

Water-stress and N-nutrition effects on photosynthesis and growth of *Brassica carinata*

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Abstract

Effects of water and nitrogen (N) supply on growth and photosynthetic response of *B. carinata* were examined in this study. Plant growth and related characteristics varied significantly in response to the availability of water and nitrogen. *B. carinata* maximized the utilization efficiency of the most limiting resources by developing physiological adaptations, such as changes in root and leaf development. The utilization of water and N was tightly linked with the availability of each resource. Instantaneous water-use efficiency (WUE) was always greater in plants with high-N nutrition [50, 100, and 150 kg(N) ha⁻¹] than in the low-N-treated plants [0 kg(N) ha⁻¹] in all watering treatments. Instantaneous N-use efficiency (PNUE) decreased significantly with increasing water stress in all N treatments. Seed yield is significantly related to PNUE ($p>0.05$) but not WUE ($p<0.05$). The positive relationship between leaf net photosynthetic rate (P_N) and seed yield suggests that P_N can be used as an important tool for selection of new strains with high seed yield.

Additional keywords: *Brassica carinata*; instantaneous water-use efficiency; instantaneous N-use efficiency; nitrogen supply; soil water potential; water stress.

Introduction

Brassica carinata A. Braun is an interesting C₃ oilseed crop with high erucic acid content, which has attracted a growing interest in using it in nonfood applications such as biodiesel, biopolymers, lubricants, soaps, and surfactants (Cardone *et al.* 2003, Taylor *et al.* 2009). In addition, the residual defatted meal of *B. carinata* can be used as a soil amendment for plant defence due to the highly biologically active compounds (*i.e.* allyl glucosinolates) in the meal. Furthermore, with good drought resistance and low pod-shattering tendency (Monti *et al.* 2009), *B. carinata* could be developed as an oilseed crop in Canada to diversify and stabilize oilseed production.

In both managed and natural systems, plants often encounter diverse environmental stresses. Since many oilseed crops are indeterminate plants, adaptation is affected by tolerance to environmental stress and by crop management to take advantage of optimum conditions for plant growth (Weiss 2000). In order to achieve optimum growth, plants develop several approaches to balance the resources and maximize the most limited resources. An

efficient use of resources reflects the ability of the plant to tolerate the variation of resource availability and therefore is a desirable trait for developing new oilseed crops.

Water and nitrogen availabilities are two major environmental factors which change dramatically during plant development. Photosynthesis is one of the primary processes to be affected by any environmental changes. Numerous studies have emphasized the plant responses to interacting environmental resources (Chapin III *et al.* 1987, Chaves *et al.* 2009); however, the study on the interactive effect of resource availability on growth and photosynthesis of *B. carinata* from the standpoint of resource-use efficiency is limited. Two major environmental resources, nitrogen and water, were assessed in this study. In order to relate photosynthetic capacity to resource availability, two indices of intrinsic resource-use efficiency was investigated, which are instantaneous PNUE, defined as the ratio of P_N to leaf N content per leaf area basis (N_{area}), and WUE, defined as the ratio of P_N to transpiration rate (E).

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Abbreviations: C_i – intercellular CO₂ concentration; E – transpiration rate; N – nitrogen; N_{area} – leaf N content per leaf area basis; P_N – net photosynthetic rate; PNUE – instantaneous N-use efficiency; WUE – instantaneous water-use efficiency.

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The main objectives of the study were: (1) to determine the effect of N and water supply on yield and yield components, (2) to evaluate the P_N , E , WUE, and PNUE under varied N and water availability regimes,

(3) to investigate the relationship between P_N , WUE, PNUE, and seed yield. In order to achieve the objectives, *B. carinata* was grown under different rates of applied N and soil water potential, in a controlled environment.

