Brassica carinata: Biology and agronomy as a biofuel crop

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Abstract
The environmental consequences of using nonrenewable fossil fuels have motivated a global quest for sustainable alternatives from renewable sources. Carinata has been developed as a low carbon intensity, non-food oilseed biomolecular platform to produce advanced drop-in renewable fuels, meal, and co-products. The crop is widely adaptable to grow in the humid subtropical and humid continental climatic regions of Asia, Africa, North America, South America, Europe, and Australia as a spring or winter crop. Carinata is heat tolerant, resistant to diseases and seed shattering with lower water-use requirements than other oilseed brassicas. Adopting carinata in double-cropping systems would require continuing research to integrate crop biology with agronomy, to understand growth and development and its interaction with agricultural inputs and management. Site-specific best management agronomic practices and crop improvement research to develop frost-tolerant, early-maturing, nutrient use-efficient, and high yielding varieties with desirable oil content and fatty acid profile will enhance the crop’s adaptability and economic viability. The exploitation of intra- and interspecific and intra- and intergeneric diversity will further enhance carinata productivity and resistance to biotic and abiotic stresses. This review attempts to present a comprehensive description of carinata's biology, beginning with its origin and current state of distribution, availability of genetic and genomic resources, and a discussion of its morphology, phenology, and reproduction. A detailed analysis of the agronomy of the crop, including planting and germination and management practices, is presented in the context of crop growth and development. This will facilitate global adoption, sustainable production, and commercialization of carinata as a dedicated biofuel oilseed crop in diverse cropping systems and growing regions of the world, including the Southeast United States.

KEYWORDS
biofuels, biomass, carinata, germplasm resources, oilseed, photosynthesis, renewable, vegetative traits
1 | INTRODUCTION

Brassica carinata A. Braun, commonly referred to as “Ethiopian mustard,” “Ethiopian rape,” “Abyssinian mustard,” or “carinata,” is being developed as a low carbon intensity, non-food oilseed feedstock to produce advanced drop-in renewable fuels, protein-rich meal, and bio-products. It exhibits a desirable oil profile, wide adaptability, and productivity under suboptimal conditions (Blackshaw et al., 2011; Cardone et al., 2002; Gesch et al., 2015). Production of carinata as a winter crop presents a unique opportunity for growers in the Southeast United States to produce a significant amount of biofuel feedstock to contribute to domestic energy needs. Carinata fits into existing cropping systems as a winter crop, providing opportunities to farm over 1.4 million hectares of winter fallow land that could translate to over 1224 million liters of jet fuel, displacing 1.4%–2.33% of petroleum-based jet fuel in the United States (Alam & Dwivedi, 2019).

Carinata seed has 18.7%–28.3% protein and 42%–52% oil content with a well-distributed fatty acid profile. Erucic acid (41%–43%) forms the primary fatty acid component, followed by linoleic, linolenic, and oleic acids (Kumar et al., 2020). After hexane extraction, the seed meal has 43.6% crude protein, 23.6% neutral detergent fiber, 13.2% acid detergent fiber, and 2.5% crude fats making carinata meal a high-value protein feed (Schulmeister et al., 2019). The species possesses agronomic traits allowing it to be grown either as a winter crop in the humid subtropical regions or as a spring-planted crop in humid continental climates. Carinata is heat tolerant, resistant to diseases and seed shattering, and has lower water-use requirements than other oilseed brassicas (Kumar et al., 1984; Malik, 1990; Raman et al., 2017; Shivpuri et al., 1997). Varieties that are frost tolerant, early maturing, nutrient use efficient, high yielding with desirable oil content and fatty acid production are needed to integrate carinata into prevalent crop rotation systems (Kumar et al., 2020; Mulvaney et al., 2018, 2019; Seepaul et al., 2018). Connecting biology with agronomy is critical for the sustainable cultivation of carinata in different production regions of the world.

