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Comparative response of *Brassica carinata* and *B. napus* vegetative growth, development and photosynthesis to nitrogen nutrition

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ABSTRACT

Nitrogen availability is a major limiting factor controlling growth, CO_2 assimilation and productivity of oilseed brassicas, however, little is known about the physiological and morphological responses of *B. carinata* to N. A greenhouse study was conducted at North Florida Research and Education Center, Quincy, Florida during 2014/2015 to determine the effects of N rate on carinata (*B. carinata* A. Braun) cv. AAC A110 and (*B. napus* L.) cv. Canterra 1918 growth, development and photosynthesis. Four N treatments (0, 33, 66 and 100% of N in full strength Hoagland solution) were imposed 30 days after planting. Plant height, leaf area, node number, branches and total biomass and its components (leaf, stem and root dry weights) in both species decreased linearly with N reduction. Intra-specific total dry matter and photosynthetic capacity did not vary 55 days after treatment (DAT). However, partitioning biomass to various plant components differed between the species and was modified by N availability. At all N rates, carinata apportioned >53% of total biomass to the stem component while in canola stems comprised 17–34% of total biomass. Roots contributed more to total dry weight in canola (33–46%) than in carinata (23–29%) except at the highest N level. In both species, root dry matter increased with decreasing N availability. At 55 DAT, total chlorophyll, *Chl*a and *Chl*b concentrations, specific leaf area and photosynthetic capacity for both species decreased with N deficiency. Parameters of leaf photosynthetic responses to photosynthetically active radiation and internal CO_2 concentration curves were also altered by N availability. During the vegetative stage, N deficiency restricted plant growth, biomass production and also modified resource allocation which may have implications for N use efficiency and recovery during reproductive development.

1. Introduction

Emerging biofuel platforms address concerns of national energy security, oil market volatility and climate change mitigation through the development of alternative, renewable energy sources to satisfy renewable policies across the US. Renewables from biomass waste, wood and biofuels accounted for 49% of the 9.69 quadrillion Btu of renewable energy produced in 2015 (U.S. Energy Information Administration, 2016). Soybean (*Glycine max* L.) and corn (*Zea mays* L.) are the primary first generation biofuel feedstocks for ethanol and biodiesel production in the US (U.S. Energy Information Administration, 2016). Dedicated innovative second generation feedstocks that competitively use natural resources for food/feed and fuel production can diversify renewable energy sources from agricultural crops without taking lands out of food production. Cash-based winter cover crops can fit seamlessly into existing southeastern US rotation systems and are amenable to current production infrastructure leading to enhanced revenue and sustainability of production systems.

Non-food plant-derived oils have an important role in addressing the needs for sustainable renewable energy sources in the emerging global bioeconomy. Currently, about 95% of global plant-derived oils are from 8 crops distributed in 6 families (FAOSTAT, 2015). These edible oils predominantly contain 16 and 18 carbon fatty acids, such as palmitic (C16:0), stearic (C18:0), oleic (C18:1), linoleic (C18:2), and linolenic (C18:3) acids. Erucic acid (C22:1) is the major very long chain fatty acid in seed oil produced from carinata (30–45%) and high erucic acid canola (35–50%). High concentrations of erucic acid produce greater yields of fuel and result in fuel chemistry similar to petroleum-derived fuels compared with other renewable plant oils. Oleiferous brassicas including carinata and high erucic acid canola are promising and competitive feedstocks for bio-based fuel industries. C_3 crops such as carinata (n = 17, BBCC) and canola (n = 19, AACC) are natural allote-

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traploids with *B. oleracea* (n = 9, CC) as a common parent. Relative to canola, carinata possesses valuable agronomic traits such as better heat and drought tolerance (Kumar et al., 1984), resistance to diseases (Shivpuri et al., 1997) and resistance to seed shattering (Zanetti et al., 2013). Spring-seeded carinata genotypes produced 20% greater seed yield than commercial canola varieties in Minnesota, US. Carinata harvest index was 0.35 compared with 0.41 for canola, mainly due to the 52% greater biomass production than canola (Gesch et al., 2015). In Central Italy, carinata seed yield was 28% lower than canola with 10% lower oil production, although the crop residues were twice that of canola (Del Gatto et al., 2015). Similar observations in relative yield and oil content responses were reported by Zanetti et al., 2009. Both crops are grown primarily for the production of oils with carinata being a dedicated industrial oilseed crop for 'drop in' aviation fuels while canola has dual edible and industrial oil applications. Carinata oil content averaged 40.2% while canola averaged 45.6%, however, the oil yield of carinata was 16% greater than canola (Gesch et al., 2015).

Brassicas are highly responsive to N application (Hocking et al., 1997) and require relatively high rates of mineral N fertilizers for optimum seed yields (Malagoli et al., 2005; Rathke et al., 2006). Nitrogen accounts for the largest energy input and production cost in oilseed production (Gan et al., 2008), therefore optimizing N for agronomic and economic efficiencies are critical for commercial success. Managing N application for uptake and utilization efficiency requires an understanding of growth and resource allocation in response to N limitation. Brassicas have relatively high N uptake during vegetative growth until flowering followed by reduced N uptake during flowering and finally incomplete N translocation from the leaves and stems to the developing seeds (Wiesler et al., 2001). Although brassicas have a high capacity for N uptake, many species have a low nitrogen use efficiency and remobilization during the vegetative phase partly due to freeze-induced abscission of N-rich leaves during cold winter months (Albert et al., 2012; Malagoli et al., 2005; Rossato et al., 2001).

Nutrient availability, allocation and translocation influence plant acclimation to variation in soil nutrient status. Nutrient limitations during early season development leads to morphological plasticity through the redistribution of biomass among plant organs to ensure reproductive fitness and accelerated completion of ontogeny. Nitrogen is an essential element for plant growth and development involved in cell differentiation and elongation. As a result, N deficiencies reduce plant growth by restricting leaf area development (Albert et al., 2012; Gammelvind et al., 1996), branching (Momoh et al., 2004) and dry matter accumulation during the vegetative phase. During the vegetative stage, the leaves represent a major nitrogen source and sink with the remobilization of nutrients from old to younger leaves or senescing leaves to reproductive tissues during bolting, flowering and seed fill (Jensen et al., 1996). Nitrogen mobilized from canola leaves and stems contributes 70% of the total N required for seed filling with the remainder mobilized from other tissues (22% from inflorescence and 8% from roots (Malagoli et al., 2005). Nitrogen uptake is usually greatest during the vegetative stage and declines at flowering and pod fill in canola (Rossato et al., 2001). Abiotic factors that affect the uptake, assimilation and allocation capacity during the pre-bolting period will modulate the reproductive performance and seed yield of oilseed brassicas (Jackson, 2000; Malagoli et al., 2004, 2005). For example, removal of 50% of the leaves present at the end of the vegetative stage resulted in a 30% decrease in seed yield in canola (Noquet et al., 2004).

The majority of N utilized by plants establishes and maintains photosynthetic apparatus which may contain up to 75% of total leaf N content in C_3 plants (Chapin et al., 1996). As a result, photosynthesis is strongly correlated with leaf N concentration (Gammelvind et al., 1996; Jensen et al., 1996). During the vegetative stage, fully developed leaves of canola maintain a high photosynthetic capacity (35–45 $\mu mol\, m^{-2}\, s^{-1}$) and stomatal conductance (1–1.5 $mol\, m^{-2}\, s^{-1}$) over 2–3 weeks (Jensen et al., 1996). Interspecific variation in nutrient uptake and gas exchange affect the biomass allocation and competitive ability in relation to nutrient and light availability (Knops and Reinhart, 2000).

Phenotyping and quantifying nitrogen response can aid in the identification of target traits to screen for N use efficiency in N-limited conditions and serve as a precursor to breeding for those traits for improved oilseed productivity. Therefore, understanding the effects of early season N deprivation on growth, development and physiology of oilseed brassica is essential for optimum N management and seed productivity. Although canola has benefitted from decades of mineral nutrition and physiology research (Rathke et al., 2006; Zanetti et al., 2013), there is a dearth of information on the growth and physiological responses of carinata to N deficiency. Therefore, the aim of this study was to quantify and compare the effects of N deficiency on carinata and canola biomass accumulation, developmental rates and gas exchange processes during the vegetative stage.

2. Materials and methods

2.1. Plant culture

This greenhouse experiment was conducted at the UF/IFAS North Florida Research and Education Center, Quincy, Florida (30° 32′ 44.7036″ N, 84° 35′ 41.0820″ W). Seeds of carinata cv. AAC A110 and open pollinated winter type canola cv. Canterra 1918 (5 seeds pot^{-1}) were planted on 1 December 2014 in 288 plastic pots (31.8 cm height × 19.7 cm diameter, 7.65 L) filled with fine sand as the growth substrate and saturated until free drainage with full strength Hoagland solution prior to planting. The Hoagland nutrient solution was modified by substituting $Ca(NO_3)_2$ with $CaCl_2$ and KNO_3 with KCl in order to achieve the specified N concentrations (Reddy and Matcha, 2010). The pH of the sand was 5.8 and had very low levels of nutrients, in kg ha^{-1}, P (17), K (12), Mg (17), Ca (294) and 0% organic matter and 0.008% N. Pots were arranged in 6 rows of 6 pots oriented in an east to west direction on sliding benches as a randomized complete block design with five replications at each harvest per N level per species. Plants were sequentially thinned to one plant per pot 7 to 14 days after planting (DAP). To minimize border effect, pots were kept equidistant from each other after each harvest and perimeter pots were not measured. The daytime temperature was maintained at 19.6 ± 2.6 °C and night temperature at 12.8 ± 1.7 °C throughout the experiment. The daytime RH was 60.4 ± 7.9% and night RH at 80 ± 10.6% throughout the experiment. Plants were grown under a 12-h/12-h light/dark photoperiod with supplemental lighting from high-pressure sodium lamps that provided a total flux ≈1200 $\mu mol\, m^{-2}\, s^{-1}$. Pots were rotated within and across benches to minimize differences in temperature heterogeneity prior to treatment imposition. To further reduce the effect of temperature differences, the pots were rotated among the four benches, three times during the experiment.

2.2. Treatments

Irrigation with full strength Hoagland solution continued to 30 DAP after which the four N treatments [0 (0 mg N l^{-1}), 33 (5 mg N l^{-1}), 66 (10 mg N l^{-1}) and 100% control (16 mg N l^{-1})] of N in full strength Hoagland solution were imposed. To ensure optimum water conditions, fertigation was supplied three times daily, at 0830, 1230 and 1630 h through a drip irrigation system metered by an ESP-LX BASIC 12 station modular irrigation controller (Rain Bird Corp., Azusa, CA).