Materials and methods

Plant material and growth conditions: In a controlled environment study, *B. carinata* line 070760EM [obtained from the Agriculture and Agri-Food Canada, Saskatoon Research Centre (AAFC-SRC) breeding program] was used as the experimental material to study the effect of different N rates [equivalent to 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, respectively] and soil water potential (0, -0.065 and -0.130 MPa) on its growth, root development, and yield components. Ten seeds were sown in 15-cm diameter plastic pots filled with 1:1 mixture of Pro-mix BX (*Premier Horticulture*, Canada) and field soil [pH 5.9; 551 kg(P_2O_5) ha^{-1} , 460 kg(K_2O_5) ha^{-1} ; 3,653 kg(Ca) ha^{-1} , 445 kg(Mg) ha^{-1} , 88 kg(S) ha^{-1} , 52 kg(nitrate-N) ha^{-1} , 0.25% N]. Seedlings were thinned to four plants pot^{-1} at the first true leaf stage, approximately seven days following emergence. A combination of incandescent and cool white fluorescent lights provided photosynthetically active radiation (PAR) of approximately $420 \pm 20 \mu\text{mol m}^{-2} s^{-1}$ 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.

Water stress imposition: Water was withheld 21 days after seedling emergence to impose water deficit. To simulate more realistic responses to drought, a cyclical water-stress method was imposed. Moisture deficit was gradually imposed by withholding water and allowing a decline in soil moisture potentials to -0.065 and -0.130 MPa, respectively. After the soil moisture potential dropped to the required level, water was added to the soil until field capacity was reached. Control pots were irrigated daily to maintain field capacity. Soil moisture potential was measured daily by using Watermark Soil Moisture Meter and Sensors (*Spectrum Technologies*, IL, USA).

N application: N was supplied by dissolving ammonium nitrate in distilled water. Each pot received 100 ml of the N solution 7 days after seeding. Other nutrients, P, K, Ca,

Mg, and S were provided from the soil mixture.

Growth variables: All of the aboveground portions of four plants pot^{-1} were collected at the time of harvest (90 days after seeding). Two plants were used to determine yield components (number of branches and pods per plant) and dry matter. Roots were washed by hand after harvest to evaluate the root dry matter and root:shoot ratio.

Photosynthetic variables: A portable gas-exchange system *ADC-LCA4* (*ADC*, Hoddesdon, Hertfordshire, UK) was used to measure P_N and E . The sixth fully expanded leaf from a branch tip was selected for photosynthetic measurements. All measurements were made under PAR of $420 \pm 20 \mu\text{mol m}^{-2} s^{-1}$ at $350 \pm 10 \mu\text{mol mol}^{-1}(\text{CO}_2)$, leaf temperature of 20°C, and relative humidity of 70%. A minimum of two measurements were taken on each of 9 fully expanded leaves per treatment. All measurements were made between 10:00 and 13:00 h in three consecutive days at the beginning of the flowering stage (50 days after seeding). Before the photosynthetic measurements, a print of the leaf was used to determine leaf area by using a leaf area meter (*Li-3000*, *Licor*, Lincoln, NE, USA) at the beginning of flowering. The same leaves were used to analyze leaf N content (note: the leaves were all dried in 60°C oven for 48 h before the analysis). Dry leaf samples were ground and analyzed for N by combustion using a Leco protein/nitrogen analyzer (*Model FP-528*, *Leco Corp.*, St. Joseph, MI). N_{area} was calculated as (leaf dry mass × leaf N content)/leaf area.

Experimental design and statistical analysis: The experiment followed a two factor (soil water potential and N rate) factorial randomized complete block design with 3 replications for each treatment. The response variables plant height, yield components (branches and pods $plant^{-1}$), root and shoot dry matter, root:shoot ratio, specific leaf area, leaf N content, N_{area} , P_N , E , WUE, PNUE, and seed yield were collected and subjected to the PROC MIXED procedure in *SAS* (*SAS Institute, Inc.*, Cary, NC, USA). Tukey's test was used to compare the differences among treatments at the 5% significant level.