2 | ORIGIN AND DISTRIBUTION

Carinata is a member of the family Brassicaceae (formerly known as Cruciferae), order Capparales, tribe Brassiceae; genus Brassica, and species carinata (Edwards et al., 2000). Although the name carinata was first given by A. Braun in 1841, it is known to have various scientific synonyms like Brassica intergrifolia var. Carinata (West) Rupr (1860), Melanosinapis abyssinica Hort. ex Regel, and Sinapis abyssinica A. Braun (1856) (Edwards et al., 2000). Carinata, an allotetraploid (BBCC-genome, 2n = 4x = 34, genome size ~1300 Mb) originated through spontaneous interspecific hybridization between wild B. nigra (BB-genome, 2n = 2x = 16, genome size ~630 Mb) and cultivated B. oleracea (CC-genome, 2n = 2x = 18, genome size ~700 Mb) in Northeastern Africa, probably in the Ethiopian Plateau and the Mediterranean coast (Gómez-Campo, 1999; Hemingway, 1995; Warwick et al., 2006). The presence of these progenitor species in the region during the emergence and domestication of carinata supports this hypothesis (Alemayehu & Becker, 2002). The origin of carinata and its relationship with diploids B. rapa (AA-genome, 2n = 2x = 20, genome size ~550 Mb), B. nigra, B. oleracea and allotetraploids B. juncea (AABB-genome, 2n = 4x = 36, genome size ~1100 Mb) and B. napus (AACC-genome, 2n = 4x = 38, genome size ~1130 Mb) species has been explained in Triangle of U (Morinaga, 1934; Nagaharu, 1935; Figure 1). Restricted fragment length polymorphism analysis of chloroplast DNA (Palmer et al., 1985) revealed that carinata has the cytoplasm of B. nigra.

FIGURE 1 The relationship among different brassica species explained using the Triangle of U
Cultivation of carinata is believed to have started in the 4th to 5th millennia BC in Northeastern Africa (Ethiopia, Sudan, and Eritrea) and surrounding areas like East Tropical Africa (Kenya, Tanzania, and Uganda), Westcentral Tropical Africa (Cameroon and the Democratic Republic of Congo), West Tropical Africa (Cote D’Ivoire), South Tropical Africa (Mozambique, Malawi, Zambia, and Zimbabwe), Southern Africa (Botswana), Western Indian Ocean (Madagascar), and Southwest Asia (Saudi Arabia and Yemen) where it was grown for production of leafy vegetable, fodder, and oilseed (Delesa, 2011; Simmonds, 1979; Warwick et al., 2009). Carinata was introduced to North America from Ethiopia in 1957 to be used as a source of leafy vegetables (Stephens, 2009). Due to its use as an alternative to napus and as an alternative energy crop with low to no indirect land-use changes, an increasing trend of cultivation of carinata is seen in different parts of the world, including Europe (Spain, Italy, Greece, and the UK), Australia, New Zealand, South America (Chile and Uruguay), and South Asia (India and Pakistan; Bozzini et al., 2007; Malik, 1990; Prakash et al., 2012; Seepaul et al., 2016; Velasco et al., 2003; Zada et al., 2013; Figure 2).

3 | GENETIC AND GENOMIC RESOURCES

3.1 | Germplasm resources

Plant germplasm resources contain the genetic information of a plant’s hereditary makeup depicting its origin and evolution. This information can identify genetically diverse parental lines for breeding and other crop improvement programs. Specifically, crop improvement leading to increased productivity and/or resistance to biotic and abiotic stressors can be facilitated by intra- and interspecific and intra- and intergeneric diversity. Eight germplasm/gene banks across the world have an extensive repertoire of carinata. These germplasm/gene banks have 1707 accessions collected from 17 countries across the world (Table 1).

3.2 | Genetic and genomic advancements

The genetic diversity of the crop is influenced by natural and artificial selection (Wang et al., 2016), which helps to unravel the crop’s evolutionary history. Carinata shows low genetic diversity due to a stronger genetic bottleneck during domestication (Khedikar et al., 2020). A recent comparative analysis of different genetic and genomic resources like nucleotide sequences, protein sequences, genes, and research articles published on carinata and other common Brassicaceae members (napus, B. juncea, and B. rapa) is provided in Table 2.

