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BRIEF COMMUNICATION

Photosynthetic and growth responses of *Camelina sativa* (L.) Crantz to varying nitrogen and soil water status

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Abstract

Water and nitrogen (N) deficiency are two major constraints limiting the yield and quality of many oilseed crops worldwide. This study was designed to assess the response of *Camelina sativa* (L.) Crantz to the availability of N and water resources on photosynthesis and yield parameters. All the measured variables, which included plant height, root and shoot dry matter, root:shoot ratio, xylem pressure potential (XPP), yield components, photosynthetic parameters, and instantaneous water-use efficiency (WUE) were remarkably influenced by water and nitrogen supply. Net photosynthetic rate (P_N) and yield components were significantly decreased more by water deficit than by N deficiency. XPP, stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) decreased substantially as the water deficit increased irrespective of the level of N application. WUE at the high N supply [100 and 150 kg(N) ha^{-1}] dropped in a large degree as the increased water deficit due to a larger decrease in P_N than transpiration rate (E). The results of this study suggest that the regulative capacity of N supply on photosynthetic and plant growth response is significantly affected by soil water status and *C. sativa* is more sensitive to water deficit than N supply.

Additional key words: instantaneous water-use efficiency; net photosynthesis; nitrogen supply; seed yield; soil water status; transpiration rate.

The unremitting growth of oilseed demand makes it necessary to explore new oilseed crops to meet this requirement. *C. sativa*, with many positive agronomic attributes such as apparent low-input requirements, adaptation to semiarid regions, tolerance of low-fertility and high disease and insect resistance (Schuster and Friedt 1998, Zubr 1997), has great potential to be grown across Canada. In order to introduce a new oilseed crop, it is necessary to determine the resource requirements of this crop.

Accurate assessment of resource-use efficiency is crucial to an understanding of how to optimize growth and yield through an improved management. The relationship among applied N rate, photosynthesis, and growth has been well documented (Field and Mooney 1986, Cechin and Fumis 2004). Many previous studies have addressed the response of stomatal behavior, leaf water status and photosynthesis to soil water status (McVetty *et al.* 1989, Reddy *et al.* 2003). However, information on the interactive effect of nitrogen and water on *C. sativa* growth and photosynthetic response is limited. Hence, this study was initiated to determine the photosynthetic and yield responses of *C. sativa* to various N and moisture regimes. The main objectives of the study were to (*1*) determine the interactive effects of N and moisture regimes on growth and yield components and (*2*) evaluate the effect of applied N and water on P_N, E, and WUE.

In a controlled environment study, *C. sativa* cv. Calena (provided by the Nova Scotia Crop Development Institute) was used to study the effect of different N rates [0, 50, 100, and 150 kg(N) ha^{-1}, which corresponded to 0, 0.088, 0.176, and 0.264 g pot^{-1} of ammonium nitrate] and soil water potential (0, –0.065, and –0.130 MPa) on its

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Abbreviations: C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; N – nitrogen; P_N – net photosynthetic rate; WUE – instantaneous water-use efficiency; XPP – xylem pressure potential.

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Table 1. Soil mixture characteristics used in the growth chamber study.

pH	P_2O_5 [kg ha^{-1}]	K_2O [kg ha^{-1}]	Ca [kg ha^{-1}]	Mg [kg ha^{-1}]	Sulfur [kg ha^{-1}]	Nitrate [kg ha^{-1}]	N [%]
5.9	551	460	3,653	445	88	52	0.25

Table 2. Interactive effects of N and soil moisture regimes on xylem pressure potential (XPP), root dry matter, root:shoot dry matter, N content, total N amount and plant height. Means ± SE (n = 6). *Different letters* within the same column indicate significant differences ($p<0.05$).