Results and discussion

Effect of N and water availability on growth and related characteristics: Growth and related characteristics of *B. carinata* were highly sensitive to the availability of water and N. Leaf area and leaf N content were markedly higher in plants supplied with N than plants without N under all watering treatments (Table 1). Leaf area decreased and leaf N content increased with water stress in all N treatments. PNUE was positively correlated with leaf area while negatively related to N_{area} (Table 5), which suggests that *B. carinata* prefers to produce large leaf size with lower N content instead of a smaller leaf area with higher N contents to optimize the utilization of leaf N in photosynthesis. The increased leaf N content and N_{area} with applied water stress suggests that *B. carinata* may regulate the internal osmotic pressure by accumulating N-based secondary metabolites to adjust the water stress. The adjustment to water stress by accumulating N-based glucosinolates in *Brassica* species has been documented in several studies (Schreiner *et al.* 2009).

Neither N nor the interaction between soil water and N availability substantially affected plant height. However, the plant height was highly sensitive to water stress and it dropped from 115 to 70 cm as the water stress increased (Table 3). Shoot dry matter, root dry matter, and root:shoot ratio were all significantly affected by the interaction between N and water availability (Fig. 1). Shoot and root dry matter increased significantly as N increased in well watered plants. In the moderate water-stress treatment, plants with N had significantly higher shoot dry matter than plants without N while the difference between N treatments was not significant. There was no significant difference in shoot and root dry matter in severely water-stressed plants at any level of N. The root:shoot ratio of plants in low N treatments [0 and 50 kg(N) ha^{-1}] increased markedly under severely water-stressed conditions while that of plants with higher N

kept statistically constant in all water regimes. The plants without N supply had the highest root:shoot ratio in all water regimes. This result indicated that extending the root proliferation is an essential strategy for *B. carinata* to resist resource insufficiency.

Both branches plant⁻¹ and pods plant⁻¹ were positively related to N supply while they were negatively affected by water deficit (Table 3 and 4). N effect on seed yield was dependent on the availability of water (Table 2, Fig. 2A). The seed yield of well watered plants increased linearly from 2.52 to 5.81 g per pot as N increased. Water stress substantially decreased the seed yield in all N treatments, but the relative magnitude varied. Plants with the highest N decreased seed yield approx. 5 fold while the seed yield of plants with 50 and 100 kg(N) ha^{-1} was reduced by half as the water stress increased. For plants without N, the seed yield decreased by 85% as water stress increased. In many studies, a positive linear relationship was found between P_N and seed yield (Richards 2000). A similar relationship was observed in *B. carinata* plants in this study (Table 5). This study suggests that P_N can be used as a tool for selection of new genotypes with high seed yield and high PNUE.

WUE: The effects of N availability on P_N , E , and WUE are not identical under different water status (Table 2). P_N and E were negatively correlated with water stress and increased with N. C_i decreased dramatically as the water stress increased in all N treatments. The high C_i in well watered conditions indicated that biochemical rather than stomatal limitations appear to account for the difference in photosynthesis among N treatment. The linear decline in C_i as the water stress increased found in this study indicates that the development of stomatal limitations to gaseous CO_2 exchange drives C_i lower, which is the dominant factor for the reduction in photosynthesis and increase in WUE. WUE was remarkably improved as the

Table 1. Interactive effects of N and soil moisture regimes on leaf area, leaf N content and leaf N content per leaf area basis (N_{area}). Means \pm SE ($n = 6$). *Different letters* within the same column indicate significant differences ($p < 0.05$).