Phenotypic analysis of 11 carinata lines for their agronomic performance and seed quality as a new potential oilseed crop in Canada did not show wide variability (Getinet et al., 1996). In contrast, Alemayehu and Becker (2002) assessed 36 accessions of carinata for 13 morphological and seed-related traits and found a wide range of genetic variability for yield-related traits. They also reported moderate variability in oil quantity and quality (glucosinolate [GSL] levels) and protein content. The use of morphological traits and biochemical markers, which are highly influenced by environmental factors, may have resulted in the detection of a wide variability among the accessions. Recently, 99 accessions of carinata were assessed for eight morphological traits and sinigrin content showed a wide variation among the traits (Teklehaymanot et al., 2019). It was found that sinigrin content, a predominant GSL in the leaves, was negatively correlated with leaf area, leaf width, primary branches, and plant height.

Genetic analysis of 39 carinata accessions using six amplified fragment length polymorphism (AFLP) primer combinations resulted in 189 polymorphic markers (Genet et al., 2005). This study segregated the accessions into seven clusters showing the presence of substantial genetic diversity in carinata. A collection of 43 accessions from five different countries was genotyped using 50 random amplified polymorphic DNA (RAPD) markers and showed high genetic diversity but no apparent geographical clustering (Teklewold & Becker, 2006). In another study, a total of 296 AFLP markers produced using four primer combinations were used to assess 66 carinata accessions that showed a low level of
genetic diversity in carinata in comparison to B. nigra and B. juncea (Warwick et al., 2006). In contrast, Jiang et al., (2007) assessed 110 accessions of carinata using 233 AFLP markers and showed high genetic diversity. Efforts are being made to develop genetic maps and to identify quantitative trait loci (QTL) for the crop. Priyamedha et al. (2012) constructed the first skeleton linkage map in carinata by using an F2 population of 150 individuals developed by crossing a resynthesized parental line Ar29 with natural cultivar PC5. They used 69 loci (23 RAPD, 29 ISSR, and 17 SSR) spanning 2166 cM on all 17 linkage groups. Guo et al. (2012) constructed the first genetic linkage map of carinata using 212 loci (151 SSR, 44 AFLP, 12 SRAP, and 5 IBP markers) on a doubled haploid population of 183 lines covering 1703 cM assigned to the eight linkage groups of the B-genome and nine linkage groups of the C-genome. They were able to identify loci governing two Mendelian-inherited traits (petal and anther tip color) and one quantitative trait (seed coat color). Zou et al. (2014) constructed a high-density genetic linkage map using 4031 DArTseq loci covering 2048.4 cM on a doubled haploid population of 185 individual lines leading to the identification of QTLs governing budding and flowering time. Genes conferring black rot resistance were identified and mapped by Sharma et al. (2016) using 160 ILP and 204 SSR markers on F2 population of 212 genotypes. Zhang et al. (2017) genotyped a panel of 81 accessions of carinata to generate 54,510 DArTseq polymorphic markers. These markers were used for genome-wide association analysis of the panel, and seven markers were significantly associated with five seed yield and quality traits (flowering time, oleic acid, linolenic acid, pod number, and seed weight). A diversity panel of 83 carinata accessions procured from the Australian Grains Genebank was assessed for pod shatter resistance (Raman et al., 2017) and led to the identification of parental lines to develop an F2 population of 300 individuals. This population was assessed using 6464 DArTseq markers to develop a genetic linkage map and for QTL identification (five QTLs distributed on chromosomes B1, B3, B8, and C5) related to pod shattering resistance (Raman et al., 2017). Recently, Khedikar et al. (2020) assessed a worldwide panel of 620 accessions to study genetic diversity, linkage disequilibrium, and haplotype patterns using 10,000 SNPs.
This analysis helped in the identification of genomic regions showing evidence of selection pressure. Carinata showed lower nucleotide diversity levels than napus suggesting the development of a genetic bottleneck during domestication.

4 | MORPHOLOGY, PHENOLOGY, AND REPRODUCTION

Carinata is an erect, annual grown as an oilseed or as a leafy vegetable. The seedling emerges epigeally, with heart-shaped cotyledons (2–3 cm) that are photosynthetically active to offset insufficient food reserves (Mnzava & Schippers, 2007; Seegeler, 1983). Carinata shows determinate growth with height averaging 1.4 m, high branching, and elongated taproots reaching up to 1 m (Barro & Martín, 1999; Zanetti et al., 2013). Stems are glabrous, waxy, reaching up to 2 cm in diameter (Seegeler, 1983) with leaves having short petiole, simple trichomes, alternate, glabrous to slightly hairy, and waxy phenotype (Al-Shehbaz, 2012; Mnzava & Schippers, 2007). Lower leaf blades are ovate to oblong with one to three deep lobes up to 20 cm long and 10 cm wide. The lower leaves’ abaxial surface is green, while the adaxial surface is paler or grayish with purple or light-green veins. In comparison, upper leaves are lighter colored and have fewer lobes, smaller in size, narrower, and less waxy (Seegeler, 1983).

