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Physiological analysis of growth and development of winter carinata (*Brassica carinata* A. Braun)

Ramdeo Seepaul¹ | Shivendra Kumar¹ | Kenneth J. Boote² | Ian M. Small¹ | Sheeja George¹ | David L. Wright¹

¹North Florida Research and Education Center, University of Florida, Quincy, FL, USA

²Agricultural and Biological Engineering, University of Florida, Gainesville, FL, USA

Correspondence

Ramdeo Seepaul and Shivendra Kumar, North Florida Research and Education Center, University of Florida, Quincy, FL 32351, USA. Email: rseepaul216@ufl.edu (R. S.); shivendrkumar@ufl.edu (S. K.)

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Abstract

Brassica carinata is a non-food, low-carbon, none-to-low indirect land-use change impact oilseed feedstock grown for sustainable biofuels, bioproducts, and high protein seed meal. Understanding carinata growth and development is critical to the development of best management practices for maximum productivity and profitability of double-cropped farming systems. Field experiments were conducted during 2017-2018 (Year 1) and 2018–2019 (Year 2) winter-spring growing seasons in Quincy, Florida, to quantify the total aboveground dry matter accumulation (TDM), allocation, growth, nutrient uptake, and seed quality. The two carinata cultivars Avanza 641 and AX17012 accumulated 10826 and 9343 kg TDM ha⁻¹ in Year 1 and 9655 and 10,642 kg TDM ha⁻¹ in Year 2, respectively, at harvest maturity. The proportion of DM in the vegetative parts such as leaves and stems decreased, and the DM in reproductive structures such as silique walls and seeds increased with maturity. Seed yield (SY) was similar between cultivars but differed between years with Year 1 (2732 kg ha⁻¹), producing 29% greater SY than Year 2 (1929 kg ha⁻¹). Carinata primary stem has 17-20 leaf nodes, with 75%-88% of the axillary meristems producing primary and secondary branches. Crop growth rate (CGR) increased from vegetative to pod development for both cultivars in Year 1, while in Year 2, AX17012 and Avanza 641 attained maximum CGR at the pod development and bolting/flowering stages, respectively. Maximum seasonal nutrient uptake in leaves, stems, and siliques generally occurred in the early, mid, and late season, respectively, in both years. Seed weight, oil, monounsaturated fatty acids, C18:3, C20:1, and C22:1 concentrations increased with plant age, whereas protein, glucosinolate, polyunsaturated fatty acids, saturated fatty acids, C18:1, and C18:2 concentrations decreased with plant maturity. These results can be used for crop modeling to predict growth, development, and yield and aid in developing in-season decision support tools.

KEYWORDS

biomass, carinata physiology, growth analysis, nutrient uptake, oilseed, seed composition, total dry matter

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1 **INTRODUCTION**

The genus *Brassica* comprises several economically important oilseed crop species that are cultivated for different purposes. It includes six interrelated members comprising three diploid progenitor species, that is, B. nigra L. Koch, B. oleracea L., and B. rapa L., and three allotetraploid species, that is, B. carinata A. Braun, B. juncea L. Czern, and B. napus L. that contribute toward meeting global edible oil, meal, and industrial oil needs. B. napus (napus) and B. rapa with high oleic acid, low erucic acid, and low glucosinolate content are grown widely as major edible oilseed crops in Europe, North America, South America, Australia, and China (Seepaul et al., 2021). Brassica juncea with high erucic acid and glucosinolate content is mostly grown in the South Asian subcontinent to meet the edible oilseed demand (Becker et al., 1995; Gómez-Campo, 1999; Kjellström, 1993). B. carinata (carinata), which also has high erucic acid and glucosinolate content, is cultivated in North-Eastern Africa mostly (Ethiopia) as a vegetable and fodder crop (Simmonds, 1979; Warwick et al., 2009) and as an industrial oilseed in North and South America (Kumar et al., 2020; Seepaul, Bliss, et al., 2016; Seepaul, George, et al., 2016).

Recently, carinata has emerged as a promising crop due to its greater adaptability, low input cost, and higher productivity in suboptimal conditions, as well as providing a source of non-food feedstock for the production of renewable fuels with a highly desirable oil profile (Blackshaw et al., 2011; Cardone et al., 2003; Gesch et al., 2015). Carinata seeds are predominantly dark yellow to brown with up to 48% oil content and 40%-45% erucic acid content, making it a desirable candidate for sustainable aviation fuel production and various other industrial applications (Bouaid et al., 2009; Falk, 1999; Kumar et al., 2020; Jadhav et al., 2005; Velasco et al., 2003). Carinata seed meal is a good source of protein for animal feed after removing glucosinolates through processing (Schulmeister et al., 2019). High glucosinolate-containing cultivars have been used for bio-fumigation (Abera et al., 2011). In recent years, carinata cultivation has expanded to Europe (Spain, Italy, Greece, and UK; Bozzini et al., 2007; Velasco et al., 2003), Australia, New Zealand, South America (Argentina and Uruguay; Seepaul, Bliss, et al., 2016; Seepaul, George, et al., 2016), and South Asia (India and Pakistan; Malik, 1990; Prakash et al., 2012; Zada et al., 2013). Efforts are being made to adopt carinata as a winter commodity cover crop in North America, especially in the Southeastern United States (Kumar et al., 2020; Marillia et al., 2014; Seepaul et al., 2020) due to its vigorous growth once established, great biomass production, nutrient scavenging ability, wide adaptability, and availability of large acreage of winter fallow land in the region (19.02 million hectares; Soil Health Census Report USA, 2019).

Understanding crop productivity in different environments and its response to management is important to widespread adoption and commercial production. Yield is a complex trait that is resultant of interaction between morphological, physiological, and environmental factors. Phenological traits of plants are often used to evaluate plant growth, which finally determines their overall performance in terms of yield and biomass (Dhondt et al., 2013; Hosoi & Omasa, 2012; Taheriazad et al., 2016). The overall growth of the plant and its final yield are influenced by various factors such as leaf area index (LAI), average photosynthetic efficiency of leaves, plant height, number of branches, pods per plant, pod area (in case of oilseed brassicas), accumulation of dry matter in leaf, and stem, pod, and total biomass which vary with the growth stages of a plant (Friedli et al., 2016; Gebbers et al., 2011; Sharma & Ritchie, 2015; Sun et al., 2017).

Leaves are an important source of carbohydrates produced during photosynthesis and are primarily responsible for biomass production in plants. The photosynthates produced by leaves drive the growth and yield in crops. Greater leaf area is important for light interception and influences plant productivity. The plant growth rate is low during the early stages of its life cycle due to incomplete plant cover on the ground and absorption of a smaller portion of solar radiation by leaves. The rate of photosynthesis increases with greater number of leaves and expansion of leaf area, leading to rapid plant growth. Maximum growth rate is realized when plants reach height and density to utilize environmental factors efficiently (Radford, 1967). Higher rates of nitrogen and sulfur fertilization result in increased seed yield, total dry matter, and harvest index in B. napus and B. juncea (Kumar et. al., 2001; Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019) due to an increase in leaf number and photosynthetic activity (Chongo & McVetty, 2001; Diepenbrock, 2000; Singh & Singh, 1983). Availability of N during seed development and maturation is also known to significantly affect oil content and fatty acid composition in carinata and napus and affect various vegetative traits such as height, leaf area, branches, and total biomass (Seepaul, Bliss, et al., 2016; Seepaul, George, et al., 2016). A study conducted by Mulvaney et al., (2019) showed that row spacing in carinata affected the total number of branches and pods per plant, influencing seed and oil yield. At the end of flowering, pods continue to contribute to photosynthesis (Jensen et al., 1996; King et al., 1997). Chloroplasts located in the outer pod wall layer are responsible for 70-100% of the assimilation of photosynthates in seeds (Bennett et al., 2011; Major & Charnetski, 1976; Quebedeaux & Chollet, 1975; Raven & Griffiths, 2015; Sheoran & Randhir, 1991; Singal et al., 1995; Singh, 1993). Seed weight and size are very important traits that contribute toward plant fitness and vield. Seed filling and seed weight depend on the process of photosynthesis in source tissue and subsequent translocation of assimilates to the seeds (Zuo & Li, 2014). Variation in pod length affects the pods' photosynthetic ability impacting seed

filling and final seed weight in different oilseed species (Bravo et al., 1980; Li et al., 2019). Aboveground biomass is also an important parameter that is central to functional plant ecology and growth analysis. Repeated measurement of biomass contributed by different stage-dependent factors such as leaf area, pod, and seed development, etc., helps in determination of total aboveground dry matter, net primary production, crop growth rate, and yield (Cornelissen et al., 2003; Poschlod et al., 2000; Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019).