Treatment	N rate [kg ha^{-1}]	Leaf area [cm^2]	Leaf N content [%]	N_{area} [mmol m^{-2}]
Well watered	0	5.73 ± 0.011^g	1.15 ± 0.035^f	0.008 ± 0.0003^c
	50	11.09 ± 0.647^b	1.91 ± 0.060^{cd}	0.010 ± 0.0004^c
	100	13.97 ± 0.779^a	1.77 ± 0.125^{cde}	0.008 ± 0.0007^c
	150	15.33 ± 0.665^a	2.07 ± 0.390^{cd}	0.009 ± 0.0017^c
Moderate water stress	0	3.35 ± 0.071^h	1.31 ± 0.049^{ef}	0.010 ± 0.0014^c
	50	9.21 ± 0.050^{de}	2.23 ± 0.240^c	0.011 ± 0.0011^c
	100	9.38 ± 0.068^{cd}	2.96 ± 0.056^b	0.015 ± 0.0013^b
	150	10.78 ± 1.01^{bc}	3.32 ± 0.390^{ab}	0.015 ± 0.0021^b
Severe water stress	0	1.44 ± 0.028^i	1.55 ± 0.121^{def}	0.021 ± 0.0015^a
	50	7.23 ± 0.023^f	3.75 ± 0.175^a	0.019 ± 0.0005^a
	100	7.65 ± 0.016^f	3.44 ± 0.145^{ab}	0.017 ± 0.0013^{ab}
	150	7.84 ± 0.040^{ef}	3.64 ± 0.177^a	0.019 ± 0.0012^a

Table 2. Interactive effects of N and soil moisture regimes on rate of net photosynthetic rate (P_N), transpiration rate (E),instantaneous water-use efficiency (WUE), internal CO_2 concentration (C_i), instantaneous N-use efficiency (PNUE) and seed yield of *B. carinata* leaves. Means \pm SE ($n=6$). *Different letters* within the same column indicate significant differences ($p<0.05$).

Treatment	N rate [kg ha^{-1}]	P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	E [$\text{mmol m}^{-2} \text{s}^{-1}$]	WUE [mmol mol^{-1}]	C_i [$\mu\text{mol mol}^{-1}$]	PNUE [$\mu\text{mol mmol}^{-1} \text{s}^{-1}$]	Seed yield [g]
Well watered	0	1.24 \pm 0.160 ^f	3.67 \pm 0.165 ^a	0.34 \pm 0.028 ^f	431.8 \pm 10.21 ^{bc}	162.54 \pm 14.6 ^{bc}	2.52 \pm 0.27 ^d
	50	2.52 \pm 0.065 ^b	2.28 \pm 0.014 ^b	1.10 \pm 0.023 ^{cd}	442.5 \pm 14.43 ^{ab}	247.76 \pm 5.08 ^b	4.63 \pm 0.087 ^{bc}
	100	3.26 \pm 0.310 ^a	3.59 \pm 0.127 ^a	0.91 \pm 0.137 ^d	451.8 \pm 17.02 ^a	411.48 \pm 41.2 ^a	5.54 \pm 0.362 ^{ab}
	150	3.52 \pm 0.285 ^a	1.90 \pm 0.070 ^c	1.85 \pm 0.101 ^a	448.7 \pm 13.04 ^a	393.90 \pm 44.1 ^a	5.81 \pm 0.056 ^a
	0	1.02 \pm 0.085 ^f	1.75 \pm 0.081 ^{cd}	0.58 \pm 0.022 ^c	427.9 \pm 15.36 ^c	100.40 \pm 6.95 ^{cd}	1.31 \pm 0.327 ^f
	50	1.99 \pm 0.020 ^{cd}	1.64 \pm 0.051 ^d	1.21 \pm 0.035 ^c	422.3 \pm 13.88 ^{cd}	184.64 \pm 16.1 ^{bc}	3.05 \pm 0.383 ^d
Moderate water stress	100	2.29 \pm 0.075 ^{bc}	2.16 \pm 0.007 ^b	1.06 \pm 0.037 ^{cd}	428.4 \pm 10.48 ^c	149.56 \pm 17.9 ^c	4.37 \pm 0.109 ^c
	150	2.12 \pm 0.100 ^{bcd}	1.15 \pm 0.025 ^f	1.85 \pm 0.128 ^a	413.7 \pm 16.98 ^{de}	141.10 \pm 15.8 ^c	4.12 \pm 0.081 ^c
	0	0.85 \pm 0.005 ^f	1.32 \pm 0.071 ^{ef}	0.64 \pm 0.030 ^e	421.1 \pm 12.93 ^{cd}	41.23 \pm 2.83 ^d	0.36 \pm 0.004 ^f
	50	1.70 \pm 0.025 ^{de}	1.41 \pm 0.053 ^e	1.20 \pm 0.025 ^c	407.6 \pm 15.84 ^e	88.51 \pm 1.42 ^{cd}	2.50 \pm 0.034 ^d
	100	1.84 \pm 0.028 ^{cd}	1.20 \pm 0.070 ^{ef}	1.54 \pm 0.073 ^b	413.3 \pm 18.20 ^{de}	109.39 \pm 9.59 ^{cd}	2.23 \pm 0.085 ^{de}
	150	1.73 \pm 0.021 ^{de}	0.90 \pm 0.014 ^g	1.92 \pm 0.065 ^a	395.4 \pm 16.19 ^f	90.49 \pm 4.94 ^{cd}	1.14 \pm 0.021 ^f
Severe water stress	0						
	50						
	100						
	150						