N [kg ha^{-1}]	Soil water potential [MPa]	XPP [–MPa]	Root dry matter [g]	Root:shoot	N [%]	Total N amount [g]	Plant height [cm]
0	0	0.81 ± 0.02^{B}	3.55 ± 0.15^{Fg}	0.41 ± 0.02^{G}	1.46 ± 0.05^{D}	$12.53 \pm 1.67^{D\text{-}g}$	72.75 ± 0.80^{Bc}
0	–0.065	1.14 ± 0.06^{De}	$4.00 \pm 0.21^{D\text{-}f}$	0.79 ± 0.05^{Cd}	1.65 ± 0.03^{Cd}	8.41 ± 1.15^{Fg}	61.00 ± 0.50^{F}
0	–0.130	1.53 ± 0.10^{G}	5.05 ± 0.3^{Cd}	1.44 ± 0.12^{A}	2.59 ± 0.07^{Ab}	9.07 ± 1.20^{Fg}	51.65 ± 0.15^{H}
50	0	0.76 ± 0.07^{A}	6.90 ± 0.48^{Ab}	0.73 ± 0.04^{D}	1.61 ± 0.08^{Cd}	$15.14 \pm 0.58^{C\text{-}e}$	70.75 ± 0.25^{Cd}
50	–0.065	1.35 ± 0.06^{Fg}	$4.55 \pm 0.45^{C\text{-}e}$	0.80 ± 0.08^{Cd}	2.49 ± 0.04^{Ab}	$14.20 \pm 1.13^{C\text{-}f}$	57.15 ± 0.35^{G}
50	–0.130	1.84 ± 0.06^{H}	3.05 ± 0.15^{Fg}	0.92 ± 0.13^{B}	2.81 ± 0.25^{A}	$9.33 \pm 1.38^{E\text{-}g}$	49.25 ± 0.75^{I}
100	0	0.83 ± 0.07^{C}	6.80 ± 0.30^{Ab}	0.56 ± 0.03^{F}	1.53 ± 0.09^{D}	18.83 ± 2.73^{Bc}	74.80 ± 1.76^{B}
100	–0.065	1.13 ± 0.05^{De}	$4.55 \pm 0.26^{C\text{-}e}$	0.61 ± 0.07^{Ef}	2.09 ± 0.05^{Bc}	$15.92 \pm 2.19^{B\text{-}d}$	65.60 ± 1.08^{E}
100	–0.130	1.38 ± 0.05^{Fg}	2.55 ± 0.15^{G}	0.88 ± 0.06^{Bc}	2.85 ± 0.37^{A}	8.16 ± 1.14^{G}	61.15 ± 0.50^{F}
150	0	0.95 ± 0.03^{Cd}	7.80 ± 0.89^{A}	0.62 ± 0.02^{Ef}	2.73 ± 0.13^{A}	34.22 ± 5.07^{A}	81.30 ± 1.36^{A}
150	–0.065	1.01 ± 0.07^{Ce}	5.70 ± 0.43^{Bc}	0.69 ± 0.04^{De}	2.63 ± 0.08^{A}	21.70 ± 1.49^{B}	69.40 ± 0.60^{D}
150	–0.130	1.20 ± 0.09^{Ef}	4.10 ± 0.31^{Df}	0.74 ± 0.09^{D}	2.42 ± 0.15^{Ab}	$13.44 \pm 1.46^{C\text{-}g}$	63.00 ± 1.50^{F}
P-value		0.001	0.002	0.001	0.011	0.003	0.001

growth and yield components. Ten seeds were sown in 15-cm diameter plastic pots filled with a 1:1(v/v) mixture of Pro-mix BX (*Premier Horticulture,* Canada) and field soil. Soil mixture characteristics are shown in Table 1. Seedlings were thinned to two plants pot^{-1} at the first true leaf stage, approximately seven days following emergence. A combination of incandescent and cool white fluorescent lights provided 350 ± 10 µmol m^{-2} s^{-1} photosynthetically active radiation (PAR) measured at the top of the plant canopy. The growth chamber was maintained at a 16-h photoperiod, with a mean day/night temperature of 25/15°C. Relative humidity was maintained at 70% ± 5%. In order to minimize variation in the growth chamber microenvironment, plants were rotated randomly within and between blocks three times during the experiment.

N was supplied by dissolving ammonium nitrate in distilled water. Sufficient amounts of other nutrients, P, K, Ca, Mg, and S were provided from the soil mixture. Each pot received 100 ml of the N solution 7 days after seeding. Moisture deficit was gradually imposed by withholding irrigation. Water was withheld 21 days after seedling emergence to impose water deficit. Withholding water allowed a decline in soil moisture potentials to –0.065 and –0.130 MPa, respectively. After the soil moisture potential dropped to the desired level, water was added to the soil until field capacity was reached. Control pots received 150 ml of water daily to maintain field capacity. The excess water from the pots was collected in plastic plates and returned to each respective pot. To simulate more realistic responses to drought, a cyclical water stress method was imposed. Soil moisture potential was measured daily by using a Watermark Soil Moisture Meter and Sensors (*Spectrum Technologies, Inc.*, IL, USA). The experiment was terminated after 60 days from first exposure to water stress.