The inflorescence is a loose, highly branched, and elongated compound raceme, with actinomorphic and perfect flowers borne terminally on the main stem and branches (Mnzava & Schippers, 2007; Seegeler, 1983). Pedicels are cylindrically shaped and 5–6 mm long. Flowers bear four green and oblong sepals (4–7 mm long) alternating with four yellow and obovate petals (6–10 mm long). Flowers also have six stamens and four nectaries. Most brassica species reproduce sexually through cross-pollination, contributing to the great diversity within species. However, carinata sets seed efficiently through both self- and cross-pollination. Carinata was reported to self-pollinate 46%–88% of the time (Labana et al., 1987) due to self-compatibility, and cross-pollinated 30% of the time due to its flower structure and delayed anthesis (Cheung et al., 2015; Velasco & Fernández-Martínez, 2009). Pollens are heavy, sticky, and are difficult to transfer from plant to plant by wind (Adeniji & Aloyce, 2012). Fruits are linear siliques up to 5 cm long, with a 2–7 mm straight or curved conical beak (Seegeler, 1983). Siliques are green and photosynthetically active when immature and turn light brown at maturity. They contain up to 20 seeds and are non-dehiscent due to their thick and highly lignified valve margins (Banga et al., 2011; Barro & Martín, 1999). Seeds are globose, finely reticulated, yellow to brown with a diameter ranging between 1 and 1.5 mm (Getinet, 1996; Mnzava & Schippers, 2004; Rahman & Tahir, 2010; Setia & Richa, 1989).

Carinata has been described as a long-day plant (Zanetti et al., 2013). However, there is a possible interactive effect between temperature and photoperiod for flowering initiation (Friend, 1968) as high temperature has been associated with accelerated phenological development under long photoperiod (Nanda et al., 1996). Flower initiation in carinata varied from 77 to 126 days across multiple locations and years in Florida depending upon genotypic, edaphic, and climatic factors (Kumar et al., 2020). Carinata lifecycle ranged from 3949 to 4288 growing degree days (GDD; 4.4°C base temperature) with an average lifecycle of 154 days for an early-maturing genotype and 165 days for a late-maturing genotype when grown as a winter crop in Florida (Kumar et al., 2020) while it reached physiological maturity at 2000–2200 GDD (4°C in Europe (Zanetti et al., 2013). Carinata variety 110994EM bolted, flowered, developed pods, and reached seed maturity around 535, 1084, 1547, and 2404 GDD, respectively (Seepaul et al., 2019).

5 | AGRONOMY OF CARINATA

Carinata is tolerant to a wide range of climatic conditions and can be fall-planted in the humid subtropical regions with mild winters and even rainfall throughout the year or spring-planted in the humid continental climate with hot and humid summers. Carinata can be fall-planted (October–November) in the Southeast United States, generally 3–4 weeks before the first frost event (Seepaul, Small, Mulvaney, et al., 2019) or spring-planted (mid-March to mid-May) in Midwest and Western states in the United States (Gesch et al., 2019). Timely fall planting facilitates asynchrony between carinata phenology and incidence of biotic and abiotic stresses. For example, timely planting allows the crop to reach the rosette stage at the time of highest frost probability (Mulvaney et al., 2018) or avoidance of pest incidence and severity during periods of greatest herbivory. There is substantial variation in flowering time within the species (Rakow & Getinet, 1998). Fall-planted carinata in Florida took 102 days to flower and 161 days to mature after planting (Kumar et al., 2020), while spring-planted carinata in Saskatchewan, Canada, took 55 days to flower and 110 days after planting to mature (Getinet et al., 1996). Spring-planted carinata was the latest maturing species (111–113 days after planting) among common oilseed crops evaluated in Minnesota (Gesch et al., 2015). The relatively long growing cycle of carinata limits its commercial production in the Prairie Provinces of western Canada, requiring the development of early-maturing varieties (Getinet et al., 1996). Scaling up production in the Southeast United States also requires early-maturing varieties to fit carinata in the double-cropped peanut–cotton rotations prevalent in the region. Whether planted in the spring or fall, carinata’s lifecycle should fit the diverse rotations
with minimal delay in planting the subsequent crop within
the growing regions where it is double-cropped (Christ et al.,
2020).