Understanding crop productivity in different environments and its response to management can be a limiting factor for the widespread adoption of new crops. Genetic, environmental, and management practices interact to influence crop morphology, phenology, physiology, and yield. Physiological and morphological traits such as leaf area index (LAI), photosynthetic efficiency of all the leaves, plant height, number of branches, pods per plant, pod area, accumulation of dry matter in leaf, stem, and pod, and total biomass are often used to evaluate plant growth and agronomic performance (Dhondt et al., 2013; Friedli et al., 2016; Gebbers et al., 2011; Hosoi & Omasa, 2012; Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019; Taheriazad et al., 2016). Detailed information of growth-related aspects of economically important Brassicaceae members such as B. napus, B. rapa, and B. juncea are available but there is a dearth of studies for carinata due to its nascent importance as a biofuel crop. Growth dynamics of various traits across two growing seasons for carinata will provide important information about the productivity of the crop. The objectives of this study were to (1) assess the growth and development of the crop across two growing seasons by evaluation of different physiological traits and (2) explore the relationship between these traits and yield components in carinata.

2 | MATERIALS AND METHODS

2.1 | Site characterization, experimental design, and management

A 2-year field trial was conducted during the year 2017–2018 and 2018–2019 winter–spring growing seasons at the University of Florida North Florida Research and Education Center (30°32′44″N, 84°35′40.7″W), Quincy, FL on a Norfolk sandy loam (Fine-loamy, kaolinitic, thermic Typic Kandiudults) with 0%–2% slopes. Two carinata cultivars (Avanza 641 and AX17012) sourced from Nuseed Canada were planted in a randomized complete block design with four replications. The two cultivars and harvest dates were randomized completely within each block. Plots were 1.5 by 30 m with 1.8 m alleys between plots. In both years, alleys were planted with carinata and mowed at physiological maturity to reduce border and alley effects. Plots were tilled using two passes made with an Athens 62 Disk Plow (Athens

Plow Company; 13 cm deep) followed by a field cultivator to create a level seedbed. Seeds treated with Prosper EverGol (Bayer CropScience, Research Triangle Park) (fungicide and insecticide seed treatment containing clothianidin, penflufen, trifloxystrobin, and metalaxyl) were planted using a R-Tech JT5DN cone planter (R-Tech Industries, Homewood) in 30 cm rows at a rate of 6.1 kg ha⁻¹.

Based on soil test recommendations, nitrogen fertilizer was applied at a rate of 89 and 111 kg ha⁻¹ in Years 1 and 2, respectively, with 20% preplant incorporated and 80% topdressed at early flowering. Phosphorous and potassium were preplant incorporated at 45 and 38 kg ha⁻¹ in Year 1 and 91 and 76 kg ha⁻¹ in Year 2. Sulfur was applied at a rate of 20 and 28 kg ha⁻¹ at early flowering in Years 1 and 2, respectively.

Carinata was planted on December 4, 2017 in Year 1 and on January 9, 2019 in Year 2. Pre-emergence herbicide pendimethalin (N-(1-ethylpropyl)-3,4-dimethyl-2,6dinitrobenzenamine) was applied at planting at an active ingredient rate of 0.73 L ha⁻¹. Lambda-Cy 1EC (Lambdacyhalothrin $[1\alpha(S^*),3\alpha(Z)]-(\pm)$ -cyano-(3-phenoxyphenyl) methyl-3-(2-chloro-3,3,3-trifluoro-1-ropenyl)-2,2-dimethyl cyclopropanecarboxylate) was applied on February 7, 2018 at a rate of 0.26 L ha⁻¹ to control aphids. Topsin 4.5 FL (Thiophanate-methyl (dimethyl [1,2-phenylene)-bis(imino carbonothioyl)]bis[carbamate])) was applied on March 22, 2018 at a rate of 1.5 L ha⁻¹. One irrigation of 15.2 mm was applied on March 20, 2019 during flowering.

2.2 | Data collection

Biomass samples were collected at 2-week intervals until harvest maturity from the inner three 1 m row length (0.91 m^2 sampled) beginning at 31 and 35 days after planting in Years 1 and 2, respectively. The growth stage was recorded using a modified BBCH scale for B. napus. Plant height was measured as the distance between the soil level and the uppermost visible mainstem node. The number of nodes, primary branches on the mainstem, and secondary branches were recorded. Plants were separated into leaves, stems, pod walls, and seed. Leaf and pod area were measured depending on growth stage to determine leaf and pod area indices using a LI-3000A Portable Area Meter connected to a LI-3050A Transparent Belt Conveyer (LI-COR Biosciences). Plant parts were dried in a forced-air oven at 55-60°C for 72 h for dry matter determination. Leaves, stems, and pods (pod walls + seeds) were ground separately to pass a 2 mm stainless steel screen and analyzed for mineral content at the Waters Agricultural Laboratories, Camilla, GA. Specific leaf area (SLA) was computed from leaf area divided by leaf mass (g). The leaf, stem, pod, and seed mass were measured in kg ha⁻¹ and LAI was computed from the fractions, ratios,

and SLA multiplied by the total biomass (kg ha^{-1}) from a 0.91 m² sample area.

Naturally desiccated carinata was harvested with a Wintersteiger Delta plot combine (Wintersteiger Inc.) on June 4, 2018 and May 30, 2019. Seeds were oven-dried at 50°C for 48 hours before weight and moisture were recorded. Yields were corrected to 8% moisture. Seed moisture content and test weight were measured with a Steinlite S195 moisture meter (Steinlite) using ~0.75 kg seeds. Two samples of 1000 seeds were randomly subsampled and weighed. Seeds were analyzed for mineral content at Waters Agricultural Laboratories. Seed and ground tissue samples were chemically digested in nitric acid in a digestion block (DigiBlock Digester ED36S, Labtech) followed by elemental quantification via inductively coupled plasma optical emission spectrometry (ICP-OES, Perkin-Elmer optima 4300 DV).

Total glucosinolates, protein content, oil content, and fatty acid composition were estimated using near-infrared reflectance spectroscopy (NIRS). Samples were analyzed using a FOSS XDSTM Rapid Content Analyzer (FOSS Inc.). Sample spectra were evaluated using the ISIscan program (FOSS Analytical) using proprietary carinata calibration equations (Nuseed Canada) developed from numerous calibration and validation samples. The proprietary prediction model developed by Nuseed Canada utilized nuclear magnetic resonance spectroscopy (Oxford MARAN Ultra Benchtop NMR System, Oxford Instruments) as well as gas chromatography (Agilent 6890N, Agilent Technologies) to develop the underlying equations (Taylor et al., 1992).