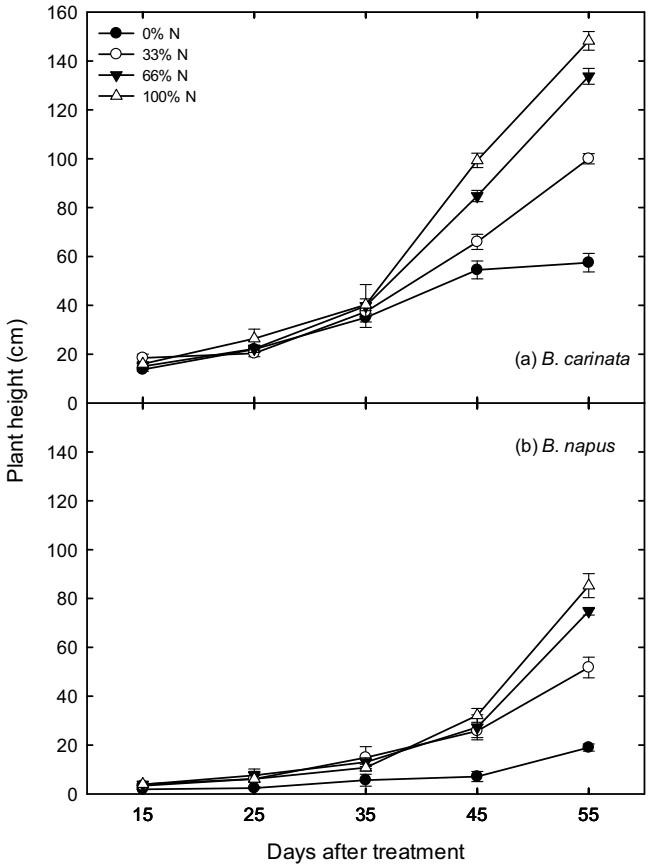

Fig. 1. Temporal variation in (a) carinata and (b) canola plant height in response to 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 10-day interval until 55 days after treatment. Each data point is the mean of 4 measurements. Bars represent the standard error of the means.

2.3. Growth measurements

Plant height was measured from the soil level to the uppermost visible mainstem node ten days after treatment at each of the five harvests that occurred at 10 days interval. The number of nodes on the mainstem and number of primary branches were also recorded. Both species were harvested and separated into leaf blades and stems (petiole and stems). Leaf blade area was measured at each harvest using a LI-3000A Portable Area Meter connected to a LI-3050A Transparent Belt Conveyer (LI-COR Biosciences, Lincoln, NE). Roots were washed over a fine screen and the maximum root length measured. All tissue samples were dried in a forced-air oven at 60 °C for 72 h before being weighed to determine dry matter accumulation partitioned to below and above-ground organs.

2.4. Pigments and gas exchange measurements

Leaf pigment concentrations (*Chl*a, *Chl*b and carotenoids) were estimated in the upper most fully expanded leaf of four plants in each treatment 55 DAT. Five leaf discs (each 38.5 mm^2) were placed in vials containing 5 mL dimethyl sulphoxide and incubated in dark at room temperature for 24 h for pigment extraction. Absorbance of the extract was measured using a spectrophotometer (Cary BIO 50, Varian, CA, USA) at 470, 648 and 664 nm to calculate *Chl*a, *Chl*b and carotenoids concentrations, respectively, using equations developed by Lichtenthaler (1987) and expressed on a leaf area basis ($\mu g\,cm^{-2}$).

Gas exchange processes [net photosynthesis (P_n), stomatal conductance (G_s) and transpiration (T_r)] of the upper most fully expanded leaf of four plants in each treatment were measured between 1000 and 1400 h using a LI-6400 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE). When measuring P_n, G_s and T_r, the PAR (provided by a 6400-02 LED light source) was set to 1200 $\mu mol\,m^{-2}\,s^{-1}$ (based on measured PAR in the greenhouse), leaf cuvette temperature set at 20 °C, leaf chamber CO_2 concentration set at 400 $\mu L\,L^{-1}$ and relative humidity maintained at ambient conditions. Photosynthetic light and C_i-response curves were measured on three plants in each treatment 55 DAP. For photosynthetic light curves, the leaf cuvette temperature was set at 20 °C, leaf chamber CO_2 concentration set at 400 $\mu L\,L^{-1}$ and relative humidity maintained at ambient conditions while the PAR increased from 0 to 2000 $\mu mol\,m^{-2}s^{-1}$. Leaves were dark adapted before logging the first measurement. When measuring C_i curves, the leaf cuvette temperature was maintained at 20 °C and the PAR set at 1200 $\mu mol\,m^{-2}\,s^{-1}$ while the CO_2 concentration was programmed to increase from 0 to 800 $\mu L\,L^{-1}$.

Table 1
Significance levels from analysis of variance for the effect of nitrogen (N) rate on growth parameters of carinata and canola measured 85 days after planting and 55 days after nitrogen treatment.

Source of variation	PH[a]	LA	LDW	SDW	RDW	TDW	RSR	Node	Branch	RL
Species	***[b]	*	***	***	***	ns	***	***	***	*
N	***	***	***	***	***	***	***	***	***	*
Species × N	**	ns	ns	ns	*	ns	ns	ns	ns	ns

[a] Plant height (PH), total leaf area (LA), leaf dry weight (LDW) stem dry weight (SDW), root dry weight (RDW), total dry weight (TDW), root:shoot ratio (RSR, unitless), mainstem node numbers (node), primary branches (branch) and maximum root length (RL).
[b] ns: not significant at $P > 0.05$; *,**,*** significance level at $P \leq 0.05$, 0.01 and 0.001.

2.5. Data analysis

To test for the interaction and main effects of nitrogen levels and species on growth, development and physiological traits, a two way ANOVA was performed using PROC GLM in SAS 9.4 (SAS Institute Inc., NC). Treatment means were separated using Fisher's protected least significant difference ($P < 0.05$). Relationships among growth, development and physiological parameters were done using correlation analysis. When correlations were detected, regressions were performed using PROC REG (SAS Institute) to derive generalized equations capable of predicting development rates. Polynomial models were used to test whether relationships between nitrogen and all measured parameters were nonlinear. The functional form of the regression relation was determined starting with the linear function, followed by addition of successively higher order polynomials. If the higher order polynomials did not substantially improve the response curve (based on r^2 values) then they were ignored. Light-saturated photosynthesis (A_{max}), dark respiration rate (R_d), apparent quantum efficiency (AQE), light compensation point (LCP) and light saturation point (LSP) from light response curves were estimated by non-linear regression by using Photosyn Assistant software (ver 1.1.2, Dundee Scientific, Scotland, UK). Maximum carboxylation rate by Rubisco (V_{cmax}), light-saturated electron transport (J_{max}) and other parameters from A/C_i were also calculated using Photosyn Assistant software. Means were separated by Fisher's protected LSD test at $P < 0.05$.

3. Results

3.1. Growth and development

Plant height, leaf area and total dry matter and biomass (leaf, stem and root dry weights) decreased linearly with N deprivation in both species (Table 1). Plant height and node numbers of car-

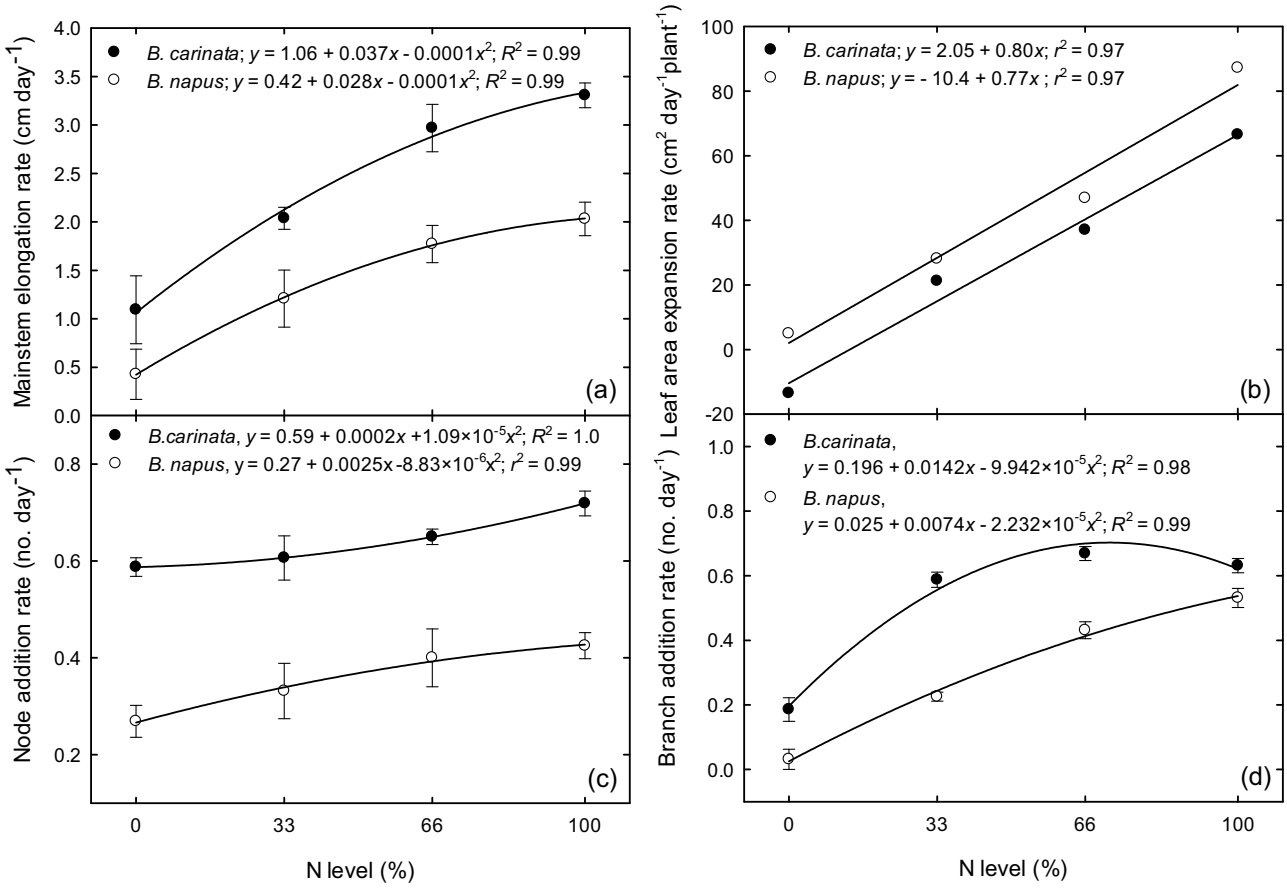

Fig. 2. Nitrogen nutrition effects (a) mainstem elongation rates (cm day^{-1}), (b) leaf area expansion rates cm day^{-1} plant^{-1}), (c) node addition rates (no.day^{-1})and (d) branch addition rates (no.day^{-1}) of carinata and canola grown at 4 levels of N (0, 33, 66 and 100% of N in Hoagland solution). Each data point is the mean of 4 measurements while bars represent the standard error of the means.