5.1  |  Planting and germination

Carinata is a very shallow-planted crop (Seepaul, Small, Mulvaney, et al., 2019) and germinates in the top portion of
the soil that usually experiences moisture deficit (Patane &
Tringali, 2011). Carinata should be planted not more 1.3 cm
depth because of its small seed size; however, deeper depths
may be considered when planting in sandy soils (Seepaul,
Small, Mulvaney, et al., 2019). Early season moisture availa-
bility in the 0.64–1.3 inches topsoil is critical for uniform
and vigorous seed germination (Patane & Tringali, 2011).
Carinata is generally seeded at 6.1 kg ha⁻¹ (129 pure live
seeds m⁻²; Kumar et al., 2020) but undergoes self-thinning
resulting from interplant competition. Due to the high de-
gree of compensatory ability, maximum seed yield can be
achieved over a wide range of plant densities from 34 to 117
plants m⁻² (Seepaul et al., 2020). Relatively higher yields were obtained from plant populations ranging from 22 to 37 m⁻² (Punia et al., 2001). Seed yield was re-
sponsive to seeding rate as high as 300 pure live seeds m⁻² in
three of the nine site-years in North Dakota (Hossain et al.,
2018). Maximum seed yields (1140–1492 kg ha⁻¹) also oc-
curred at a relatively high seeding rate (9–13.5 kg ha⁻¹) in
South Dakota (Alberti, 2017). Similarly, carinata planted
at 10 kg ha⁻¹ produced 2890 kg seed ha⁻¹ (Bozzini et al.,
2007) in Italy, while 8 kg ha⁻¹ produced 1592 kg ha⁻¹ in
Ethiopia (Tadesse et al., 2012). In Florida, maximum seed
yield (2761 kg ha⁻¹) was produced at a 3 kg ha⁻¹ seeding
rate (Mulvaney et al., 2019). Higher seeding rates may re-
duce stem diameter and increase lodging potential but may
be necessary for no-till systems to compensate for increased
seedling mortality (Alberti, 2017). Changing the plant ge-
ometry through seeding rate and row spacing alters the leaf
arrangement and canopy architecture, which controls light
interception and photosynthetic productivity (Sarlikioti et al.,
2011). Carinata has phenotypic plasticity to modulate plant
architecture to optimize light interception (Mulvaney et al.,
2019), especially at low plant populations, by producing
more branches, racemes, and pods. This phenotypic plasticity
is modulated by environmental conditions and resource avail-
ability (Hossain et al., 2018). Carinata growth and yield are
influenced more by row spacing than seeding rate (Mulvaney
et al., 2019) in Florida. Single rows spaced 36 cm apart maxi-
mized carinata yield (2761 kg ha⁻¹) in Florida (Mulvaney
et al., 2019), while a 30-cm row spacing produced 9%–11%
greater yield than a 60-cm row spacing carinata in India
(Kaur, 2002). Wider row spacings favor branching and in-
crease the number of pods per plant (Mulvaney et al., 2019).