Physiological analysis at each measurement date included (a) leaf area index (LAI = leaf area $[m^2]/0.9144 m^2$), (b) specific leaf area (SLA $[cm^2 g^{-1}] = leaf$ area $[cm^2]/$ leaf weight [g]), (c) leaf weight ratio (LWR [g g^{-1}] = leaf dry weight [g]/plant dry weight [g]), and (d) leaf area ratio (LAR [cm² g⁻¹] = leaf area per plant [cm²]/plant dry weight[g]). Further analysis was done by grouping stages into four growth stages (GS) (vegetative [Year 1, GS 1.2-1.6; Year 2, GS, 1.4–1.7], bolting/flowering [Year 1, GS 1.6–6.2; Year 2, GS 1.7-6.7], pod development [Year 1, GS 6.2-8.5; Year 2, 6.7-7.2], and senescence [Year 1, GS 8.5-9.9; Year 2, GS 7.2-9.9] Table 1). These include calculations of various growth and development factors at each of these four stages: (a) leaf area duration (LAD [days] = $(L_1 + L_2)/2 \times (t_2 - t_1)$, where $L_1 = LAI$ at the first stage, $L_2 = LAI$ at the second stage $(t_2 - t_1)$ = time interval in days), (b) net assimilation rate (NAR [g g⁻¹ day⁻¹] = { $(W_2 - W_1)/(t_2 - t_1)$ }×{ $(\log_e$ $L_2 - \log_e L_1 / (L_2 - L_1)$, where W_1 and $W_2 = dry$ weight of whole plant (g) at time t_1 and t_2 (days), respectively, L_1 and L_2 are leaf weights (g) at time t_1 and t_2 (days), respectively, $(t_2 - t_1)$ = time interval in days), (c) relative growth rate (RGR [g g⁻¹ day⁻¹] = (log_e W₂ - log_e W₁)/($t_2 - t_1$), where W_1 and W_2 are whole plant dry weight at t_1 and t_2 , respectively, $t_2 - t_1$ = time interval in days), (d) absolute growth rate $(AGR [cm² day⁻¹] = (h_2 - h_1)/(t_2 - t_1)$, where h₁ and h₂ are plant height at t_1 and t_2 times, respectively), (e) crop growth rate (CGR [kg ha⁻¹ day⁻¹] = $(W_2 - W_1)/\rho (t_2 - t_1)$, where W_1 and W_2 = dry weight of whole plant (g) at time t_1 and t_2 (days), respectively, ρ = ground area on which W₁ and W₂ are recorded [0.9144 m²]), (f) harvest index (seed yield/total above ground dry matter) \times 100), (g) translocation percentage (TP [%] = [(straw weight at flowering - straw weight at harvest)/(pod weight at flowering - pod weight at harvest]), and (h) dry matter efficiency (DME = {(grain yield [kg ha^{-1})/ TDMP) \times (100/duration of crop)}), where TDMP = total dry matter produced over the crop cycle). Seed nutrient

TABLE 1	Sampling number, sampling date	, days after planting,	cumulative growing	degree days,	and carinata	growth-stage di	aring the 2017–
2018 and 2018	-2019 winter-spring growing se	asons at North Florida	a Research and Educa	ation Center,	Quincy, FL		

	2017-2018				2018-2019			
Sample no.	Date	DAP	GDD	Growth stage	Date	DAP	GDD	Growth stage
1	1/4/2018	31	370	1.2	2/13/2019	35	476	1.4
2	1/18/2018	45	486	1.4	2/27/2019	49	814	1.7
3	1/31/2018	58	634	1.6	3/13/2019	63	1106	5.1
4	2/14/2018	72	908	3.1	3/27/2019	77	1372	6.7
5	2/28/2018	86	1320	6.0	4/10/2019	91	1712	7.1
6	3/14/2018	100	1526	7.1	4/24/2019	105	2071	7.2
7	3/28/2018	114	1825	7.2	5/8/2019	119	2519	8.9
8	4/11/2018	128	2143	8.5	5/21/2019	132	2955	9.9
9	4/25/2018	142	2493	9.5				
10	5/9/2018	156	2907	9.7				
11	5/23/2018	170	3405	9.9				

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uptake was calculated by multiplying seed yield by elemental concentration.

2.3 | Data analysis

Dry matter accumulation, plant height, and mainstem node data were fitted with a three-parameter Sigmoidal function while leaf area index was fitted with a Gaussian peak model. Each year's stand, yield, test weight, 1000-seed weight, oil content, oil yield, seed nutrient concentration, and uptake were analyzed using general linear model procedures in SAS (SAS Institute Inc.) with cultivar as fixed effect and year and replication as random effects. Temporal 1000-seed weight, oil content, and fatty acid composition were similar between cultivars; hence, the data were pooled and analyzed by year using PROC MIXED procedure in SAS with sampling date as a fixed effect and replication as a random effect. Sampling date was considered as a repeated measure and responses were evaluated at the 0.05 probability level. Differences among sampling date were separated using the PDIFF option in PROC MIXED procedure. Responses in Year 1 were tested with orthogonal polynomial contrasts. When linear, quadratic, and cubic functions were detected, the functional form of the regression relation was determined by starting with the linear function, then adding successively higher-order polynomials in conjunction with plotting the data and making visual observations. If it was determined that the higher-order polynomial did not substantially improve the explanation of the response curve (based on r^2 values), then those higher-order polynomials were ignored. Correlations among measured traits were determined by correlation analysis (PROC CORR) on the combined Years 1 and 2 data. When correlations were detected, regressions

were performed using PROC REG in SAS to quantify the relationship.

3 | **RESULTS AND DISCUSSION**

3.1 | Seasonal growth conditions

The total growing season precipitation in Year 1 was 74% greater than Year 2 with 38% and 47% of the precipitation occurring in the first 3 months after planting in Year 1 and Year 2, respectively (Figure 1). A 60% higher than average precipitation in May of Year 1 delayed seed maturity and harvest. Season-long precipitation in Year 1 was similar to the 30-year long-term average (LTA, 767 mm), while Year 2 precipitation (537 mm) was 24% less in comparison to the LTA. Carinata seed yield is directly influenced by precipitation along with weed management and fertilization (Hossain et al., 2018). A recent report showed that carinata seed yield was greater at locations with higher precipitation in north Florida than locations with lower precipitation (Kumar et al., 2020). Higher precipitation influences plant growth by increasing the production of branches and pods and root length and surface area which enhanced crop yield (Hossain et al., 2018; Kumar et al., 2020; Liu et al., 2011). This increased crop yield trend with greater precipitation was evident for both cultivars in Year 1 compared with Year 2 (Table 2). The mean growing season air temperatures in both years were 0.5°C greater than the LTA. Mean temperatures were similar between years (17.2°C); however, Year 1 mean temperature in January was 3.0°C lower than Year 2. Temperatures in February for both years were 4.6°C greater than the LTA. In Year 1, 13 of the 15 hard freeze events ($\leq 0^{\circ}$ C) lasting longer than 6 hours occurred in January 2018 while only four



FIGURE 1 Monthly average air temperatures and monthly total rainfall for 2017–2018 and 2018–2019 winter–spring growing seasons compared with 30-year normals at North Florida Research and Education Center, Quincy, FL

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TABLE 2Plant stand, seed yield, test weight, 1000-seed weight, oil content, and oil yield of two carinata cultivars during the 2017–2018 and2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

	Avanza 641		AX17012	
	2018	2019	2018	2019
Stand, plants m ⁻²				
Early-season stand	92.5 a	82.0 b	92.8 a	77.8 b
Post-harvest stand	84.5 a	43.3 b	72.8 b	41.8 b
Seed yield, kg ha ⁻¹	2892.1 a	1886.0 b	2572.6 a	1971.4 b
Test weight, kghL	58.6 b	65.2 a	56.0 b	65.2 a
1000-seed weight, g	4.3 a	3.7 b	4.8 a	3.7 b
Oil content, %	52.8 a	46.4 b	52.6 a	46.9 b
Oil yield, L ha ⁻¹	1659.6 a	950.3 b	1469.7 a	1005.0 b

hard freeze events were recorded in Year 2, three of which occurred in January 2019. A hard freeze lasting 8 hours during flowering on March 15, 2018 may have reduced pod set and seed fill in Year 1. The number of growing degree days (GDD) accumulated over the growing season in Year 1 (3405 GDD) was 13% greater than Year 2 (2955 GDD), primarily due to the longer growing season in Year 1.