Table 2
Effects of nitrogen (N) rates on carinata growth traits and dry matter partitioning at 85 days after planting and 55 days after nitrogen treatment. Data are mean ± S.E. of four replicates.

N level (%)	PH[a]	LA	LDW	SDW	RDW	TDW	RSR	Nodes	IL	PB	RL
	cm	m^2 plant^{-1}	g plant^{-1}					no. plant^{-1}	cm node^{-1}	no. plant^{-1}	cm
0	57.5 ± 3.8	0.06 ± 0.01	3.93 ± 0.83	15.92 ± 2.65	8.17 ± 0.77	28.01 ± 1.83	0.43 ± 0.08	36.0 ± 1.73	1.61 ± 0.12	11.75 ± 4.33	50.5 ± 7.86
33	100.0 ± 2.1	0.22 ± 0.03	9.96 ± 1.0	29.67 ± 2.43	16.13 ± 0.74	55.76 ± 2.5	0.41 ± 0.02	38.0 ± 1.22	2.64 ± 0.1	32.75 ± 0.63	47.75 ± 1.8
66	133.8 ± 3.3	0.31 ± 0.01	12.72 ± 0.92	42.31 ± 3.44	17.11 ± 1.11	72.14 ± 1.95	0.32 ± 0.04	40.0 ± 0.71	3.35 ± 0.14	36.0 ± 2.86	38.0 ± 1.78
100	148.3 ± 3.8	0.46 ± 0.05	17.99 ± 1.56	39.36 ± 3.04	17.56 ± 0.65	74.92 ± 3.12	0.31 ± 0	43.25 ± 1.11	3.43 ± 0.12	35.0 ± 1.78	37.0 ± 4.14
OPC[b]	L***,Q***	L***	L***	L***,Q**	L***,Q***	L***,Q***	L***,Q***	L***,Q**	L***,Q***	L***	ns

*,**,*** Orthogonal polynomial contrasts, linear (L), quadratic (Q) significant at the 0.05, 0.01 and 0.001 levels, respectively.

[a] Plant height (PH), total leaf area (LA), leaf dry weight (LDW) stem dry weight (SDW), root dry weight (RDW), total dry weight (TDW), root:shoot ratio (RSR), mainstem node numbers (nodes), internode length (IL), primary branches (PB) and maximum root length (RL).

Table 3
Effects of nitrogen (N) rates on canola growth traits and dry matter partitioning at 85 days after planting and 55 days after nitrogen treatment. Data are mean ± S.E. of four replicates.

N level (%)	PH[a]	LA	LDW	SDW	RDW	TDW	RS	Nodes	IL	PB	RL
	cm	m^2 plant^{-1}	g plant^{-1}					no. plant^{-1}	cm node^{-1}	no. plant^{-1}	cm
0	19.0 ± 1.5	0.09 ± 0.01	9.93 ± 0.85	4.71 ± 0.21	12.49 ± 0.73	27.14 ± 1.68	0.86 ± 0.03	19.75 ± 0.48	0.96 ± 0.07	0 ± 0	42.75 ± 1.80
33	51.8 ± 4.2	0.23 ± 0.01	16.23 ± 1.28	12.24 ± 2.36	21.57 ± 1.56	50.03 ± 3.78	0.77 ± 0.07	24.5 ± 0.65	2.13 ± 0.22	9.0 ± 3.08	40.0 ± 2.38
66	74.8 ± 1.6	0.36 ± 0.01	20.48 ± 1.57	25.51 ± 2.58	28.34 ± 2.26	74.33 ± 2.12	0.62 ± 0.06	28.75 ± 0.48	2.60 ± 0.04	17.25 ± 1.11	31.75 ± 3.17
100	85.3 ± 4.9	0.52 ± 0.04	32.97 ± 3.73	23.67 ± 2.75	28.26 ± 1.47	84.9 ± 4.39	0.50 ± 0.02	30.0 ± 1.08	2.87 ± 0.26	21.25 ± 2.84	37.25 ± 3.20
OPC[b]	L***,Q***	L***	L***	L***,Q**	L***,Q***	L***,Q***	L***,Q***	L***,Q**	L***,Q***	L***	ns

[a] Plant height (PH), total leaf area (LA), leaf dry weight (LDW) stem dry weight (SDW), root dry weight (RDW), total dry weight (TDW), root:shoot ratio (RSR), mainstem node numbers (nodes), internode length (IL), primary branches (PB) and maximum root length (RL).

[b] *,**,*** Orthogonal polynomial contrasts, linear (L), quadratic (Q) significant at the 0.05, 0.01 and 0.001 levels, respectively.

Table 4
Significance levels from analysis of variance for the effect of nitrogen level on development, pigments and gas exchange parameters of carinata and canola.

Source of variation	SER[a]	NAR	LAER	BAR	TDM	GR	SLA	Chla	Chlb	Total Chl	N	Carotenoids	P_n	G_s	T_r	C_i
Species	***[b]	***	***	***	ns	ns	***	***	**	***	***	*	ns	ns	ns	ns
N	***	***	***	***	***	***	***	***	***	***	***	***	***	ns	ns	ns
Species × N	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns

[a] Stem elongation rate (SER), node addition rate (NAR), leaf area expansion rate (LEAR), primary branch addition rate (BAR), total dry matter (TDM), growth rate (GR), specific leaf area (SLA), chlorophyll a (chla), chlorophyll *b* (chlb), total chlorophyll (Total Chl), carotenoids, leaf N concentration (N), net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r) and internal CO_2 concentration (C_i).
[b] ns: not significant at $p > 0.05$; *,**,*** significance level at $p \leq 0.05$, 0.01 and 0.001.

Table 5
ANOVA, OPC and mean photosynthesis light response curve parameters of carinata and canola leaves grown at 4 N levels (0, 33, 66 and 100% of N in Hoagland solution) and measured 55 days after treatment.

Species	N level (%)	R_d[a]	φ	Convexity	A_{max}	LCP	LSE
		μmol CO_2 m^{-2} s^{-1}	μmol CO_2 (μmol photons)$^{-1}$		μmol CO_2 m^{-2} s^{-1}	μmol photons $m^{-2}s^{-1}$	μmol photons $m^{-2}s^{-1}$
B. carinata	0	−1.37	0.07	0.03	20.2	19.4	319.7
	33	−1.14	0.07	0.18	26.4	16.8	412.0
	66	−2.31	0.08	0.29	34.6	30.7	492.5
	100	−1.49	0.07	0.36	34.9	21.1	536.6
	OPC[b]	ns	ns	L***,Q***	L**,Q***	ns	L***,Q***
B. napus	0	−2.11	0.09	0.05	13.1	24.6	178.3
	33	−2.31	0.08	0.11	22.3	28.0	299.3
	66	−2.14	0.06	0.52	34.6	32.6	570.3
	100	−2.65	0.08	1.0	36.9	34.2	516.0
	OPC	L*,Q**	ns	L***,Q***	L***,Q***	L***,Q***	L**,Q**
ANOVA	S	0.0001	0.1079	0.4356	0.1724	<0.0001	0.2079
	N	0.0854	0.1459	0.237	<0.0001	0.0008	<0.0001
	S*N	0.0133	0.0057	0.69	0.2292	0.0549	0.1936

[a] Photosynthesis parameters are dark respiration rate (R_d), apparent quantum efficiency (φ), convexity, maximum photosynthesis rate (A_{max}), light compensation point (LCP), and light saturation estimate (LSE).
[b] *,**,*** Orthogonal polynomial contrasts, linear (L), quadratic (Q) significant at the 0.05, 0.01 and 0.001 levels, respectively.

Table 6
ANOVA, OPC and mean CO_2 assimilation/internal CO_2 (A/C_i) curve parameters of carinata and canola plants grown at 4 N levels (0, 33, 66 and 100% of N in Hoagland solution) and measured 51 days after treatment.

Species	N level (%)	A_{max}[a]	CE	Resp	V_{cmax}	J_{max}	TPU
		μmol CO_2 m^{-2} s^{-1}		μmol CO_2 m^{-2} s^{-1}	μmol CO_2 m^{-2} s^{-1}	μmol CO_2 m^{-2} s^{-1}	Pi m^{-2} s^{-1}
B. carinata	0	42.1	0.31	−10.5	49.0	212	14.9
	33	51.9	0.34	−8.7	50.8	223	15.4
	66	60.5	0.47	−12.5	60.6	306	18.6
	100	62.4	0.41	−7.6	64.2	374	19.7
	OPC[b]	L***,Q***	L*Q**	ns	L***,Q***	L***,Q***	L**,Q**
B. napus	0	65.0	0.28	−11.1	47.1	202	15.0
	33	66.5	0.28	−9.9	42.8	179	13.1
	66	57.6	0.30	−4.4	55.0	247	16.5
	100	65.3	0.27	−4.1	52.9	234	16.2
	OPC	ns	ns	L**,Q**	L**	L**,Q**	Q**
ANOVA	S	0.0120	0.0096	0.0365	0.0421	0.0230	0.6271
	N	0.0466	0.0032	0.1848	0.0320	0.0350	0.0357
	S*N	0.0623	0.0959	0.0012	0.0623	0.7242	0.0543

[a] CO_2 assimilation parameters are maximum photosynthesis rate (Amax), carboxylation efficiency (CE), dark respiration rate (R_d), V_{cmax}, J_{max} and rate of triose phosphate utilization (TPU).
[b] *,**,*** Orthogonal polynomial contrasts, linear (L), quadratic (Q) significant at the 0.05, 0.01 and 0.001 levels, respectively.