5.2  |  Growth and development

Carinata development is divided into vegetative (seedling,
rosette), transition (bolting), and reproductive growth stages
(flowering, pod development, and seed ripening) (Figure 3).
At physiological maturity, carinata typically has 30 main-
stem nodes, 53% producing primary branches with 25 sec-
dorary branches bearing 280 pods per plant when fertilized
with 90 kg N ha⁻¹ (Seepaul et al., 2020). Leaves contributed
52% of the total dry matter (DM) during the vegetative stage
and decline sharply to 0% at maturity while the stem fraction
increased from 48% at the vegetative stage to a maximum of
73% at flowering and decline to 37% at maturity (Seepaul
et al., 2019). Seeds contributed 25% of the DM production
(Seepaul, Marois, et al., 2019). Carinata self-defoliates with
the onset of reproductive development as photo-assimilates
and nutrients are translocated from leaves to the developing
seeds (Seepaul et al., 2018) resulting in decreased leaf area
with plant maturity (Seepaul, Small, Marois, et al., 2019).
The reduction of photosynthetic leaf area through artificial
defoliation reduces seed yield by 22 and 8 kg ha⁻¹ for every
percent defoliation at the vegetative or reproductive stage,
respectively, when carinata was defoliated once (Baldwin
et al., 2021). Complete defoliation through excision at the
post-flowering stage leads to decreased seed numbers per pod
and 1000-seed weight by 32% and 25%, respectively, in cari-
ndata (Ramana & Ghildiyal, 1997). Carinata is a high biomass
producer accumulating 14,224 kg ha⁻¹ in spring-planting
in Minnesota, USA (Gesch et al., 2015), and 7017 kg ha⁻¹
as a fall-planted crop in Florida, USA (Seepaul, Marois,
et al., 2019). Harvest index (HI) ranged from 0.28 to 0.37
in Minnesota and from 0.30 to 0.34 in Florida (Gesch et al.,
2015; Seepaul, Marois, et al., 2019).
Green pods contain chloroplasts in the outer pod wall layer and are responsible for 70%–100% of assimilation of photosynthates in seeds in later stages of plant development (Andrews & Svec, 1975; Bennett et al., 2011; Major & Charnetski, 1976; Raven & Griffiths, 2015; Sheoren & Randhir, 1991; Singal et al., 1995).

Yield is dependent on the number of branches, number of seeds per pod, number of seeds per pod, and 1000-seed weight (Ozturk, 2010; Setia et al., 1995). Seed size and yield are positively correlated with aboveground DM yield, suggesting that high DM accumulation at all growth stages throughout the crop growth cycle in stress-free conditions is key to optimizing yield components and yield (Enjalbert et al., 2013; Seepaul, Marois, et al., 2019).

5.3 | Management practices

Nitrogen (N) availability alters the early season and post-bolting physiology, morphology, and biomass distribution patterns in carinata. Nitrogen accounts for the largest energy input and production costs in oilseed production (Gan et al., 2007); therefore, understanding biomass accumulation and allocation, nutrient concentration, and uptake can help synchronize in-field N application with crop growth for optimum uptake and utilization. Carinata is highly responsive to N application (Alberti et al., 2019; Pan et al., 2011; Seepaul, Marois, et al., 2019) and requires adequate N fertilization for optimum seed yields (Johnson et al., 2013; Montemurro et al., 2016; Prakash et al., 1999; Seepaul et al., 2016, 2020; Seepaul, Marois, et al., 2019; Seepaul, Small, Marois, et al., 2019). Height, node numbers, primary branches, secondary branches, and pod numbers increased by 38.3, 6.7, 64.5, 146.1, and 128.2, % from 0 to 135 kg N ha$^{-1}$, respectively (Seepaul et al., 2020). Carinata grown with limited N (0 mg N L$^{-1}$) had 47% lower photosynthesis (21.2 μmol m$^{-2}$ s$^{-1}$) than plants grown with optimal N (16 mg N L$^{-1}$; 31.0 μmol m$^{-2}$ s$^{-1}$; Seepaul et al., 2016). Suboptimal N availability modified carinata canopy architecture by reducing leaf size, early abscission and senescence, and vertical distribution of leaves on the main stem (Seepaul et al., 2016). Modification in canopy architecture in response to N deficiency adversely affected canopy photosynthesis and the production of flowers (Seepaul et al., 2016). Bolting is a period of rapid stem elongation in carinata and is a critical period for N fertilization. The limitation of N at the onset of bolting induces morphological changes such as reducing leaf area, light interception, and canopy photosynthetic activity (Seepaul et al., 2016). Limiting N during carinata reproductive development resulted in a 62% yield penalty indicating that carinata is sensitive to N limitation (Seepaul, Small, Mulvaney, et al., 2019). Under non-limiting N conditions (16.1 mg N L$^{-1}$),
Carinata growth and seed yield are also responsive to sulfur application up to 45 kg S ha⁻¹; however, the economically optimal S rate was 36 kg S ha⁻¹ (Bhattarai, 2019; Verma et al., 2018). The application of 40 kg S ha⁻¹ increased seed yield by 33%–34% over a non-treated control by increasing the number of primary branches, the number of pods per plant, and seeds per pod (Bhattarai, 2019; Verma et al., 2018). There is a dearth of information on phosphorous and potassium as well as the effect of micronutrients on carinata growth, development, and productivity.