Plant stands at the first measurement date were similar between cultivars in each of the 2 years (93 and 87 plants m^{-2} in Years 1 and 2, respectively). Across cultivars, stands declined by 20.5% (74 plants m^{-2}) and 51.4% (43 plants m^{-2}) at the end of the growing season in Years 1 and 2, respectively.

3.2 | Total dry matter (TDM) accumulation

The two cultivars (Avanza 641 and AX17012) followed similar sigmoidal pattern of growth when expressed on a cumulative thermal time basis, with a slow rate of increase, followed by an exponential increase ending with a decrease in the rate of TDM accumulation in both years of the study (Figure 2). Modeled TDM over time reached a maximum at GS 9.9 in both years. Avanza 641 and AX17012 accumulated 10826 and 9343 kg TDM ha⁻¹ in Year 1 and 9655 and 10642 kg TDM ha⁻¹ in Year 2, respectively, at harvest maturity. A similar TDM (9800 kg TDM ha⁻¹) was reported for carinata cultivar 110994EM grown in north Florida (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019).

The longer growing season in Year 1 (170 days, 3405 GDD) favored Avanza 641 which accumulated 16% greater TDM, whereas the shorter growing season in Year 2 (132 days, 2955 GDD) favored AX17012, which accumulated 10% greater TDM (Figure 2), although the GDD required to accumulate 50% of total seasonal DM was similar between cultivars averaging 1772 and 1578 GDD in Years 1 and 2, respectively. The average TDM accumulation rate represented as the reciprocal to t_{50} was 5.64^{E-04} in Year 1 and 6.34^{E-04} in Year 2. Maximum TDM increase in Year 1,

144%, occurred from stem elongation (GS 3.1) to flowering (GS 6), accumulating 174 kg TDM $ha^{-1} day^{-1}$ during this period. However, in Year 2, maximum TDM increase occurred during the vegetative stage from GS 1.4 to 1.7, accumulating 51 kg TDM $ha^{-1} day^{-1}$. In both years, the increase in TDM resulted primarily from significant increases in the stem fraction (250% and 950% in Years 1 and 2, respectively). The stem fraction was the major contributor to TDM for both cultivars across years reaching a maximum at GS 7.1. Silique walls contributed to TDM starting from GS 7.2 while seeds contributed to TDM at GS 8.5 onwards. Silique walls along with seeds comprised more than 50% of the TDM at the time of harvest (Figure 2) showing similar trends as B. rapa (rapa) where dry matter accumulation increased until pod development stage and declined thereafter (Barłóg & Grzebisz, 2004). During the vegetative growth stage, the source/sink ratio is high, and the accumulation of dry matter occurs primarily in leaves, stems, and root tissues of the plant. This trend changes during the reproductive stage when the source/ sink ratio decreases, leading to leaf senescence and mobilization of biomass from vegetative tissues to pods as observed in rapa (Jullien et al., 2009).

3.3 | Dry matter (DM) allocation

Although there was a similar TDM accumulation trend, the relative allocation of DM to plant organs differed between cultivars and years. The contribution of leaf and stem mass fractions to TDM decreased at GS 8.5 in Year 1 and GS 7.2 in Year 2 for both the cultivars (Figure 2), indicating simultaneous leaf abscission and translocation of assimilates from vegetative tissues to siliques for pod development (Jullien et al., 2009). Maximum leaf mass fraction (LMF) was similar between cultivars and years with 84% LMF at GS 1.2–1.4 followed by a gradual decline over the season until complete leaf abscission at GS 9.7 and 8.0 for Avanza 641 and AX17012, respectively. Avanza 641 mean stem mass

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FIGURE 2 Total aboveground dry matter accumulation and relative allocation of aboveground dry matter to stems, leaves, silique walls, and seeds of two carinata cultivars during the 2017–2018 (a and b) and 2018–2019 (c and d) winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

fraction (SMF) differed between years, increasing from 18% (GS 1.2) to 83% (GS 7.2) and subsequently declining to 55% (GS 9.9) in Year 1 while in Year 2, SMF increased from 20% (GS 1.4) to 86% (GS 6.7) and gradually declined to 50% (GS 9.9). Stem mass fraction for AX17012 was similar between years, increasing from 16% (GS 1.2–1.4) to 80% (GS 6.7–7.1) and declining to 41% (GS 9.9). Oilseed crops generally attain maximum growth rate at anthesis, and the TDM produced till this stage is mobilized to support pod development (Barłóg & Grzebisz, 2004; Major et al., 1978). A linear relationship between the aboveground TDM accumulation at anthesis and its translocation to seeds during the reproductive stage in safflower (*Carthamus tinctorius* L.) was observed,

contributing 65%–92% of total seed weight (Koutroubas et al., 2004). Mean silique mass fraction (SiMF = silique wall + seed mass) increased from 10% at GS 7.2 to 52% at GS 9.9 in Year 1 and from 4% at GS 7.1 to 57% at GS 9.9 in Year 2. Mean seed fraction (SdMF) was similar between cultivars but differed between years, increasing from 2% (GS 8.5) to 26% (GS 9.9) in Year 1 and from 1% (GS 7.2) to 20% (GS 9.9) in Year 2. Seed yield (SY) extrapolated from the whole plot harvested at the end of the season was similar between cultivars but differed between years. Mean SY in Year 1 (2732 kg ha⁻¹) was 29% greater than Year 2 (1929 kg ha⁻¹). Carinata self-defoliates with the initiation of leaf abscission at the onset of flowering and continues until

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100% leaf abscission at seed maturity. The decline in the leaf mass fraction is associated with a concomitant increase in the stem, and reproductive fractions as assimilates are translocated from the leaves to the metabolic sinks. The decline in post-anthesis TDM accumulation is mainly due to defoliation, leaf shading by pod development, and leaf senescence (Gabrielle et al., 1998). Although pods can photosynthesize actively (Müller & Diepenbrock, 2006), pod photosynthesis cannot compensate for the decreased TDM accumulation (Diepenbrock, 2000). Contrary trends were observed in *B. napus*, where leaves contribute 37% of assimilates to the developing seed, whereas pod walls and stems contribute 32% and 31%, respectively (Brar & Thies, 1977).