All of the aboveground portions of two plants pot^{-1} were collected at the time of harvest. Plant height was measured at harvest. Two plants were used to measure the xylem pressure potential (XPP) with a *Scholander* pressure bomb (*PMS Instrument, Co. Corvallis*, Oregon, USA), as an indicator of plant water status (*e.g.* Mason 1969) and the same plants were used to determine yield components (number of branches and pods per plant) and dry matter following XPP measurement. Roots were washed by hand after harvest to evaluate the root dry matter and root:shoot ratio. Two shoot samples were ground and analyzed for N by combustion (*AOAC*, 1990, Method 968.06) using a Leco protein/nitrogen analyzer (*Model FP-528, Leco Corp.*, St. Joseph, MI). Total shoot N was calculated by the product of shoot dry matter and shoot N content.

A portable gas-exchange system *ADC-LCA4* (*ADC Inc.,* Hoddesdon, Hertfordshire, UK) was used to measure P_N, E, g_s and C_i. The sixth fully expanded leaf from a branch tip was selected for photosynthetic measurements. The selected leaves were fully developed, with horizontal positions and on upper parts of unshaded shoots. A minimum of two measurements were taken on each of 6 fully expanded leaves per treatment. All measurements were made between 10:00 and 13:00 h over two consecutive days. Before the photosynthetic measurements, the print of the leaf was used to determine leaf area by using a leaf area meter (*Li-3000, Licor,*

Table 3. Nitrogen effect on yield components (branches plant^{-1} and pods plant^{-1}) and shoot dry matter. Means ± SE ($n = 6$). *Different letters* within the same column indicate significant differences ($p<0.05$).

N rate [kg ha^{-1}]	Branches plant^{-1}	Pods plant^{-1}	Shoot dry matter [g]
0	7.80 ± 0.83^{B}	74.9 ± 13.7^{B}	5.73 ± 0.96^{B}
50	8.00 ± 0.45^{B}	82.2 ± 11.1^{B}	6.13 ± 1.15^{B}
100	8.67 ± 0.75^{A}	94.7 ± 11.7^{A}	7.58 ± 1.78^{A}
150	8.75 ± 0.86^{A}	99.3 ± 11.6^{A}	8.78 ± 1.41^{A}
P-value	0.023	0.031	0.015

Table 4. Water deficit effect on yield components and shoot dry matter. Means ± SE ($n = 6$). *Different letters* within the same column indicate significant differences ($p<0.05$).

Soil water potential [MPa]	Branches plant^{-1}	Pods plant^{-1}	Shoot dry matter [g]
0	10.25 ± 1.28^{A}	123.6 ± 12.8^{A}	10.70 ± 1.22^{A}
–0.065	7.00 ± 0.93^{B}	79.5 ± 11.5^{B}	6.66 ± 0.51^{B}
–0.130	7.06 ± 0.56^{B}	62.3 ± 4.5^{C}	3.81 ± 0.41^{C}
P-value	0.038	0.003	0.029

Lincoln, NE, USA*)* at the start of the flowering stage. WUE was derived by the ratio of P_N to E.

The experiment followed a two factor factorial randomized complete block design with 3 replications for each treatment. The first factor was soil water potential at three levels (0, –0.065, and –0.130 MPa) and the second factor was N at four levels [0, 50, 100 and 150 kg(N) ha^{-1}]. The response variables plant height, XPP, yield component (branches and pods plant^{-1}), root and shoot dry matter, root:shoot ratio, shoot N content, P_N, E, g_s, C_i, and WUE were collected and subjected to the PROC MIXED procedure in *SAS*. *Tukey*'s test was used to compare the differences among treatments at 5% significant level.