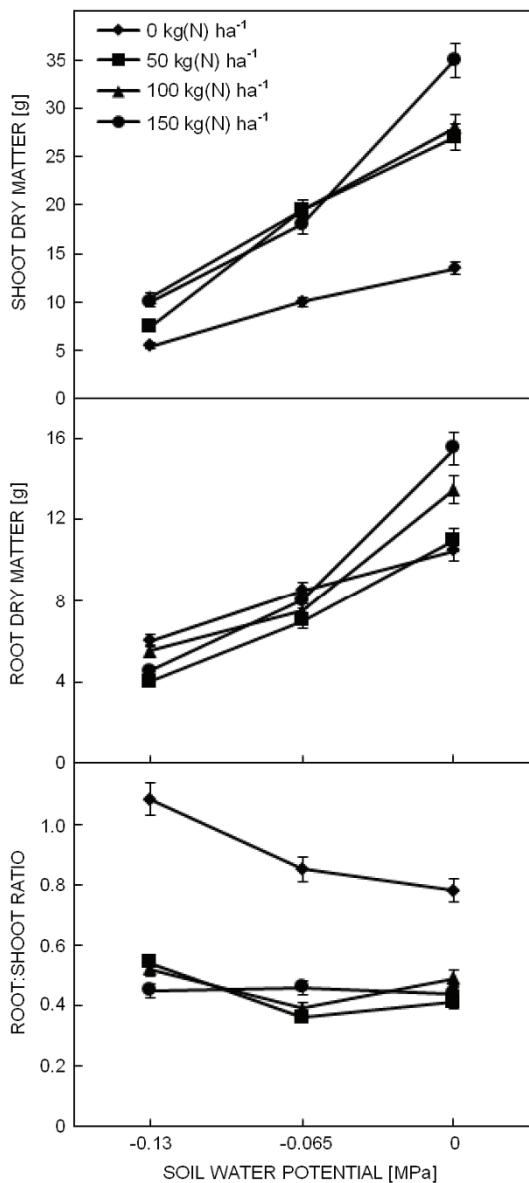


Fig 1. Interactive effects of N and soil moisture regimes on shoot dry matter, root dry matter and root:shoot ratio. Each value in this figure is the mean of three replicates and corresponding standard error bars.

drought intensity increased in all N treatments except for the plants given 150 kg(N) ha⁻¹, in which WUE was statistically consistent across all the soil water status (Fig. 2B). Plants at the high-N nutrition had significantly larger value of WUE than plants in the low-N treatment with all watering treatments.