3.4 | Morphology and physiology of carinata

Plant height (PH) and mainstem node numbers (MNN) of both cultivars followed a similar sigmoidal growth pattern

in both years of the study: however, the height differed in Year 1 only, with Avanza 641 being 21% taller and having 11% greater MNN than AX17012 (Figure 3). Plant height and MNN were similar from GS 1.4 to 6.0 but differed at later growth stages in Year 1 between the cultivars but were similar at all GS in Year 2. The maximum PH and MNN for Avanza 641 were 125 cm and 20.3 nodes, and 108 cm and 17.3 nodes for AX17012 in Year 1. The two cultivars averaged 134 cm and 18.8 nodes in Year 2. Plant height increased by 7% and 19% for Avanza 641 and AX17012, respectively, in Year 2 compared to Year 1, demonstrating consistent growth across years in different environmental conditions. Primary (PB) and secondary branch (SB) numbers were similar in both cultivars at all GS (Figure 4). Maximum PB (14.8) occurred at 1372 GDD or GS 6.7 followed by a gradual decline to 8 at GS 9.9 (Figure 4). As PB numbers declined, SB increased from 0.5 at GS 6.7 to 18.5 at harvest maturity. Secondary branch numbers were positively correlated with seed yield (r = 0.64, p = < 0.0001;



FIGURE 3 Plant height (a and b), mainstem node numbers (c and d), and leaf area index (e and f) at different growth stages and cumulative growing degree days base of two carinata cultivars during the 2017–2018 and 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

FIGURE 4 Primary and secondary branch numbers of two carinata cultivars at different growth stages and cumulative growing degree days base during the 2018– 2019 winter–spring growing season at North Florida Research and Education Center, Quincy, FL



Table 3). Seed yield was positively correlated with stem mass fraction (r = 0.91, p = <0.0001) and pod mass fraction (r = 0.88, p = <0.0001) but negatively correlated with leaf mass fraction (r = -0.45, p = <0.0001; Table 3). The stem mass fraction positively correlated with primary branches (r = 0.80, p = < 0.0001). Total aboveground dry matter accumulation was positively correlated with seed yield $(r = 0.72, p = \langle 0.0001; \text{ Table 3})$ similar to an earlier report by Seepaul, Marois, et al. (2019) and Seepaul, Small, et al. (2019), indicating that high DM accumulation at all phenostages is key to optimizing oilseed yield components and seed yield. Growth involves the production of shoot apical meristem, nodes, internodes, leaves, axillary meristems, and branches that form the plant's aerial architecture. Carinata primary stem bears around 17–20 leaf nodes, with 75%–88% of the axillary meristems producing primary branches and later secondary branches. All reproductive branches terminate in an unbranched raceme inflorescence that flowers acropetally. The leaf size and orientation, and branching patterns are important morphological traits in plant architecture that may influence radiation interception, canopy photosynthesis, and yield (Chongo & McVetty, 2001; Diepenbrock, 2000; Singh & Singh, 1983). Agronomic factors that regulate leaf and branching patterns (planting date, tillage, seeding rate, row spacing, and nutrient management) are also known to affect seed yield in carinata (Mulvaney et al., 2019). Parameters such as leaf area, leaf weight ratio, and leaf area ratio provide an estimate of photosynthetic area per unit biomass (Horak & Loughin, 2000). The interception of photosynthetically active radiation by plants is determined by its leaf area index (LAI), canopy architecture, and physiological capacity, which, in turn, determines the overall growth and productivity of the crop (Ewert, 2004; Tripathi

et al., 2018). A linear relationship that exists between LAI, leaf area duration, and biomass production has been found in different crops, including oilseed rape (Larson & Isebrands, 1972; Liu et al., 2012; Stockle & Kiniry, 1990). The leaf area per unit ground surface area or leaf area index (LAI) differed between cultivars and years in the current study (Figure 3). Maximum LAI (MLAI) for Avanza 641 occurred at GS 7.1 (3.3) and 6.0 (2.9) in Years 1 and 2, respectively. MLAI for AX17012 was at GS 6.0 in both years (2.2 in Year 1 and 2.1 in Year 2). LAI sharply declined to 0 from peak LAI at GS 9.5 in Year 1 and GS 8.5 in Year 2. Avanza 641 exhibited 22% and 36% greater LAI than AX17012 in Years 1 and 2, respectively. Specific leaf area was similar between varieties at all growth stages in both years, except at GS 1.7, 5.1, 7.1, and 8.9 in Year 2 (Figure 5a,b). Over the growing season. SLA increased from 156 to 229 $\text{cm}^2 \text{ g}^{-1}$ in Year 1 but decreased from 280 to 194 cm² g⁻¹ in Year 2. Greater SLA values indicate greater leaf surface area per unit biomass produced, affecting canopy light interception and light use efficiency. The leaf weight ratio (LWR) of both varieties decreased linearly (Figure 5c,d) over time in both years as the plants partitioned more DM to the stems and reproductive structures. Leaf weight ratio decreased from 0.84 to 0 g g^{-1} in Year 1 and from 0.82 to 0 g g^{-1} in Year 2. Specific leaf area is responsive to environmental changes and therefore has greater variability than LWR. Leaf area ratio (LAR) was similar between varieties but differed between years. In Year 1, LAR increased from 130 to 183 cm² g⁻¹, and subsequently declined to 0. In Year 2, maximum LAR occurred at GS 1.4 (230 cm² g⁻¹) and gradually declined to 0 at GS 9.9 (Figure 5e,f).

In oilseed crops, including brassicas, one of the primary sources of photosynthesis in the later growth stages is pods,

TABLE Center, Q	3 Corr uincy, FL	relation a	nalyses of	.B. carina.	<i>ta</i> traits f	or two v	'arieties	produce	d during t	he 2017	'-2018 aı	nd 2018-	-2019 w	inter-sp	ring gro	wing sea	asons at]	Vorth Fl	orida Res	earch ar	ıd Educa	ation	
Trait	Height	Node	Pribran	Secbran	TDM	LMF	SMF	PMF	SdMF H	П	L AI A	eaf rea L	AI L.	AR L	WR J	AD S	ILA	SLW	AGR N	IAR I	RGR (CGR T	Ч
Node	0.95	-																					
Pribran	0.72	0.80	1																				
Secbran	0.85	0.74	0.49	1																			
TDM	06.0	0.83	0.58	0.92	1																		
LMF	0.15	0.32	0.41	-0.32	-0.03	1																	
SMF	0.89	0.86	0.80	0.82	0.91	0.23	1																
PMF	0.70	0.58	0.23	0.83	0.88	-0.40	0.61	1															
SdMF	0.55	0.44	0.15	0.64	0.72	-0.45	0.52	0.82	-														
IH	0.58	0.45	0.15	0.64	0.72	-0.47	0.52	0.82	0.99 1														
PAI	0.70	0.61			0.84	-0.32	0.66	0.92	0.80 0	82 1													
Leaf Area	0.23	0.41	0.53	-0.01	0.01	0.83	0.28	-0.36	-0.46 -	0.47 –	-0.28 1												
LAI	0.15	0.34	0.50	-0.22	-0.06	0.94	0.23	-0.44	-0.47 -	0.49 -	-0.37 0.	92 1											
LAR	-0.90	-0.86	-0.66	-0.76	-0.88	-0.10	-0.84	-0.72	-0.56 -	0.59 -	- 77.0-	0.13 -	0.05 1										
LWR	-0.93	-0.94	-0.68	-0.81	-0.88	-0.15	-0.86	-0.70	-0.54 -	0.57 -	-0.73 -	0.25 -	0.17 0.	91 1									
LAD	0.36	0.55	0.75	0.20	0.25	0.66	0.50	-0.08	-0.28 -	0.29 0	.35 0.	74 0.	99 –).35 –	0.40								
SLA	0.06	0.16	0.00	-0.14	-0.06	0.12	0.04	-0.18	-0.20 -	0.19 0	.05 0.	43 0.	41 0.		0.20 (0.20	1						
SLW	-0.12	-0.20	-0.08	0.09	-0.02	-0.15	-0.11	0.12	0.15 0	.14 –	-0.10 -	0.42 -	0.40 –(0.17 0.	- 22	-0.20	-0.89	1					
AGR	0.37	0.48	0.72	0.44	0.05	0.66	0.18	-0.15	-0.23 -	0.23 -	-0.39 0.	64 0.	- (99).12 –	0.24 (.39	0.34	-0.36	_				
NAR	0.48	0.38	0.14	0.45	0.61	-0.14	0.51	0.60	0.56 0	51 0	- 87	- 60.0	0.15 –(- 64.0	0.49 (. 20	-0.19	0.26	0.15 1				
RGR	-0.71	-0.60	-0.71	-0.92	-0.76	0.38	-0.67	-0.72	-0.66 -	0.68 -	-0.80 0.	28 0.	38 0.	70 0.	- 54	-0.19	0.45	-0.51	- 111 -	-0.13 1			
CGR	0.48	0.54	0.37	0.26	0.52	0.25	0.57	0.36	0.04 -	0.02 0	.63 0.	28 0.	23 –(- 84.0	0.49 (. 64	-0.11	0.12	0.21 0	- 62	-0.19 1		
TP	0.38	0.67	0.08	-0.16	0.33	0.00	0.74	-0.42	- 0.07	0.34 0	. 69.	0.	. 00	•).38 .			-0.16 .	'	-0.25 (.22 1	
DME	-0.26	-0.53	-0.16	0.14	-0.05	0.00	-0.50	0.56	0.29 0	41 -	-0.43 .	0.	. 00	•		-0.43 .			0.42 .		- 11	-0.41 -	-0.6
Abbreviatio ratio; NAR branches; S	ons: AGR, , net assim LA, specif	absolute g ilation rate ïc leaf are:	rowth rate; ?; node, nun a; SLW, spe	CGR, crop nber of maii scific leaf w	growth ra nstem nod 'eight; SN	tte; DME les; PMF, IF, stem 1	, fry matt pod mas nass fract	er efficier s fraction ion; TDM	cy; HI, hai ; pod LAI, 1, total abo	vest inde PAI, pod veground	ex; LAD, l l area inde d dry matt	leaf area (:x; pribrai er; TP, tr	luration;] 1, primary anslocatic	LAI, leaf branche	area ind s; RGR, tage.	ex; LAR, relative g	leaf area 1 rowth rate	atio; LM ; SdMF,	∃, leaf mas seed mass :	ss fraction; fraction;	n; LWR, secbran,	leaf weig secondar	y ht



