK.

FAO. 2008. FAOSTAT. Available at http://faostat.fao.org/default.aspx. FAO, Rome, Italy (verified 13 Jan. 2010).

Gunasekera, C.P., L.D. Martin, K.H.M. Siddique, and G.H. Walton. 2006. Genotype by environment interactions of Indian mustard (*Brassica juncea* L.) and canola (Brassica napus L.) in Mediterranean-type environments II. oil and protein concentrations in seed. Eur. J. Agron. 25:13–21.

Hall, B. 2006. Growing degree day modelling for spring canola. [Online]. Available at http://www.ontariosoilcrop.org/User/Docs/Grant-Reports/Canola.GeorgianCentral. pdf. (accessed 14 Oct. 2008; verified 14 Oct. 2008). Ministry of Agriculture, Food and Rural affairs, Guelph, ON.

Johnston, A.M., D.L. Tanaka, P.R. Miller, S.A. Brandt, D.C. Nielsen, G.P. Lafond, and N.R. Riveland. 2002. Oilseed crops for semiarid cropping systems in the northern Great Plains. Agron. J. 94:231–240.

McCaffery, D. 2004. Irrigated canola—Management for high yields. Grain Research and Development Corporation, Griffith, Australia.

Manitoba Agriculture Food and Rural Initiatives. 1999. Moisture and target yields. Available at http://www.gov.mb.ca/agriculture/soilwater/soil/fbd04s00.html (verified 13 Jan. 2010). Manitoba Agriculture, Food and Rural initiatives, Winnipeg, MB.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. London. Ser. B 281:277–294.

Marshall, T.J., and J.W. Holmes. 1988. Soil physics. 2nd ed. Cambridge Univ. Press, UK.

Nel, A.A., J.W. Lodewyckx, W. Jansen, and N.A. Nkosi. 2007. The nitrogen requirement of canola under irrigation. Available at www.arc.agric.za/home.asp?pid=370&toolid=30&itemid=1471 (verified 13 Jan. 2010). ARC- GCI, Potchefstroom, Republic of South Africa.

Nielsen, D.C. 1997. Water use and yield of canola under dry land conditions in the Central Great Plains. J. Prod. Agric. 10:307–313.

Patel, N.R., A.N. Mehta, and A.M. Shekh. 2001. Canopy temperature and water stress quantification in rainfed pigeonpea (*Cajanus cajan* (L.) Millsp.). Agric. For. Meteorol. 109:223–232.

Payne, R.W. D.A., Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2007. GenStat for Windows®, 10th ed. Introduction. VSN International, Hemel Hempstead, UK.

Reyes, S.U. 2007. Canola oil. Available at http://www.ats.agr.gc.ca/asean/4359_e.htm (verified 15 Jan. 2010). Agriculture and Agri-Food Canada.

Richards, F.J. 1969. The quantitative analysis of growth. p. 3–76. *In* F.C. Steward (ed.) Plant physiology: A treatise. Academic Press. London, UK.

Sinclair, T.R. 1984. Leaf area development in field-grown soybean. Agron. J. 76:141–146.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames, IA.

Soil Classification Working Group. 1991. Soil classification. A taxonomic system for South Africa. Dep. of Agric. Development, Pretoria, South Africa.

Sovero, M. 1993. Rapeseed, a new oilseed crop for the United States. p. 302–307. *In* J. Janick and J.E. Simons (ed.) New crops. Wiley, NY.

Szumigalski, A.R., and R.C. Van Acker. 2006. Nitrogen yield and land use efficiency in annual sole crops and intercrops. Agron. J. 98:1030–1040.

Tanveer, A., M. Ayub, A. Ali, and M.A. Nadeem. 2005. Effect of soil incorporated herbicides on weeds and yield of canola (*Brassica napus* L.). Pakistan J. Bot. 37:661–665.