inata control (100% N) vs 0N treated plants decreased by 61 and 17% while those for canola decreased by 78 and 32%, respectively (Tables 2 and 3). Carinata height was significantly greater than that of canola at each measurement date across all N rates. During the first 35 DAT, there were no differences in plant height among N treatments for both species (Fig. 1). For carinata, heights were different at all N treatments at 45 DAT while canola height were different at 55 DAT onwards. Mainstem elongation rate (MSER) of carinata, derived from the linear phase of mainstem height over time, was greater at all levels of N than canola. At 55 DAT, MSER rate showed a quadratic relationship with N level for both species. Maximum MSER occurred at 100% N for both carinata (3.31 cm day^{-1}) and canola (2.03 cm day^{-1}) (Fig. 2). Averaged across N rates, carinata had 90% greater plant height, 52% more mainstem nodes and 141% more primary branches than canola. Primary branch numbers decreased by 66% (carinata) and 100% (canola) from control to 0N treated plants (Tables 2 and 3). Leaf area generally increased with time, except in the 0N treated plants (Fig. 3), and differed with species and N level at 55 DAT (Table 2). At 55 DAT, leaf area decreased by 87% and 83% with N reduction from 100% N control to 0N in carinata and canola plants, respectively (Tables 2 and 3). For the 0N treated plants, premature leaf abscission occurred after 15 DAT for carinata and 35 DAT for canola resulting in a decrease in leaf area (Fig. 2). Plant height was closely related to mainstem node numbers for carinata ($y = 17.045 + 0.1602x$; $r^2 = 0.88$) and canola ($y = 28.224 + 0.1001x$; $r^2 = 0.78$). Although carinata was taller and more highly branched at optimum conditions, its total leaf area accumulation was more sensitive to N deficiency than canola

(Table 2). Under limited N supply, both species produced leaves that were smaller than those grown at optimum conditions (Fig. 4). Carinata had smaller sized leaves compared with canola for a given leaf number (Fig. 4). Mainstem internode lengths, derived from plant height and mainstem node numbers, showed a quadratic relationship with N level for carinata ($y = 1.5817 + 0.0404x - 0.0002 \times 2$; $R^2 = 0.99$) and canola ($y = 0.98 + 0.0392x - 0.0002^{\times 2} +$; $R^2 = 0.99$). Mainstem node numbers increased linearly with time across all N rates for both species (Fig. 5). Carinata had greater node addition rates than canola across all N levels over the treatment period (Fig. 2).

3.2. Biomass allocation

Vegetative morphology and biomass distribution patterns were altered by N limitation. Total dry weight did not differ between the species and showed a quadratic relationship with N level ($y = 27.25 + 1.0557x - 0.005^{\times 2}$; $R^2 = 0.97$) (Tables 2 and 3). Plants grown under limited N supply accumulated less biomass and plant component dry weights (Fig. 6) similar to previous reports (Pan et al., 2011). Biomass distribution to various plant components differed between the species and was modified by N availability (Tables 2 and 3, Fig. 6). Carinata apportioned 53–59% of total biomass to the stem component across all N rates while canola stems comprised 17–34% of total biomass (Tables 2 and 3). Carinata allocated 14–24% of total dry weight to leaves while canola allocated 28–39% across all N rates. Roots contributed more to TDW in canola (33–46%) than carinata (23–29%) except at the highest N level (Tables 2 and 3). Root biomass increased linearly with N level for both species (Tables 2 and 3). Maximum root length did not vary with N availability (Tables 2 and 3) but may have been restricted by the pot size used in this study. Root:shoot ratio decreased linearly with increasing N availability across species. Carinata (0.42–0.31) had a lower root:shoot ratio than canola (0.86–0.50) across all levels of N supply (Tables 2 and 3).

3.3. Leaf N, pigment concentration, SLA

Leaf N, leaf total chlorophyll, *Chl*a and *Chl*b and carotenoid concentrations at 55 DAT differed among N levels and species (Table 4). Leaf N concentration decreased linearly with N deprivation from 42.8 to 19.5 g kg^{-1} (4arinata, $y = 20.80 + 0.2281x$; $r^2 = 0.98$) and from 37.3 to 10.9 g kg^{-1} (canola, $y = 11.91 + 0.2536x$; $r^2 = 0.98$) (Fig. 8a). Leaf N content per g dry leaf was positively correlated with leaf N per unit area for both species (Fig. 8b). Similar to leaf N, leaf total chlorophyll, *Chl*a and *Chl*b and carotenoid concentrations decreased linearly with N deficiency for both species (Fig. 9). The 0N treated plants had 69 and 73% lower *Chl*a, 58 and 80% lower *Chl*b, 67 and 76% lower total chlorophyll and 54 and 49% lower carotenoid concentrations than carinata and canola 100% N treated plants, respectively. Across species and N level, carinata had 40% lower *Chl*a, 28% lower *Chl*b, 16% lower total chlorophyll and 16% lower carotenoid concentration than canola. There was a linear relationship between leaf nitrogen and total chlorophyll concentration for carinata ($y = 8.53 - 1.3553x$; $r^2 = 0.77$) and canola ($y = 1.36 + 1.6142x$; $r^2 = 0.76$).

Specific leaf area (SLA), a function of leaf dry-matter and leaf area, differed between the species (Table 4) ranging from 165 to 200 cm^2 g^{-1} in carinata and 106 to 177 cm^2 g^{-1} in canola with increasing N level (Fig. 10). Specific leaf area increased linearly with N concentration for carinata ($y = 0.27 - 0.0455x$; $r^2 = 0.78$) and canola ($y = 18.87 - 5.5434x$; $r^2 = 0.64$). Photosynthesis also linearly increased with SLA for carinata ($y = 6.66 - 0.1502x$; $r^2 = 0.71$) and canola ($y = 14.54 + 0.0735x$; $r^2 = 0.77$). Transpiration linearly increased with SLA for carinata ($y = 3.7917 + 0.0144x$; $r^2 = 0.50$) and canola ($y = 3.091 + 0.0225x$; $r^2 = 0.72$). No significant relationships existed between SLA and stomatal conductance and internal CO_2 concentration. Leaf biomass also increased with SLA for carinata ($y = 121.0 - 0.9323x$; $r^2 = 0.71$) and canola ($y = 1.80 - 0.5249x$; $r^2 = 0.83$). Across species, biomass traits, plant height ($r = 0.87$, $P < 0.0001$), node numbers ($r = 0.92$, $P < 0.0001$), LDW ($r = 0.80$, $p < 0.0001$), SDW ($r = 0.89$, $P < 0.0001$), and RDW ($r = 0.82$, $P < 0.0001$) positively correlated with SLA. Root:shoot ratio negatively correlated with SLA ($r = -0.90$, $P < 0.0001$).

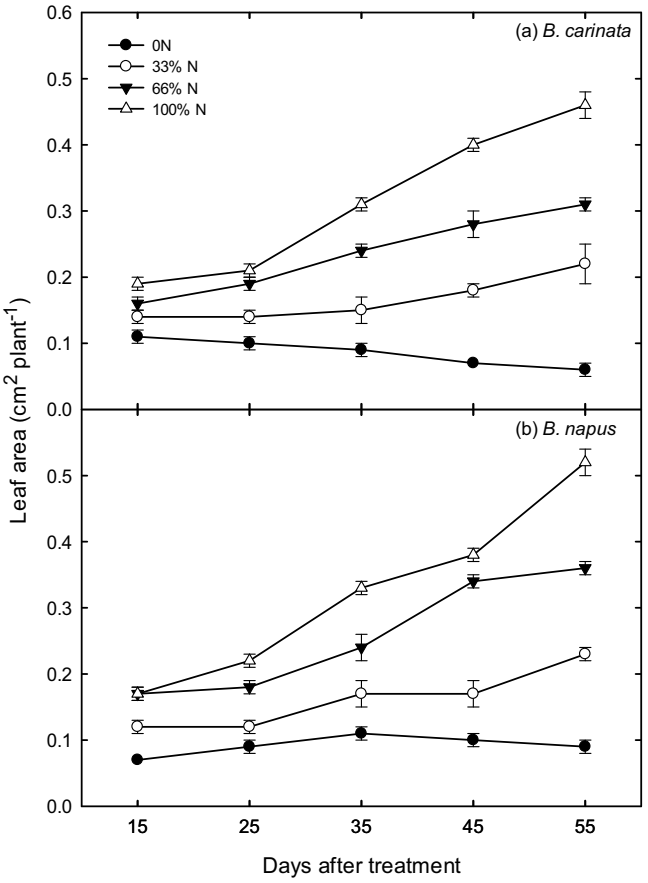

Fig. 3. Temporal variation in (a) carinata and (b) canola plant total leaf area in response to 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 10-day interval until 55 days after treatments. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

3.4. Gas exchange processes

At 55 DAT, pre-bolting leaf-level P_n of the uppermost fully expanded leaf did not differ between the species but decreased linearly with N deprivation (Fig. 11). The 0N treated plants (21.2 μmol m^{-2} s^{-1}) produced 47% less photosynthates than 100% N plants (31.0 μmol m^{-2} s^{-1}) when averaged across species. The photosynthetic capacity of both species is closely related to the leaf N ($y = 13.92 + 0.31x$; $r^2 = 0.80$) and total chlorophyll ($y = 13.917 + 0.428x$; $r^2 = 0.72$) concentrations of the leaf, similar to findings reported by Jensen et al. (1996).

3.5. Leaf photosynthetic responses to PAR and C_i

Leaf photosynthetic responses to photosynthetically active radiation (PAR) exhibited similar exponential increases in net photosynthesis for both species across all N levels (Fig. 12). Nitrogen supply had significant effects on maximum photosynthesis (A_{max}), light compensation point (LCP) and light saturation estimate (LSE) but not dark respiration (Rd), apparent quantum efficiency (AQE)

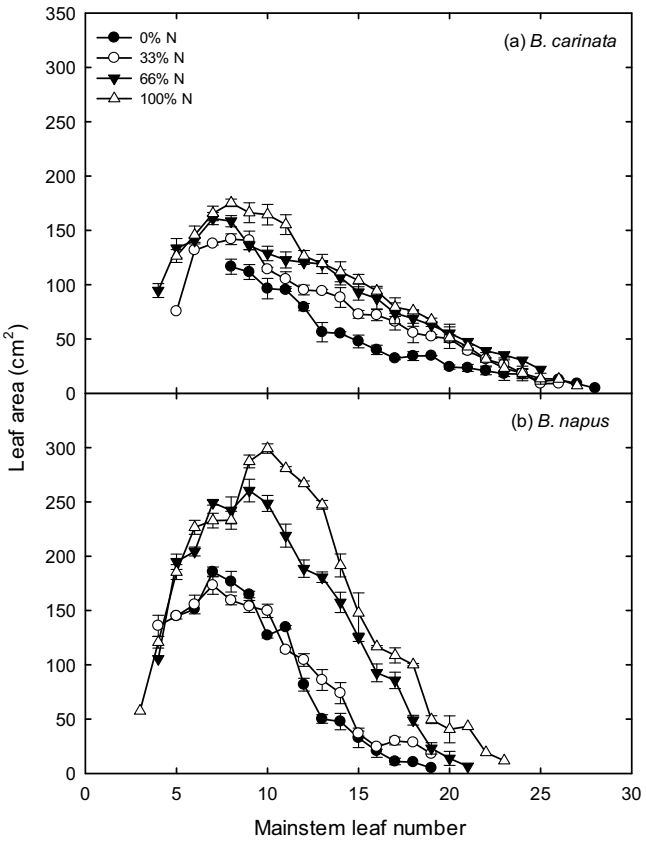

Fig. 4. Nitrogen nutrition effects on (a) carinata and (b) canola leaf size distribution on the mainstem 55 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