FIGURE 5 Specific leaf area (a and b), leaf weight ratio (c and d), and leaf area ratio (e and f) of two carinata cultivars at different growth stages and cumulative growing degree days base during the 2017–2018 and 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

which contains chloroplasts located in the outer pod wall layer and are responsible for 70–100% of assimilation in seeds (Bennett et al., 2011; Raven & Griffiths, 2015). Seed weight and size are very important attributes of plant fitness and yield. Pod area index (PAI) in the current study did not differ between the cultivars and increased linearly from GS 7.1 to 9.9 (y = 0.002x - 2.72, $r^2 = 0.88$; Figure 6).

Maximum leaf area duration (MLAD) of both cultivars occurred from bolting/flowering to pod development stage (64 days) in Year 1 (Figure 7a.i). In Year 1, Avanza 641 maintained its canopy for 10 days longer than AX17012 while in Year 2, MLAD occurred earlier at the vegetative to bolting/ flowering stage, with Avanza 641 maintaining its photosynthetic canopy for 6.7 days longer than AX17012 (Figure 7a. ii). Net assimilation rate (NAR), the increase in plant dry matter per unit leaf dry weight, and unit time increased with plant maturity, reaching a maximum at the pod development stage in both years (Figure 7b.i,ii). The increase in NAR in initial stages can be attributed to an increase in leaf number and leaf area, which helps capture more CO₂ and thus enhances the photo-assimilation rate. Net assimilation rate increased in both cultivars through the pod development stage, emphasizing pods' role in photosynthesis during the later growth stages. In addition, the increased day length, availability of solar radiation, and warmer temperatures during pod development may also enhance photosynthesis. Net assimilation rate was similar between the cultivars during the earlier growth stages in both years; however, during the pod development stage, AX17012 recorded 55% and 85% greater NAR in Years 1 and 2, respectively.

The relative growth rate (RGR), the rate of accumulation of new dry weight per unit of existing dry weight, of Avanza 641 was greater than AX17012 at vegetative and bolting/flowering stages but not at the pod development stage in Year 1; however, both cultivars had similar RGR at all growth stages in Year 2 (Figure 7ci,ii). RGR in most crops is highest in the beginning of the crop cycle and decreases gradually with leaf senescence and maturity. Similarly, maximum RGR in carinata occurred at bolting/flowering and vegetative stages in Years 1 and 2, respectively. The absolute growth rate (AGR), which represents the increase in height per unit of time, was similar between cultivars at all growth stages except at pod development in Year 1 and senescence in Year 2 (Figure 7d.i,ii). Mean maximum AGR occurred at bolting/flowering in Year 1 (2.5 cm day⁻¹) and Year 2 (2.2 cm day⁻¹). Crop growth rate (CGR), increase in aboveground dry matter per unit ground area per unit time, increased from vegetative to pod development for both cultivars in Year 1 (Figure 7e.i,ii). In Year 1, Avanza 641 accumulated 16 and 48% greater DM than AX17012 at the pod development and senescence stages, respectively. AX17012 reached maximum CGR at the pod development stage in Year 2, whereas Avanza 641 reached peak CGR at the bolting/flowering stage. Harvest index (HI), ratio of seed to total aboveground dry matter, was similar between cultivars but differed by year, increasing from 1.6 and 12.1 at the pod development stage to 25.1 and 19.7 at senescence in Years 1 and 2, respectively (Figure 7f.i,ii). Avanza 641 translocated 86 and 66% of photo-assimilates from the biomass to the seed from flowering to harvest in Years 1 and 2, respectively, whereas AX17012 translocated a mean of 46%



FIGURE 6 Pod area index of two carinata cultivars at different growth stages and cumulative growing degree days base during the 2018–2019 winter–spring growing season at North Florida Research and Education Center, Quincy, FL



FIGURE 7 Leaf area duration (a.i and a.ii), net assimilation rate (b.i and b.ii), relative growth rate (c.i and c.ii), absolute growth rate (d.i and d.ii), crop growth rate (e.i and e.ii), and harvest index (f.i and f.ii) of two carinata cultivars at different growth stages during the 2017–2018 and 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL



FIGURE 8 Translocation percentage (a) and dry matter efficiency (b) of two carinata cultivars during the 2017–2018 and 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

in both years (Figure 8a), suggesting that silique walls contribute significant quantities of photosynthates. Avanza 641 was 27 percentage points more efficient than AX17012 at translocating assimilates. Although the translocation percentage (TP) varied between the seasons and cultivars, the dry matter accumulated, measured as dry matter efficiency (DME) in the seed from the total dry matter produced over the crop growth period, was similar between cultivars in both years with an average of 20% of TDM accumulated in the seed over the growing season (Figure 8b).

3.5 | Nutrient uptake in plant parts

The optimal availability of highly mobile nutrients such as nitrogen during the season can delay the transition to bolting and flowering and therefore prolong the translocation of N from vegetative to the reproductive tissues resulting in increased leaf duration, photosynthesis, and seed yield. Understanding seasonal nutrient uptake patterns is essential to optimized scheduling of nutrient application to increase nutrient use efficiency. The seasonal nutrient uptake trends were similar between cultivars but differed between years; hence, the data were pooled by variety and analyzed by year.

Maximum N uptake (89.4 kg ha⁻¹) occurred at GS 7.2 (1825 GDD) with 31%, 50%, and 19% uptake in leaves,

stems, and pods, respectively, in Year 1 (Figure 9a). In Year 2, the maximum N uptake (94.6 kg ha^{-1}) also occurred at GS 7.2 (2071 GDD); however, the contribution from leaves, stems, and pods were 13%, 19%, and 68% (Figure 10a). Peak N uptake in leaves, stems, and pods occurred at GS 7.1, 7.1, and 9.7 in Year 1 (Figure 9a) and GS 6.7, 6.7, and 8.9 in Year 2 (Figure 10a). As a percent of total N uptake, maximum seasonal uptake in leaves (87%-97%), stems (55%-64%), and pods (75%-77%) occurred in early (GS 1.2-1.4), mid (6.7-7.1), and late season (9.7–9.9), respectively, in both years.