Results of this study clearly demonstrate that limiting water and N during growth of *C. sativa* can directly influence several aspects of growth. Under well-watered conditions, yield components increased significantly as the N supply increased up to 100 kg(N) ha^{-1} (Table 3). Yield components of plants with 150 kg(N) ha^{-1} supply were not significantly higher than 100 kg(N) ha^{-1}, which suggests that plants with 150 kg(N) ha^{-1} may absorb N but may not be utilized for photosynthetic functions or for growth. It is well documented that an increase in N usually leads to larger leaf area, high leaf N, with an increase in leaf photosynthetic capacity and growth (Field and Mooney 1986). The response of *C. sativa* to a water deficit differed with N application rate. Soil moisture deficit adversely affected total shoot N at all N levels and the degree of reduction was highly correlated to N supply (Table 2). The greatest decrease of 61% was observed with the 150 kg(N) ha^{-1} treatment, while the lowest reduction (28%) was observed in the 0 kg(N) ha^{-1} treatment (Table 2). The number of branches plant^{-1} and pods plant^{-1} decreased from 10 to 7 and 124 to 62 as the soil water potential decreased from 0 to –0.130 MPa (Table 4). In contrast, water deficit reduced the pods plant^{-1} by 50% while N deficit decreased pods plant^{-1} only by 20% (Table 3 and 4) suggesting that water deficit can be more detrimental to yield than N supply. The response of root dry matter to water deficit varied in relation to the N supply. Without N supply, root dry matter increased significantly from 3.55 to 5.05 g with the increasing water deficit. There was, however, an inverse relationship between root dry matter and water deficit for all plants that received N. Plants that received the highest N supply produced the highest root dry matter (4.1 g to 7.8 g) irrespective of the soil water status (Table 2). Although shoot dry matter was not affected by the interactive effect of N and water supply, it was significantly influenced by N and water levels independently. Table 3 shows that shoot dry matter increased by 53% (5.73 –8.78 g) as N rate increased from 0 to 150 kg(N) ha^{-1} and decreased by 64% (10.7–3.81 g) with the decreasing soil water potential from 0 to –0.130 MPa (Table 4). The root:shoot ratio increased significantly as the increased water deficit at all N rates but the relative magnitude of these increases varied with the level of N. Table 2 shows that at the 0 N level the root:shoot increased 2.5 times (0.41 to 1.44) in response to water deficit, which was significantly greater when compared to the plants that received N application. The increases of root:shoot were only 26% (0.73 to 0.92), 57% (0.56 to 0.88) and 19% (0.62 to 0.74) in 50, 100 and 150 N kg ha^{-1} treatments, respectively. The significant increase in root:shoot ratio in water deficit condition indicated that there is preferential allocation of carbon towards root growth. This would have increased hydraulic conductance since hydraulic conductance is directly related to root volume.

The results in this study also showed that all the measured photosynthetic parameters were remarkably influenced by water and nitrogen supply (Fig. 1). Under well-watered conditions, a positive relationship between