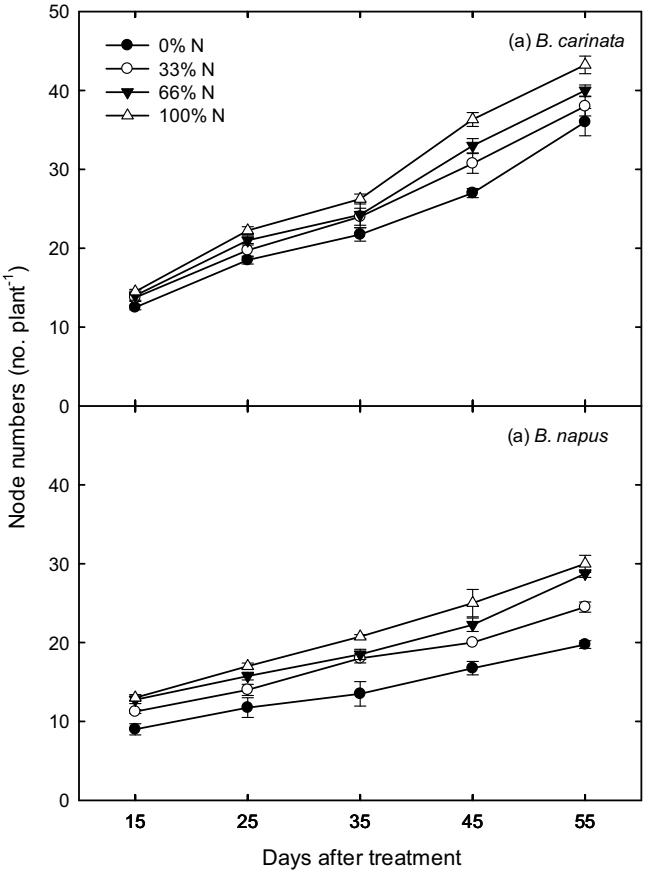

Fig. 5. Temporal variation in (a) carinata and (b) canola mainstem node numbers in response to 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 10-day interval until 55 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

and convexity of carinata and canola leaves in response to irradiance. Leaves with higher N content utilize PAR more effectively for photosynthesis than those with lower N content, hence the positive correlation between leaf N and photosynthesis ($r = 0.81$, $P < 0.0001$). Although, leaf N content of carinata was greater than canola (Fig. 8), A_{max} did not differ between the species (Table 5). At low PAR (<200 μmol m^{-2} s^{-1}), photosynthesis did not vary with N level across species. Averaged across species, at 2000 μmol m^{-2} s^{-1}, plants that received 100% N accumulated 19 μmol m^{-2} s^{-1} more photoassimilates than 0N treated plants (Fig. 12). The dark respiration rate, R_d, the rate at which CO_2 is released to the atmosphere at 0 PAR, differed between species but did not vary with N level (Table 5). Averaged across N level, carinata (−1.6 μmol m^{-2} s^{-1}) had a greater dark respiration rate than canola (−2.3 μmol m^{-2} s^{-1}) (Table 5). The LCP, PAR value at which net assimilation rate is zero, varied with species and N level and was generally greater in canola (29.8 μmol photons m^{-2} s^{-1}) than carinata (22.0 μmol photons m^{-2} s^{-1}). Across species, mean LCP of 100% N treated plants was 20% higher than the 0N treated plants. Curve convexity, the transition from light-limited to light-saturated photosynthetic rate or the ratio of physical to total resistance to diffusion of CO_2 into the chloroplast, did not vary with species or N level (Table 5). The light saturation estimate (LSE), the PAR where photosynthesis first reaches its maximum rate, did not vary between the species but generally increased with N level from 249 to 526 (mmol photons m^{-2} s^{-1}). Apparent quantum efficiency (AQE, φ), the initial slope of the PAR curve as a measure of the photosynthetic efficiency, did not differ with species or N level.

Net photosynthesis was sensitive to the changes of internal leaf CO_2 concentration (C_i) and was modulated by the leaf N concentration. Treatment N level had significant effects on maximum photosynthesis rate (A_{max}), maximum rate of Rubisco carboxylation (V_{cmax}), maximum rate of election transport for RUBP regeneration (J_{max}) and CE (carboxylation efficiency) but not dark respiration (R_d) and triose phosphate utilization (TPU) of carinata and canola leaves in response to C_i (Table 6). Modelled maximum photosynthesis of 100% N treated carinata leaves increased by 33% over 0N treated plants while that of canola did not differ with N availability (Table 6). The increase in carinata A_{max} with N level resulted from increases in the regulation of the potential electron transport rate and the maximum Rubisco activity. At 0 CO_2 μL L^{-1}, CO_2 evolves from the mitochondria under lighted conditions and represents dark respiration which did not vary with species or N level. The initial slope of the relationship between photosynthetic rate and internal CO_2 concentration (~200 CO_2 μL L^{-1}) represents the area of Rubisco limitation to photosynthesis emanating from the saturation of ribulose bisphosphate. The V_{cmax} did not differ between the species averaging 53 μmol m^{-2} s^{-1} across N level and was upregulated by 23 and 11% from 0N treated to 100% N treated leaves across species (Table 6). In addition to the biochemical limitations to photosynthesis as a function of N, stomatal resistance also reduced the rate of A_{max} below its potential. Stomatal limitation, calculated as the difference in photosynthesis at ambient (400 CO_2 μL L^{-1}) and intracellular CO_2 concentrations, increased from 14 and 6% (0N treated plants) to 22 and 11% (100% N treated plants) for carinata and canola, respectively. Carboxylation efficiency (CE), the increase in photosynthetic rate per unit increase in CO_2 at the site of CO_2 fixation, of carinata was higher than canola at all levels of N. The upper part of CO_2 response curve from 300 μL L^{-1} and higher is influenced by two photosynthetic parameters. First, the

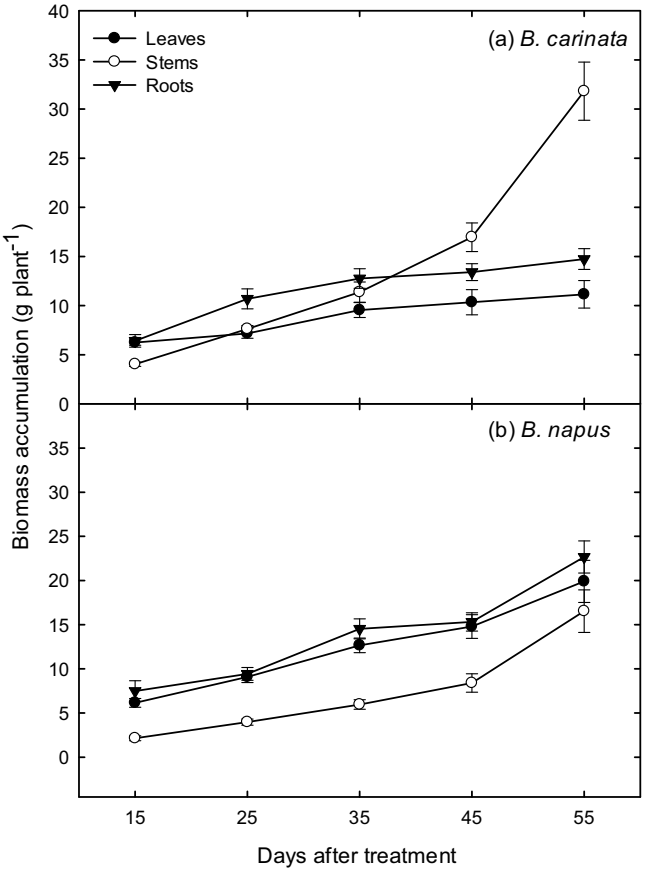

Fig. 6. Temporal variation in (a) carinata and (b) canola biomass allocation averaged 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 10-day interval until 55 days after treatments. Each data point is the mean of 8 measurements. Bars represent the standard error of the means.

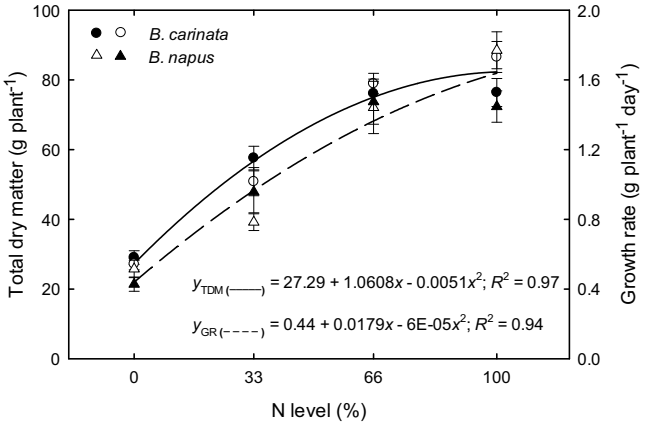

Fig. 7. Nitrogen nutrition effects on carinata and canola total dry matter accumulation (TDM, g plant^{-1}) and crop growth rate (GR, g plant^{-1}day^{-1}). Each data point is the mean of 4 measurements while bars represent the standard error of the means.

rate of regeneration of RuBP (J_{max}) and second, the availability of inorganic phosphate in leaves (TPU). Nitrogen level increased the rate of electron transport in carinata 23% more than canola. The J_{max} of 100% N treated leaves increased by 43 and 14% over 0N plants for carinata and canola, respectively. The RuBP regeneration is limited by the availability of inorganic phosphate arising from the failure of triose phosphate utilization in the Calvin cycle under suboptimal conditions.