Phosphorus uptake was maximum at GS 7.2 in both years $(19.4 \text{ kg ha}^{-1})$ in Year 1 (Figure 9b) and in Year 2 (12 kg ha^{-1}) (Figure 10b) with 71% uptake in stems in Year 1 and 70% uptake in pods in Year 2 at GS 7.2. Peak P uptake in leaves, stems, and pods occurred at GS 7.1, 7.2, and 9.7 in Year 1 (Figure 9b) and GS 6.7, 6.7, and 7.2 in Year 2 (Figure 10b). Similar to N uptake, maximum seasonal P uptake in leaves (100%), stems (73-76%), and pods (82%-86%) occurred in early (GS 1.2-1.4), mid (GS 6.7-7.1), and late season (GS 9.9), respectively, in both years.

Potassium uptake was greatest at GS 9.7 (130.9 kg ha⁻¹) and 8.9 (222.4 kg ha⁻¹) in Years 1 (Figure 9c) and 2 (Figure 10c) with 54% and 45% uptake in pods and stems in both years. Maximum seasonal K uptake in leaves (86%-96%), stems (73%-82%), and pods (54%-64%) occurred in early (GS 1.2-1.4), mid (GS 6.7-7.1), and late season (GS 9.7-9.9), respectively, in both years.

Magnesium, calcium, sulfur, boron, copper, and zinc uptake were greatest at GS 9.7 and 8.9 in Years 1 and 2, respectively (Figures 9d-k and 10d-k). Manganese uptake was greatest at GS 7.2 in both years, whereas iron uptake was greatest at GS 9.9 and 8.9 in Years 1 and 2. Pods accounted for 50%-82% uptake while 18%-50% uptake occurred in stems. Maximum seasonal uptake for Mg, Ca, S, B, Zn, Mn, Fe, and Cu in leaves, stems, and pods generally occurred in the early (GS 1.2-1.4), mid (GS 6.7-7.1), and late season (GS 9.9) in both years.

Uptake patterns in the current study differ from previous findings (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019) where maximum N uptake occurred between 50% bolting and 50% flowering while maximum P, K, Ca, Mg, S, B, Mn, Fe, Zn, and Cu uptake occurred between 50% flowering and pod formation. In the current study, maximum N, P, and Mn uptake occurred during pod development while the K, Ca, Mg, S, B, Fe, Zn, and Cu uptake occurred closer to physiological maturity or later. These differences in uptake patterns may be related to the interannual variability in ecoedaphic conditions that influence root morphology, root-shoot relations, translocation, and redistribution of nutrients from roots to shoots as well as soil-root interactions (Seepaul, Bliss, et al., 2016; Seepaul, George, et al., 2016).

Improving the uptake, assimilation, and utilization of applied nutrients is crucial to the agronomic, environmental,

and economic competitiveness and commercial success of carinata (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019). The identification of growth stages associated with maximum nutrient uptake may aid in synchronizing the time of nutrient application with critical growth stages corresponding to maximum nutrient uptake (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019) to optimize nutrient use while minimizing nutrient loss to the environment. Similar to previous findings, nutrient application, specifically N, should be synchronized with maximum nutrient uptake; therefore, providing adequate N during this period should be a key goal of nutrient management (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019). In the current study, maximum nutrient uptake occurred during pod development or closer to physiological maturity. Maximum nutrient uptake was closely related to biomass production and occurred at these growth stages primarily due to the increases in reproductive structures. To increase the uptake and utilization efficiency of applied fertilizers especially in soils where the leaching potential is high, fertilizer applications should be informed by the 4 R Nutrient Stewardship Framework. Therefore, the rate of fertilizer application should be informed by the quantification of the crop's nutrient requirements timed with crop growth stages with maximum uptake and the nutrient supplying capacity of the soil as determined by soil tests.

3.6 Seed nutrient uptake

The relative nutrient removal rates differed between cultivars and years. Avanza 641 removed greater quantities of all nutrients than AX17012 except for N, K, and S in Year 1 and K and S in Year 2 (Table 4). Mean nutrient removal quantities ranked in descending order: N>S>P=K>Ca>Mg>Fe>Zn>Mn>B>Cu. Similar to aboveground tissue nutrient uptake, seed nutrient uptake was positively correlated with seed nutrient concentration (r ranged from 0.80 to 0.98). Accumulation of nutrients in the seed is derived from the mobilization and translocation of nutrients stored in the shoot rather than uptake from the soil pool. In B. napus, more than 48% of the N taken up by the plant is translocated to the pods during seed development (Rossato et al., 2001). Nutrient uptake was also affected by the longer season in Year 1 in comparison with Year 2. The average nutrient uptake of N, P, K, Mg, Ca, and S was 25.3, 5.6, 5.85, 2.25, 3.2, and 7.1 kg ha⁻¹, respectively, greater in Year 1 between cultivars in comparison to Year 2 (Table 4), although the rate in Year 1 was lower than Year 2. This emphasizes that a longer growing season helps in better nutrient utilization during the season. Also, higher N uptake results in higher LAI (Rathke et al., 2006) evident in Year 1, leading to an extended period of photosynthetic activity.



FIGURE 9 Mean total aboveground N, P, K, Mg, Ca, S, B, Zn, Mn, Fe, and Cu (a through k) accumulation at different growth stages and cumulative growing degree days base during the 2017–2018 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL



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FIGURE 10 Mean total aboveground N, P, K, Mg, Ca, S, B, Zn, Mn, Fe, and Cu (a through k) accumulation at different growth stages and cumulative growing degree days base during the 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

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TABLE 4 Nutrient concentration and uptake of two carinata cultivars during the 2017–2018 and 2018–2019 winter–spring growing seasons at North Florida Research and Education Center, Quincy, FL

	2018				2019			
	Concentratio	n ^a	Uptake ^b		Concentratio	n	Uptake	
Element	Avanza 641	AX17012	Avanza 641	AX17012	Avanza 641	AX17012	Avanza 641	AX17012
Nitrogen	3.5	3.9	94.5	95.8	3.4	4.0	73.6	66.1
Phosphorous	0.8	0.7	23.0	17.6	0.8	0.7	17.8	11.6
Potassium	0.7	0.9	18.0	22.1	0.6	1.0	13.3	16.0
Magnesium	0.4	0.3	9.9	8.1	0.4	0.3	7.8	5.7
Calcium	0.5	0.4	14.3	8.8	0.5	0.4	10.7	5.9
Sulfur	0.8	1.0	22.1	25.3	0.8	1.0	16.4	16.8
Boron	10.5	11.0	28.6	27.2	10.0	11.0	21.7	18.3
Zinc	39.3	41.5	107.3	103.0	39.0	40.8	84.7	68.0
Manganese	27.3	27.5	74.4	67.9	27.5	27.0	59.7	45.1
Iron	71.5	64.5	195.3	161.5	70.5	63.3	152.7	106.0
Copper	3.0	2.8	8.2	6.8	2.8	2.8	5.9	4.6

a^bN, P, K, Mg, Ca, and S concentrations and uptake are in % and kg per ha, whereas B, Zn, Mn, Fe, and Cu concentrations and uptake are in ppm and g per ha.