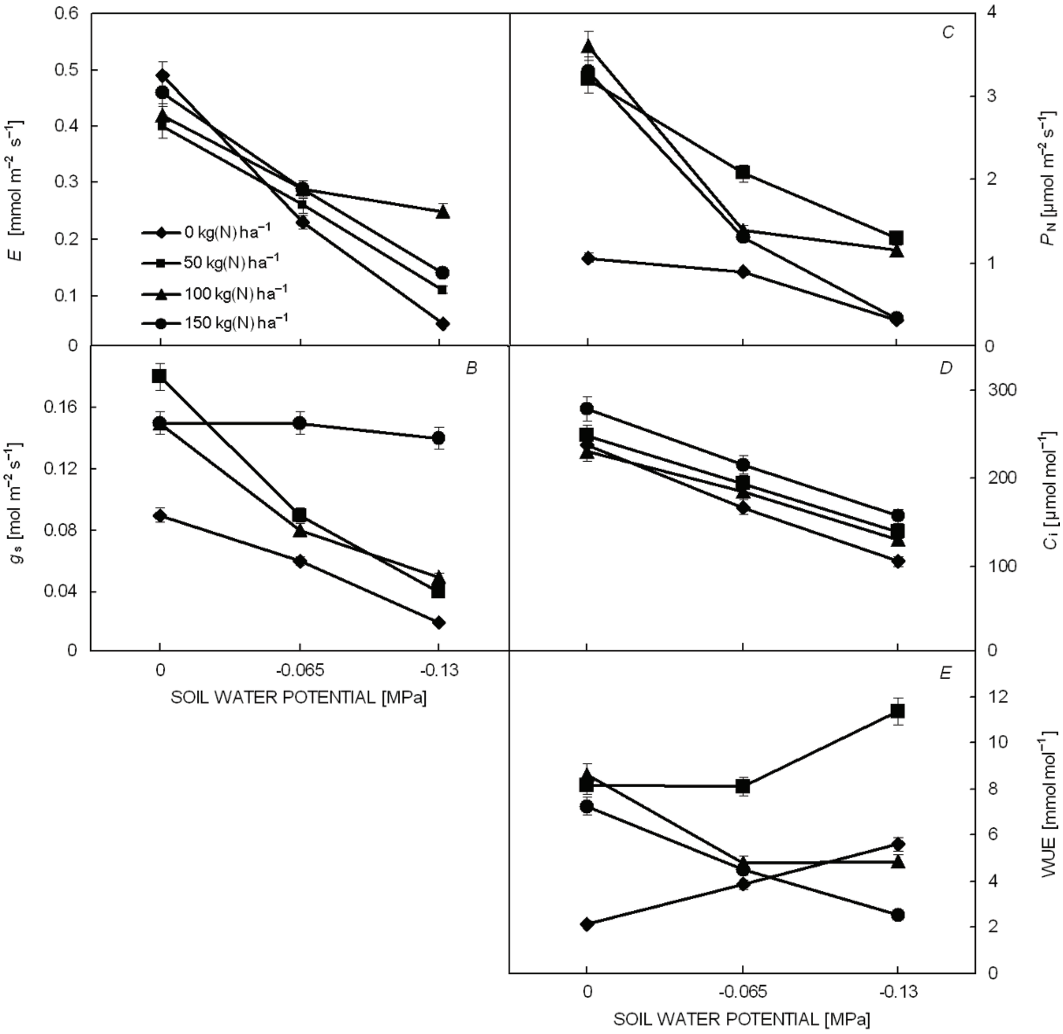

Fig. 1. Interactive effects of N and soil moisture regimes on transpiration rate, E (*A*), stomatal conductance, g_s (*B*), rate of net photosynthetic rate, P_N (*C*), internal CO$_2$ concentration, C_i (*D*) and instantaneous water-use efficiency, WUE (*E*) of *Camelina sativa* leaves. Each value in this figure is the mean of six measurements and corresponding standard error bars.

N supply and P_N was found until the N application reached 100 kg(N) ha^{-1} (Fig. 1*C*). Relatively high amounts of C_i and g_s in well-watered condition suggest that the difference of P_N among varied N treatments was more related to the biochemical limitations rather than stomatal limitations (Fig. 1*B*,*D*). WUE was significantly higher in the plants that received N than those that did not (Fig. 1*E*). As the decreased soil water potential, P_N dropped in all N treatments. Plants that received 50 kg(N) ha^{-1} had the highest P_N while at 150 kg(N) ha^{-1}, P_N was significantly inhibited (Fig. 1*C*). Greater photosynthetic sensitivity to water deficit was found in plants with high N level, which is similar to those reported for beans (Shimshi 1970) and wheat (Morgan 1986). Walters and Reich (1989) reported that this greater sensitivity might be related to the low hydraulic conductance or another aspect of water transport caused by lower root:shoot ratio in high N treatment. Even though the plants that received N supply had significantly higher P_N and yield components than plants without N supply, only a small degree of variation was observed [between 50 and 100 kg(N) ha^{-1}]. This small effect can be explained by several factors. First, significantly less total N content in plants under water deficit for all N treatments suggests that less soil water availability may have reduced the N uptake. Secondly, the low soil water potential can affect the relationship between available N and photosynthesis by increasing stomatal resistance, and generally results in reduced photosynthetic capacity (Walters and Reich 1989). Both g_s and C_i decreased substantially as the water deficit increased irrespective of the level of N application. The similar response of g_s to water deficit was also reported by Reddy *et al.* (2003) and Tognetti *et al.* (2007). The decreased C_i and g_s (Fig. 1*B,D*) indicates that both stomatal and biochemical limitations appear to account for the decline in P_N. In contrast, P_N decreased more by water deficit than by N deficiency. E decreased with water deficit (Fig. 1*A*). WUE differed between high and low N rate treatments (Fig. 1*E*). WUE decreased 64% (7.26–2.57 mmol mol^{-1}) in 150 kg(N) ha^{-1} and 44% (8.64–4.88 mmol mol^{-1}) in 100 kg(N) ha^{-1}. This sharp decrease in WUE in plants under high N treatment was due to a significant decrease in P_N than in *E*. However, WUE in the low N treatment increased substantially with water deficit, which was 1.6 times (2.12 to 5.62 mmol mol^{-1}) in 0 N treatments and 39% (8.14 to 11.34 mmol mol^{-1}) in 50 kg(N) ha^{-1} treatments. WUE was always greater at 50 kg(N) ha^{-1} treatment for any level of water status.

In conclusion, the results of this study suggest moisture deficit singly or in combination with different N rates significantly affects photosynthetic parameters and thus, growth and yield components. Under low water availability, photosynthesis is highly related to both biochemical and stomatal limitations and *C. sativa* has a N requirement of approximately 100 kg(N) ha^{-1} for achieve optimum performance; under nonlimiting moisture conditions, biochemical limitation is the major constraint for photosynthesis and a N rate of 150 kg(N) ha^{-1} can be effectively assimilated by the crop.

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