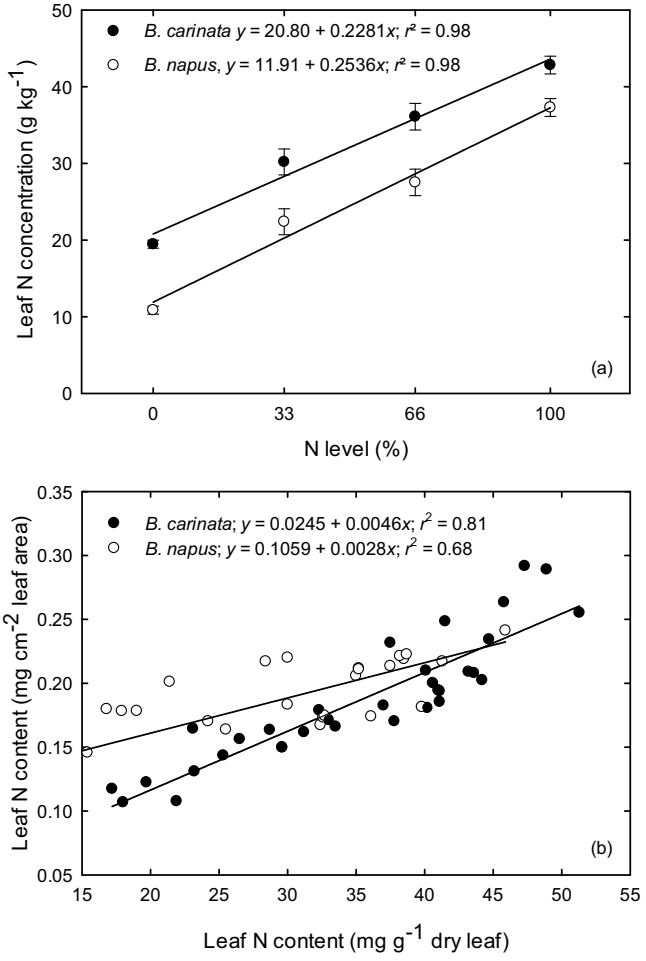

Fig. 8. (a) Relationship between nitrogen nutrition and leaf N concentration (g kg^{-1}). (b) Relationship between leaf N content (mg g^{-1} dry leaf) and leaf area N content (mg cm^{-1} leaf area) 55 days after treatment.

4. Discussion

4.1. Growth and development

Plants were grown under non-limiting N conditions and then transferred to varying levels of limited N supply 30 DAP, was a successful approach to quantify growth, development and physiological responses of oilseed brassicas to N deficiency. The cultivars evaluated in this study were selected based on similarities in temperature tolerance when grown as winter crops in the North Florida region. Carinata does not have a lengthy repressed rosette stage as canola and transitions earlier to bolting than canola. Following bolting, carinata axillary buds form branches that grow rapidly producing secondary and tertiary branching while only the upper axillary buds form primary branches in canola.

Early season shoot development involves the production of shoot apical meristem, leaves, nodes, internodes, axillary meristems and branches that form the aerial architecture of the plant. Limiting N during the early season reduced all plant growth and development parameters, altering the aerial architecture of both species in this study. Although both species have comparable sensitivity to N deprivation, the morphology and phenology differed which explains the intraspecific growth and development variation observed in this experiment. Oilseed yields are dependent on the number of raceme-bearing branches, the number of siliques per raceme and the number of seeds per silique produced by each plant (Öztürk, 2010). Nutrient management strategies that promote high

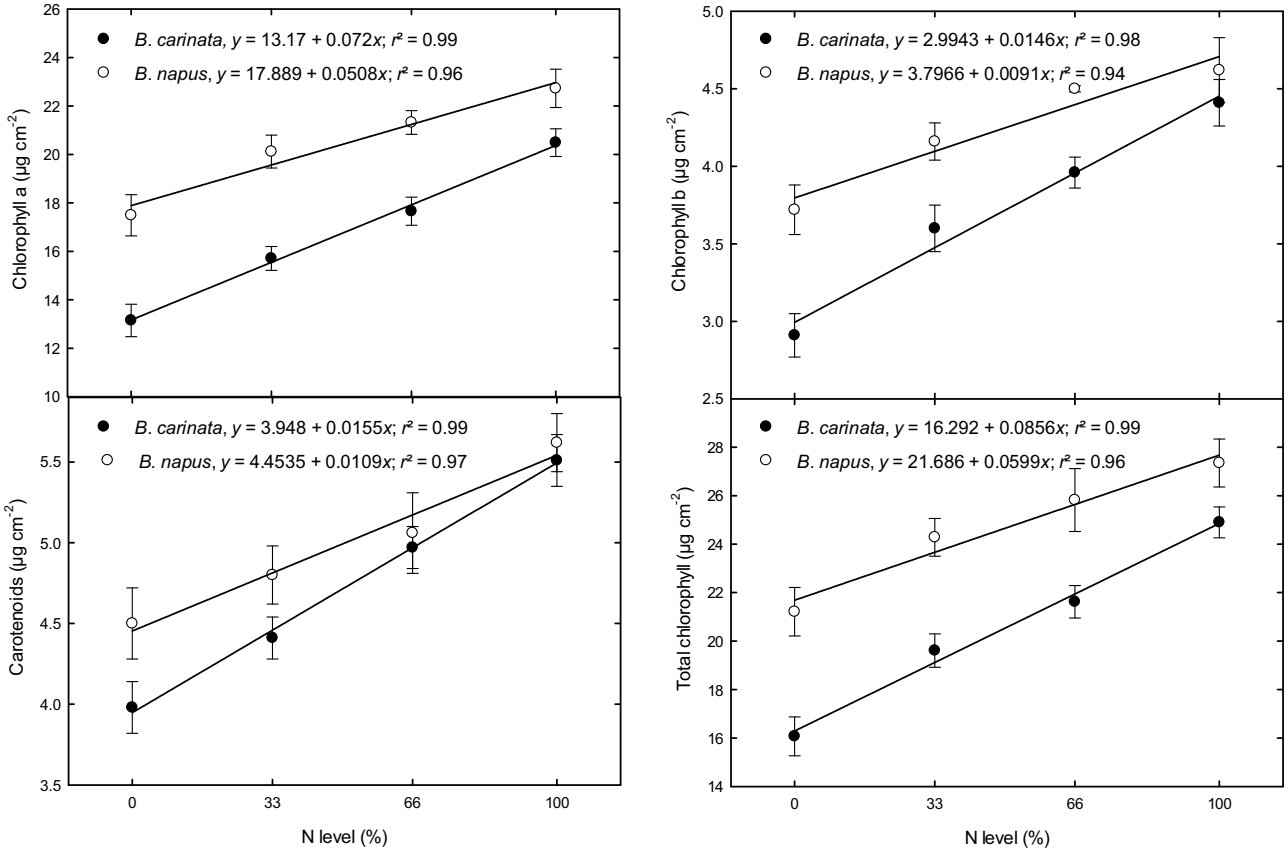

Fig. 9. Leaf chlorophyll a ($\mu g\,cm^{-2}$), chlorophyll *b* ($\mu g\,cm^{-2}$), carotenoids ($\mu g\,cm^{-2}$) and total chlorophyll concentrations of ($\mu g\,cm^{-2}$) of carinata and canola grown with 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 55 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

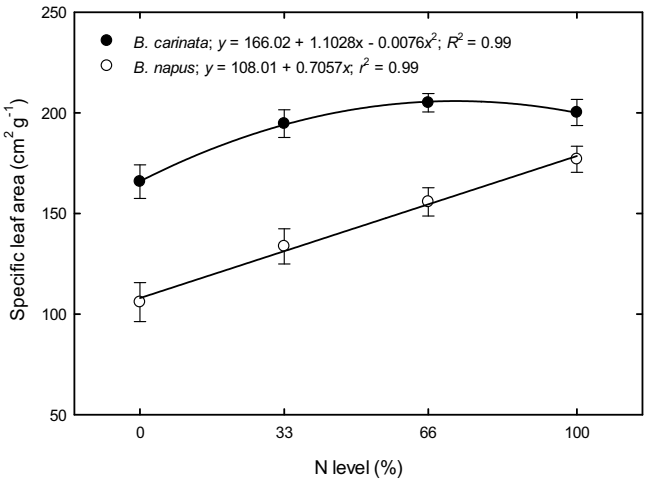

Fig. 10. Mean specific leaf area (SLA, $cm^2\,g^{-1}$) of carinata and canola grown with 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 55 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

numbers of reproductive branches will enhance the productivity of oilseed brassicas. Early season accumulation of leaf area not only enhances PAR interception and photosynthetic capacity of oilseed brassicas, but also minimizes soil water loss through evaporation and weed growth. Leaf area expansion rate increased linearly with N level for both species with canola producing 20.7 cm^2 leaf day^{-1} more than carinata under optimum conditions (Fig. 2). Plants require an adequate supply of nutrients to maintain the leaf area and lower the root:shoot ratio resulting in maximized photosynthetic capacity and reproductive fitness of the plant. Suboptimal N availability reduced the leaf sizes and increased leaf senescence and abscission as N is remobilized from older leaves to support new growth and initiate reproductive tissue. The source capacity of crop plants is determined primarily by the leaf area, leaf area duration, rate of photosynthesis, respiration and amino acid synthesis, all of which are influenced by N availability. As a result, extending the early season leaf duration allows maximum photoassimilates to be translocated to the developing seed during suboptimal conditions (Papantoniou et al., 2013).