3.7 | Temporal change in seed chemical composition

Seed development is a complex process of cell division, histodifferentiation, cell expansion, reserve deposition, and dehydration that combines genetic, metabolic, physiological pathways, and environmental cues. The seed undergoes morphological, physiological, chemical, and functional changes from fertilization to harvest maturity. The magnitude of these changes is moderated by water deficits, high or low temperatures, nutrient deficiency, and shading. The stage of seed development at harvest can influence carinata yield and seed quality, similar to B. napus (Elias & Copeland, 2001). Maximum seed quality usually occurs at the end of the seed filling stage, described as physiological maturity. Carinata seed weight increased with plant maturity in both years, increasing by 7.0 (Year 1) and 1.47 mg GDD^{-1} (Year 2) from initial seed development to harvest maturity (Table 5). Photo-assimilates are translocated from source tissue (leaves, stems, and pods) to the developing seed, followed by protein and triacylglycerol synthesis and deposition of stored reserves (Bewley et al., 2013). Oil content increased with maturity in both years, whereas protein content decreased with crop age (Table 5). Monounsaturated fatty acids, C183, C201, and C221 concentrations also increased with plant maturity, whereas polyunsaturated fatty acids, saturated fatty acids, C181, and C182 concentrations decreased with plant maturity (Table 5). The variation in seed constituents may be related to the seasonal variation in temperature and precipitation during flowering, pod set, and seed development stages (Seepaul et al., 2018).

4 | SUMMARY AND CONCLUSION

Physiological processes play an important role in variation in yield and selection of varieties for various crop improvement programs. Quantitative analysis of these processes is required for biological and economical yield enhancement in the crop. Biological yield is the total biomass of the crop, that is, economic yield × harvest index while economic yield is the economically useful part of the plant. Biological yield is the product of growth rate and duration of vegetative period and determines the economical yield (Diepenbrock, 2000). Measurement of different growth-related aspects of plants' life cycle such as leaf area, plant height, relative growth rate, net assimilation rate, LAI, and management practices during the growing season provides an estimate of overall plant growth. In the current analysis, Avanza 641 showed higher accumulation of TDM (16%) in Year 1 due to longer growing season (GDD 3405) while shorter growing season in Year 2 (GDD 2955) favored AX17012 which showed higher TDM accumulation (10%) in comparison to Avanza 641. The contribution of vegetative parts such as leaves and stem toward TDM accumulation was higher in initial growth stages of carinata's life cycle which was overtaken by reproductive parts such as silique wall and seeds in the later stages showing similar trends in both the cultivars. Higher TDM accumulation during different growth stages is known to directly impact post-harvest traits such as seed yield and oil content in carinata (Seepaul, Marois, et al., 2019; Seepaul, Small, et al., 2019), which is also evident in the current analysis. The GDD value for Year 1 was 13% higher in comparison to Year 2 which also impacted the yield of the cultivars. The average yield of carinata cultivars

TABLE 5 Mei Research and Educ	an Temporal ation Center	1000-seed we , Quincy, FL	sight, oil conte	ent, fatty a	icids, and oil c	composition o	f carinata se	ed during the	2017–2018 a	nd 2018–2019) winter-spring	growing seaso	ns at Nor	h Florida
Growth stage	1000 SW	Oil	Protein	GSL	ONOM	POLY	LCFA	VLCFA	SATS	C181	C182	C183	C201	C221
2018														
8.5	$2.2 c^{a}$	34.0 c	26.4 a	61.7 a	56.0 с	37.7 a	43.3 a	56.7 b	10.0 a	18.2 a	26.5 a	9.0 d	3.1 d	27.6 a
9.5	3.0 b	44.3 b	23.4 b	57.9 ab	62.7 b	33.6 b	32.0 b	68.0 a	7.9 b	14.7 b	21.6 b	10.4 c	5.0 c	32.6 b
9.7	4.3 a	50.7 a	21.9 bc	51.7 bc	64.2 b	32.4 c	31.1 b	68.9 a	5.6 c	8.0 c	13.1 c	16.7 a	6.2 b	50.1 с
9.6	4.5 a	50.0 a	21.6 c	46.5 c	62.4 a	32.3 c	42.4 a	57.6 b	5.8 с	3.1 d	13.4 c	15.2 b	7.9 a	44.9 d
OPC^{b}	L^{***}, Q^{*}	L***,Q***	L^{***}, Q^{**}	L^{***}	L***,Q***	L^{***}, Q^{***}	L**,Q***	L**,Q***	L***,Q***	L***,Q***	L***,Q***	L***,Q***	L^{***}	L***,Q***
LSD	0.4	1.7	1.6	9.0	1.3	0.8	2.5	2.5	0.4	2.0	1.3	0.9	0.7	2.8
2019														
7.2	2.4 c	36.0 c	25.3 a	33.8 c	59.9 с	34.7 a	33.5 a	66.5 b	10.2 a	17.2 a	26.8 a	7.5 с	1.3 c	27.0 c
8.9	3.1 b	42.9 b	24.1 b	51.1 b	64.6 a	31.6 b	22.8 b	77.2 a	8.5 b	11.4 b	20.9 b	10.8 b	2.3 b	37.7 b
9.9	3.7 а	47.2 a	23.6 b	61.2 a	62.4 b	32.6 b	37.6 a	62.4 b	5.8 с	6.2 c	14.4 c	14.7 a	7.9 a	46.0 a
LSD	0.3	2.9	1.6	8.6	1.7	1.1	4.9	4.9	1.0	3.1	2.7	1.7	0.5	4.8
^a Within column, mea	ns followed by	v the same lower	rcase letters are	not differe.	int $(p > 0.05)$ us:	ing PDIFF optic	on in PROC N	AIXED.						

^bOPC, orthogonal polynomial contrasts (L, linear; Q, quadratic).

** and *** represent linear (L) and quadratic (Q) significant at 0.01 and 0.001 levels, respectively.

in Year 1 was 42% higher in comparison to Year 2 while the overall oil content was 13% higher in Year 1 than Year 2. A simulation study conducted by Habekotté (1997) also revealed delayed maturity to be the most important factor for obtaining higher seed yield in oilseed rape, demonstrating the importance of growth duration in oilseed crops. Plant density is another factor that determines different components of plant growth such as primary and secondary branching, number of pods, and, in turn, seed yield of individual plants and overall yield (Diepenbrock, 2000). The average early season stand count for cultivars was 92.7 and 80 plants per m^2 in Year 1 and Year 2, respectively, which decreased to 78.5 and 42.5 plants per m² in Year 1 and Year 2, respectively, at the end of the season showing variation in seed yield in two seasons. Seed nutrient uptake value for the cultivars was also affected by a longer season in Year 1 in comparison with Year 2. The average nutrient uptake of N, P, K, Mg, Ca, and S was 25.3, 5.6, 5.85, 2.25, 3.2, and 7.1 kg per ha greater in Year 1 between cultivars in comparison to Year 2, although the rate of application of nutrients in Year 1 was lower than Year 2. This fact emphasizes that a more extended growing season helps in better nutrient utilization during the season. Also, higher N uptake results in higher LAI (Rathke et al., 2006) evident in Year 1, leading to extended period of photosynthetic activity. Crop simulation models have been used widely for different crops including napus which helps in determination of crop response to various factors such as weather, soil, crop management practices, and genetic characteristics. Growth analysis of different aspects of the carinata's life cycle can help develop a similar crop simulation model for carinata which will help identify factors governing crop yield and productivity.

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AUTHORS' CONTRIBUTIONS

R.S. and S.K. planned and designed the research. R.S. and S.K. wrote the manuscript. R.S. and S.K. made the figures and tables. R.S., S.K., K.J.B, I.M.S., S.G., and D.L.W. reviewed and edited the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Ramdeo Seepaul https://orcid.org/0000-0001-6246-0385 Shivendra Kumar https://orcid.org/0000-0002-2192-2069 Kenneth J. Boote https://orcid.org/0000-0002-1358-5496 Ian M. Small https://orcid.org/0000-0001-5406-3486 Sheeja George https://orcid.org/0000-0001-9046-683X David L. Wright https://orcid.org/0000-0003-1574-9738

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