PNUE: Plants with sufficient N had significantly higher PNUE than the plants with insufficient N, in all watering treatments (Fig. 2C). In well watered conditions, higher PNUE in high-N supplied plants suggested that N allocation to the photosynthetic apparatus is a major factor for the difference in photosynthesis among N treatments. The

difference of PNUE between the N treatments declined dramatically in water-stressed plants; this may be explained by a higher amount of leaf N being used as defensive compounds (such as N-based glucosinolate) instead of in the photosynthetic apparatus (Schreiner *et al.* 2009). The significantly positive correlation

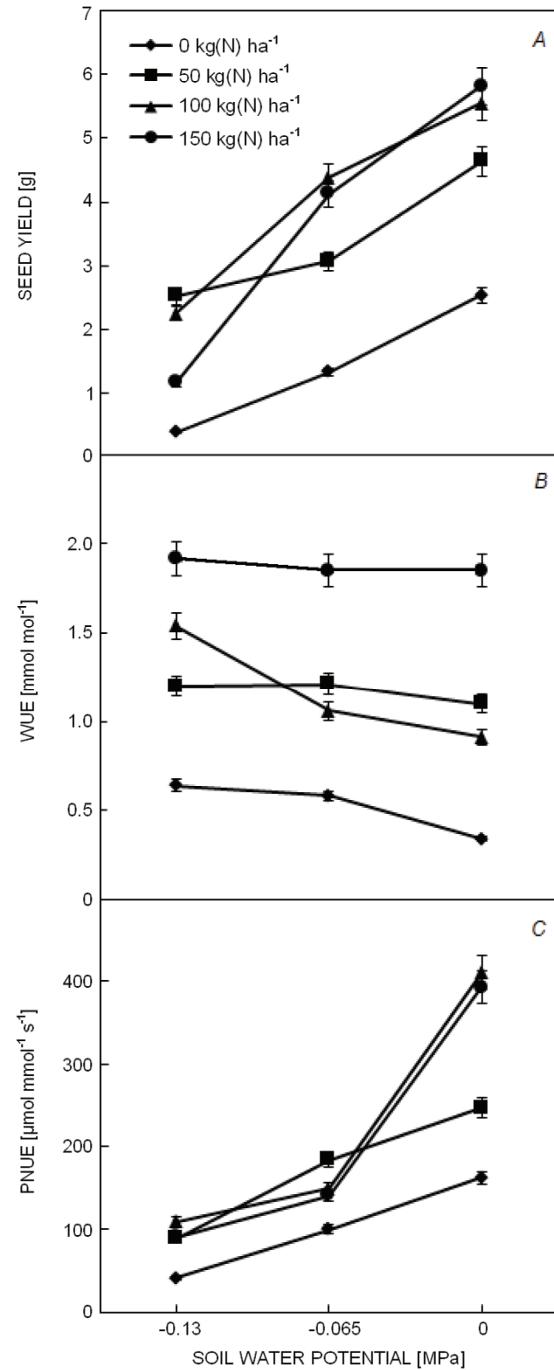


Fig 2. Interactive effects of N and soil moisture regimes on seed yield, instantaneous water-use efficiency (WUE) and instantaneous N-use efficiency (PNUE) of *B. carinata* leaves. Each value in this figure is the mean of six measurements and corresponding standard error bars.

Table 3. Water deficit effect on plant height, branches plant⁻¹ and pods plant⁻¹. Means \pm SE ($n = 6$). Different letters within the same column indicate significant differences ($p < 0.05$).

Soil water potential [MPa]	Plant height [cm]	Branches plant ⁻¹	Pods plant ⁻¹
0	115 \pm 3.97 ^a	9 \pm 1.35 ^a	42 \pm 5.08 ^a
-0.065	105 \pm 2.74 ^b	7 \pm 0.674 ^b	31 \pm 2.90 ^b
-0.13	70 \pm 1.2 ^c	5 \pm 0.349 ^b	17 \pm 1.70 ^c
P-value	0.037	0.002	0.001

Table 4. Nitrogen effect on branches plant⁻¹ and pods plant⁻¹. Means \pm SE ($n = 6$). Different letters within the same column indicate significant differences ($p < 0.05$).