4.2. Biomass allocation

Changes in nutrient availability may result in metabolic changes in the leaves and stems with concomitant adjustments of assimilate transport to the roots. Roots are heterotrophic organs that accumulate biomass through translocation of assimilates from the leaves. In N limited conditions, both species shift the allocation of assimilates to the roots restricting shoot morphogenesis and aboveground biomass accumulation. Reduction of root:shoot ratio was mainly related to inhibition of stem development for carinata and leaves for canola. Increasing biomass partitioning to the roots under N deprivation may be an adaptive mechanism for crop plants to improve water and nutrient acquisition and to regulate the transport and homeostasis of nutrients. This plasticity in management of source/sink relationship confers the ability to withstand suboptimal conditions of nutrient availability and ensure reproductive success. Heteroblastic growth and development responses to N availability did not modify the global biomass productivity

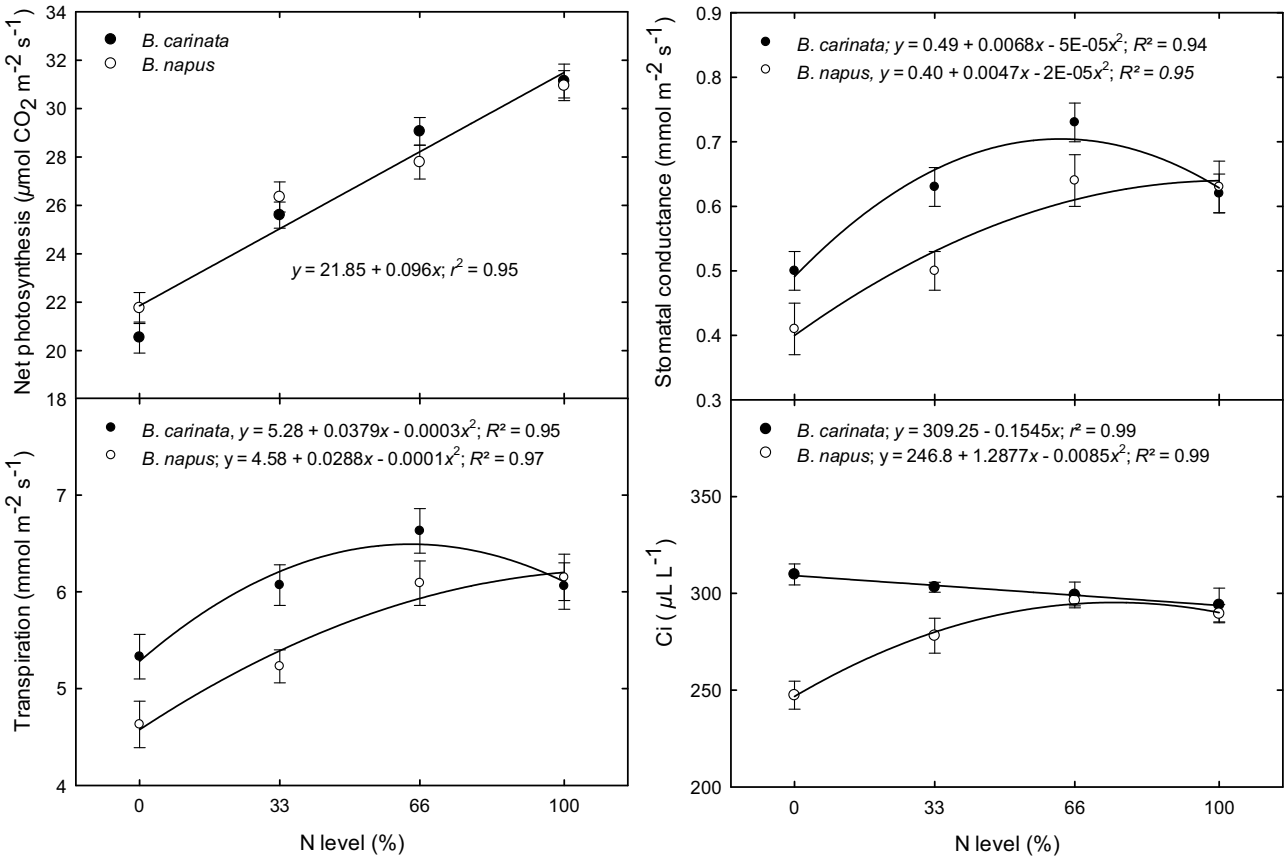

Fig. 11. Gas exchange processes, leaf photosynthesis net photosynthesis (μmol CO_2 m^{-2} s^{-1}), stomatal conductance (mmol CO_2 m^{-2} s^{-1}), transpiration (mmol CO_2 m^{-2} s^{-1}) and chlorophyll *b* (μg cm^{-2}), carotenoids (μg cm^{-2}) and internal CO_2 concentrations (μmol CO_2 m^{-2} s^{-1}) of carinata and canola with 4 levels of nitrogen (0, 33, 66 and 100% of N in Hoagland solution) and measured at 55 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

of both species in this study. However, the intraspecific variation in vegetative shoot morphogenesis responses that changes canopy architecture and branching patterns may offer agronomic advantages of one species over the other.

4.3. Leaf N, pigment concentration, SLA

In addition to tradeoff in biomass allocation between above and belowground tissues, leaf anatomy is also modified under limiting nutrient availability (Knops and Reinhart, 2000). Greater SLA may indicate greater leaf thickness and density accountable for a larger proportion of spongy mesophyll with increased intercellular air spaces that enhance light scattering and radiation capture. Across species, a high SLA was associated with a high relative growth rate (Figs. 7 and 10). The variation in SLA with N may play a role in plant adaptation strategies to N deficient conditions by changing biomass distribution patterns and opportunistic resource acquisition. Despite carinata having a greater SLA, it had no advantage over canola with respect to total biomass productivity and gas exchange during the vegetative stage. However, morphological plasticity to N may influence the reproductive productivity as N is remobilized from leaf tissue to the developing seed.

4.4. Gas exchange processes

Photosynthetic capacity in plants is related to plant architecture, leaf anatomy and morphology. Sub-optimal N availability modified aerial architecture (canopy structure, leaf size and duration and vertical distribution of leaves on the mainstem) for both species, thus changing whole plant light interception which may result in lowered canopy photosynthesis and seed productivity in these oilseed brassicas. Under well-watered conditions, Pan et al. (2011) reported a similar trend in P_n for carinata, although the values were many fold lower at high N levels. Unlike P_n, stomatal conductance (G_s) and transpiration (T_r) differed across species and increased with N supply from 0 to 66%N but declined to similar levels at 100%N (Fig. 11). These reductions in gas exchange processes when N is limited not only decreased the whole plant photosynthetic capacity but also altered source-sink distribution of photoassimilates in oilseed brassicas similar to Jensen et al. (1996). In addition, limiting N supply reduced leaf N and total chlorophyll concentrations and photosynthesis similar to sorghum (*Sorghum bicolor* L.), castor (*Ricinus communis* L.), corn and soybean (Muchow and Sinclair, 1994; Reddy and Matcha, 2010; Zhao et al., 2003). Higher leaf N concentrations increases photosynthetic assimilation rate by increasing the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase in the Calvin Cycle and in the electron transfer chain in the thylakoids (Evans, 1989; Suresh et al., 1996). At higher N rates, leaves accumulated more N per unit of mass which increased the N concentration per unit area (Fig. 8) and SLA (Fig. 10). The gain in leaf area may have enhanced radiation capture resulting in photosynthetic carbon gain and increased crop growth rate of both species (Fig. 7). Modifications in canopy architecture in response to nutritional deficiencies affect PAR capture and the production of structures involved in sexual reproduction. Canopy photosynthesis of canola may be greater than carinata since canopy photosynthesis is closely related to leaf area (Muller et al., 2005; Scott et al., 1973). However, carinata better elevates its photosynthetic structures for more effective PAR capture at the vegetative stage than canola. At this stage, canola has a dense rosette of leaves with

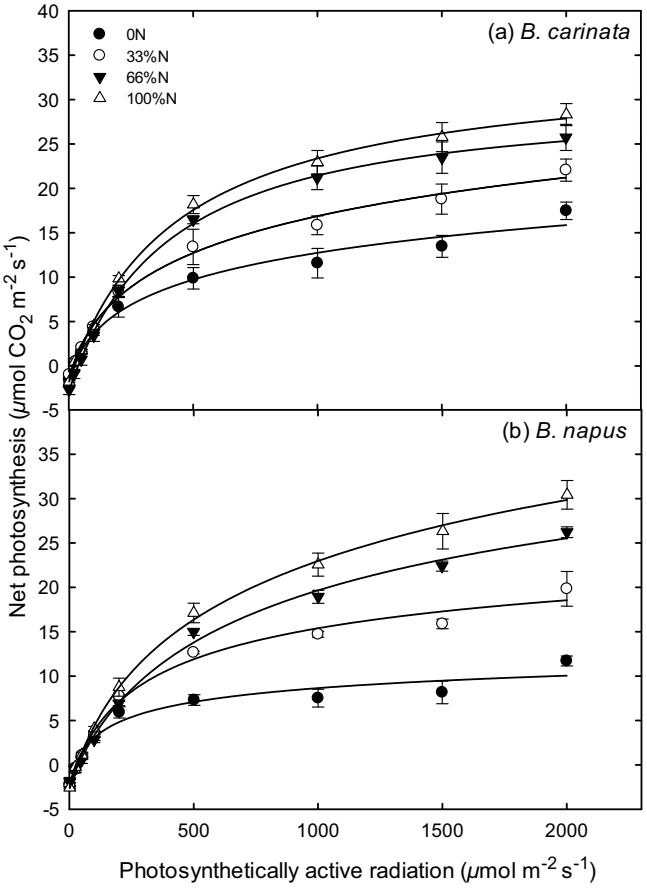

Fig. 12. Net photosynthesis of carinata and canola as a function of photosynthetically active radiation for leaves grown at 4 levels of N (0, 33, 66 and 100% of N in Hoagland solution) and measured at 51 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

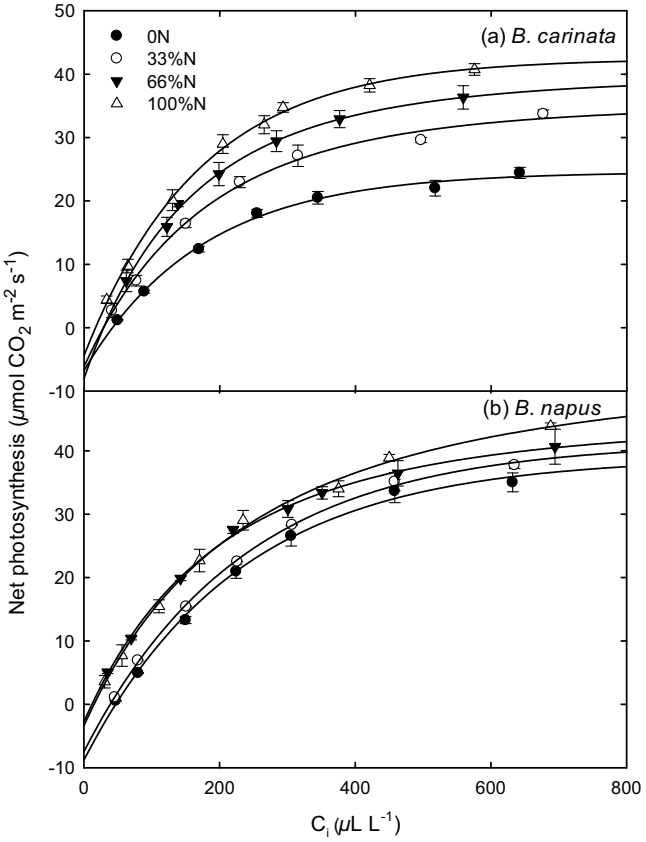

Fig. 13. CO_2 assimilation/internal CO_2 (A/C_i) curves of carinata and canola leaves grown at 4 levels of N (0, 33, 66 and 100% of N in Hoagland solution) and measured at 51 days after treatment. Each data point is the mean of 4 measurements while bars represent the standard error of the means.

shorter internodes and a higher proportion of shade leaves. Since greater photoassimilate production is associated with increased seed yield, N sufficiency during the vegetative phase will maximize yield potential (Pan et al., 2011). The magnitude of PAR responses and photosynthetic parameters to N indicates that carinata is less sensitive to changes in PAR under limited N conditions than canola.

4.5. *Leaf photosynthetic responses to PAR and* C_i

Photosynthetically active radiation and C_i response curves reveal the light-dependent and light-independent characteristics of the photosynthetic process and the modulation of these characteristics with changing environmental conditions. Under N limited conditions, our results indicate that higher V_{cmax}, J_{max} and CE in carinata leaves did not confer higher photosynthetic rates relative to canola, although the down regulation of photosynthesis was greater in leaves with low N supply than those at higher N supply for both species. When N is non-limiting (100%), both species had similar photosynthetic rates regardless of differences in V_{cmax}, J_{max} and CE. When CO_2 is at ambient and supra-ambient concentrations, the photosynthetic rates of carinata was more responsive to N deficiency than canola. A reduction in CO_2 concentration below ambient (<400 CO_2 $\mu L L^{-1}$) lowers photosynthetic capacity and Calvin Cycle intermediates which affect the activity of Rubisco and other enzymes (Long and Bernacchi, 2003). Results from modelling A-Ci curves indicate leaves of canola reached maximum photosynthetic rate at higher C_i than carinata across N rates (Fig. 13).

5. Conclusions

These results demonstrated that N deficiency induces a series of morphological changes in carinata and canola aerial architecture inhibiting leaf and stem development. During the vegetative growth phase, limiting N restricted plant height and number of nodes and branching patterns, reduced leaf expansion and lowered photosynthetic capacity. Across N rates, carinata had greater leaf N concentration and specific leaf area than canola. These differences did not have an effect on the photosynthetic capacity or total biomass accumulation of both species 55 DAT. Nitrogen deprivation changed the biomass allocation patterns. Carinata had a lower root:shoot ratio than canola across all levels of N supply resulting from the relative inhibition of stem development for carinata and leaves for canola. Photosynthetically active radiation curve responses to N supply indicates that carinata is less sensitive to changes in PAR under limited N conditions than canola. Similarly, at ambient and supra-ambient CO_2 concentrations, the photosynthetic rates of carinata was less sensitive to N deficiency than canola. Despite intraspecific morphological variation, carinata and canola photosynthetic capacity and total biomass accumulation were comparable across N rates. However, species-specific resource partitioning responses to N limitations may have implications for N use efficiency and recovery during reproductive development when N is translocated from the leaves to the reproductive structures. Increasing oilseed brassica productivity will require nutrient management strategies that time N application with critical phenostages corresponding to maximum N uptake to extend pre-bolting leaf area duration and avert yield-deleterious resource reallocation among plant organs.

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References

Albert, B., Le Caherec, F., Niogret, M., Faes, P., Avice, J., Leport, L., Bouchereau, A., 2012. Nitrogen availability impacts oilseed rape (*Brassica napus* L.) plant water status and proline production efficiency under water-limited conditions. Planta 236, 659–676.

Chapin III, F.S., Field, B.A.J., Waring, R.H., 1996. Plant response to multiple environmental factors. Bioscience 37, 49–57.

Del Gatto, A., Maria, G.M., Salvatore, A.R., Sandro, P., Lorella, M., Daniela, P., Marco, S., Daniele, D., Ester, F.D., Chiara, M., 2015. A comparative study of oilseed crops (*Brassica napus* L. subsp. *oleifera* and *Brassica carinata* A. Braun) in the biodiesel production chain and their adaptability to different Italian areas. Ind. Crops Prod 75, 98–107.

Evans, J., 1989. Photosynthesis and nitrogen relationships in leaves of C-3 plants. Oecologia 78, 9–19.

FAOSTAT, 2015. Agricultural Data: Crops and Livestock Primary and Processed. FAO, Rome [Online] Available at http://faostat.fao.org. (Accessed 12.05.15).

Gammelvind, L., Schjoerring, J., Mogensen, V., Jensen, C., Bock, J., 1996. Photosynthesis in leaves and siliques of winter oilseed rape (*Brassica napus* L.). Plant Soil 186, 227–236.

Gan, Y., Malhi, S.S., Brandt, S., Katepa-Mupondwa, F., Stevenson, C., 2008. Nitrogen use efficiency and nitrogen uptake ofjuncea canola under diverse environments. Agron. J. 100, 285–295.

Gesch, R.W., Isbell, T.A., Oblath, E.A., Allen, B.L., Archer, D.W., Brown, J., Hatfield, J.L., Jabro, J.D., Kiniry, J.R., Long, D.S., Vigil, M.F., 2015. Comparison of several Brassica species in the north central U: S. for potential jet fuel feedstock. Ind. Crops Prod. 75, 2–7.

Hocking, P., Randall, P., DeMarco, D., 1997. The response of dryland canola to nitrogen fertilizer: partitioning and mobilization of dry matter and nitrogen, and nitrogen effects on yield components. Field Crops Res. 54, 201–220.

Jackson, G., 2000. Effects of nitrogen and sulfur on canola yield and nutrient uptake. Agron. J. 92, 644–649.

Jensen, C., Morgensen, V., Mortensen, G., Andersen, M., Schjoerring, J., Thage, J., Koribidis, J., 1996. Leaf photosynthesis and drought adaptation in field-grown oilseed rape (*Brassica napus* L.). Aust. J. Plant Physiol. 23, 631–644.

Knops, J., Reinhart, K., 2000. Specific leaf area along a nitrogen fertilization gradient. Am. Midl. Nat. 144, 265–272.

Kumar, A., Singh, P., Singh, D.P., Singh, H., Sharma, H.C., 1984. Differences in osmoregulation in *Brassica* species. Ann. Bot. 54, 537–541.

Long, S., Bernacchi, C., 2003. Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. J. Exp. Bot. 54, 2393–2401.

Malagoli, P., Laine, P., Le Deunff, E., Rossato, L., Ney, B., Ourry, A., 2004. Modeling nitrogen uptake in oilseed rape cv capitol during a growth cycle using influx kinetics of root nitrate transport systems and field experimental data. Plant Physiol. 134, 388–400.

Malagoli, P., Laine, P., Rossato, L., Ourry, A., 2005. Dynamics of nitrogen uptake and mobilization in field-grown winter oilseed rape (Brassica napus) from stem extension to harvest – I. Global N flows between vegetative and reproductive tissues in relation to leaf fall and their residual. N. Ann Bot. 95, 853–861.

Momoh, E., Song, W., Li, H., Zhou, W., 2004. Seed yield and quality responses of winter oilseed rape (*Brassica napus*) to plant density and nitrogen fertilization. Indian J. Ag. Sci. 74, 420–424.

Muchow, R., Sinclair, T., 1994. Nitrogen response of leaf photosynthesis and canopy radiation use efficiency in field-grown maize and sorghum. Crop Sci. 34, 721–727.

Muller, J., Behrens, T., Diepenbrock, W., 2005. Measurement and modelling of canopy gas exchange of oilseed rape. Agric. For. Meterol. 132, 181–200.

Noquet, C., Avice, J., Rossato, L., Beauclair, P., Henry, M., Ourry, A., 2004. Effects of altered source-sink relationships on N allocation and vegetative storage protein accumulation in *Brassica napus* L. Plant Sci. 166, 1007–1018.

Öztürk, Ö., 2010. Effects of source and rate of nitrogen fertilizer on yield, yield components and quality of winter rapeseed (*Brassica napus* L.). Chil. J. Agric. Res. 70, 132141.

Pan, X., Lada, R., Caldwell, C., Falk, K., 2011. Water-stress and N-nutrition effects on photosynthesis and growth of *Brassica carinata*. Photosynthetica 49, 309–315.

Papantoniou, A., Tsialtas, J., Papakosta, D., 2013. Dry matter and nitrogen partitioning and translocation in winter oilseed rape (*Brassica napus* L.) grown under rainfed Mediterranean conditions. Crop Pasture Sci. 64, 115–122.

Rathke, G., Behrens, T., Diepenbrock, W., 2006. Integrated nitrogen management strategies to improve seed yield, oil content and nitrogen efficiency of winter oilseed rape (*Brassica napus* L.): a review. Agric. Ecosyst. Environ. 117, 80–108.

Reddy, K., Matcha, S., 2010. Quantifying nitrogen effects on castor bean (*Ricinus communis* L.) development growth, and photosynthesis. Ind. Crops Prod. 31, 185–191.

Rossato, L., Laine, P., Ourry, A., 2001. Nitrogen storage and remobilization in *Brassica napus* L. during the growth cycle: nitrogen fluxes within the plant and changes in soluble protein patterns. J. Exp. Bot. 52, 1655–1663.

Scott, R., Ogunremi, E., Ivins, J., Mendham, N., 1973. Effect of sowing date and season on growth and yield of oilseed rape (*Brassica napus*). J. Agric. Sci. 81, 277–285.

Shivpuri, A., Chipa, H.P., Gupta, R.L., Sharma, K.N., 1997. Field evaluation of mustard genotypes against white rust, powdery mildew and stem rot. Ann. Arid Zone 36, 387.

Suresh, K., Lakkineni, K., Nair, T., 1996. Relationship between leaf nitrogen and photosynthetic characteristics in *Brassica juncea* and *B-campestris*. J. Agron. Crop Sci. 177, 107–113.

U.S, 2016. Energy Information Administration. Monthly Energy Review July 2016 (accessed 8.11.16) http://www.eia.gov/totalenergy/data/monthly/pdf/mer.pdf.

Wiesler, Behrens, Horst, 2001. Nitrogen efficiency of contrasting rape ideotypes. In: Horst, et al. (Eds.), Plant Nutrition: Food Security and Sustainability of Agro-ecosystems Through Basic and Applied Research.

Zanetti, F., Vamerali, T., Mosca, G., 2009. Yield and oil variability in modern varieties of high-erucic winter oilseed rape (*Brassica napus* L. var. oleifera) and Ethiopian mustard (*Brassica carinata* A. Braun) under reduced agricultural inputs. Ind. Crops. Prod. 30, 265–270.

Zanetti, F., Andrea, M., Marisol, T.B., 2013. Challenges and opportunities for new industrial oilseed crops in EU-27: A review. Ind. Crops. Prod. 50, 580–595.

Zhao, D., Reddy, K., Kakani, V., Read, J., Carter, G., 2003. Corn (*Zea mays* L.) growth leaf pigment concentration, photosynthesis and leaf hyperspectral reflectance properties as affected by nitrogen supply. Plant Soil 257, 205–217.