N [kg ha ⁻¹]	Branches plant ⁻¹	Pods plant ⁻¹
0	5 \pm 0.520 ^c	19 \pm 2.54 ^c
50	6 \pm 0.898 ^b	29 \pm 3.58 ^b
100	7 \pm 0.726 ^b	31 \pm 4.71 ^b
150	10 \pm 1.640 ^a	40 \pm 6.94 ^a
P-value	0.029	0.018

Table 5. Summary of Pearson correlation coefficients describing the relationship among leaf characteristics and leaf water and nutrient status for *B. carinata* plants. P_N – net photosynthetic rate; E – transpiration rate; WUE – instantaneous water-use efficiency; N_{area} – leaf N content per leaf area basis; PNUE – instantaneous N-use efficiency. * significant at the 0.05 level of probability; ** significant at the 0.01 level of probability; *** significant at the 0.001 level of probability. NS – not significant.

	Leaf area	Leaf N content [%]	P_N	WUE	Leaf mass	N_{area}	PNUE
P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	0.941***						
Leaf N content [%]	NS			NS			
E [$\text{mmol m}^{-2} \text{s}^{-1}$]	NS	-0.62***		NS			
WUE [mmol mol^{-1}]	0.542**	0.719***	0.489*				
Leaf mass [g]	0.974***	NS	0.913***	0.421*			
N_{area} [mmol m^{-2}]	-0.444**	0.676***	NS	NS	-0.494*		
PNUE [$\mu\text{mol mmol}^{-1} \text{s}^{-1}$]	0.817***	NS	0.876***	NS	0.819***	-0.712***	
Seed yield [g]	0.910***	NS	0.885***	NS	0.919***	-0.548**	0.807***

potentials were not significantly negatively correlated ($p > 0.05$), there was a negative association between WUE and PNUE. In well watered plants, PNUE was high, whereas WUE was low. In severely water-stressed plants, this association was reversed with PNUE ultimately decreasing 4-fold, and WUE increasing by a smaller extent.

Conclusion: The interactive effect of water and N availability had significant effects on photosynthesis and growth of *B. carinata*. In this study, plants exhibit changes in all physiological systems, such as changes in root and leaf development, to maximize the utilization efficiency of the most limiting resources. N use modified the water use in all water regimes. Plants with N supply had significantly higher WUE than plants without N supply in all water treatments. Even though,

between P_N and PNUE (Table 8) found in this study suggested that all the factors which affected the P_N also had a similar effect on PNUE. Therefore, the carbon economy is closely related to the N economy within the whole plant. This positive relationship was also reported by Field and Mooney (1986) and Anand *et al.* (2007).

WUE vs. PNUE: The negative correlation between WUE and PNUE has been reported in many studies (Reich *et al.* 1989). Although mean values of WUE and PNUE for combinations of N treatments and soil water

B. carinata exhibits many strategies to respond to water deficiency, reduced use of water only increased WUE in a small range and resulted in a significant decrease in both PNUE and seed yield. The seed yield is strongly related to PNUE. Under adequate water conditions, increasing N supply up to 100 kg(N) ha⁻¹ significantly increased PNUE and seed yield. Under moderate drought conditions, plants with higher N supply had the ability to maintain the high WUE but had significantly lower PNUE and seed yield. As water stress increased, PNUE and seed yield decreased to a much larger extent in all N treatments and the application of 50 kg(N) ha⁻¹ appears to be sufficient to achieve maximum yield. The negative association between WUE and PNUE suggested that many economic considerations such as input cost and yield benefits should be included in determining the optimum water and N application in the future study.

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