Carinata is sensitive to drought stress, evidenced by decreased leaf size, reduced dry weight of plant parts, stomatal conductance, and photosynthesis (Ashraf & Mehmoood, 1990; Husen et al., 2014; Pan et al., 2011). Drought stress reduced the root length by 6%, shoot length by 9%, the number of leaves by 15% in a controlled environment study (Husen et al., 2014). To overcome drought stress for a short period and protect leaves against dehydration, there is increased wax deposition and partial stomatal closure in carinata leaves to limit water loss (Albert et al., 2012; Husen et al., 2014). Nitrogen and water-limiting conditions also stimulate elongation of the main and lateral roots in carinata, which can increase root exploration for efficient nutrient and water uptake (Hossain et al., 2019; Qin et al., 2019; Singh & Singh, 2018). Drought stress lowers leaf water potential leading to reduced turgor, stomatal conductance, photosynthesis (Kumar & Singh, 1998), biomass production (Husen et al., 2014), and seed and oil yields (Gesch et al., 2019). In Fort Collins, Colorado, irrigation increased biomass production, height, and pod density by 103%, 94%, and 7%, respectively, over rainfed carinata (Enjalbert et al., 2013). Maximum seed yield (2057 kg ha⁻¹), quality, and water use efficiency were achieved when irrigation was applied at the seedling stage, 50% flowering and pod development stages in the semiarid regions of India (Verma et al., 2018). Carinata is better suited as a rainfed crop for regions with adequate growing season rainfall than in arid or semiarid regions. A significant intraspecific variation for drought resistance exists within the carinata species that can be exploited to improve the drought tolerance of carinata through selection and breeding (Ashraf & Sharif, 1998; Lohani et al., 2019).

In addition to N and drought stress, high-temperature stress is also detrimental to carinata’s growth and yield, especially during flowering (Gan et al., 2004). Under high-temperature stress (35/15°C day/night temperatures), only early formed floral primordia develops into flowers and pods (Angadi et al., 2000). Improved carinata lines that can maintain pod production and seed development under high temperatures are needed to contribute to increased yield (Gan et al., 2004). Under extreme temperatures (heat and cold), brassicas tend to increase the production of antioxidant defenses, responding to an increase in reactive oxygen species (ROS; Soengas et al., 2018). In the absence of the antioxidant
defense mechanism, there is an increased production of ROS in the chloroplasts, which decreases the chlorophyll content and elicits photoinhibition, thereby reducing CO₂ fixation and loss of dry weight (Soengas et al., 2018).

Sequential flowering in carinata produces a mixture of pods with different maturity (Seepaul et al., 2018). Delayed maturity of current varieties (Kumar et al., 2020) requires agronomic management tools to accelerate uniform maturity of the crop to allow timely land preparation and planting of summer row crops (Seepaul et al., 2018). Carinata can be swathed in arid or semiarid regions or chemically desiccated in the Southeast United States (Seepaul et al., 2018). For safe seed storage, carinata must be at 10% seed moisture or less. If moisture is greater than 10%, seeds can be dried with forced air at low temperatures or air-dried (Seepaul et al., 2018).

5.4  Pest management

Carinata is resistant to diseases that commonly affect other oilseed brassica species (Katiyar et al., 1986), including black rot caused by Xanthomonas campestris pv. Campestris ( Sharma et al., 2016; Tonguc & Griffiths, 2004) and blackleg or stem canker caused by Leptosphaeria maculans (Gugel et al., 1990; Rimmer & Vandenbarg, 1992). Disease reports include those for turnip mosaic virus ( Babu et al., 2013), sclerotinia stem rot caused by Sclerotinia sclerotiorum ( Young et al., 2012), alternaria black spot caused by Alternaria alternata ( Dunbar et al., 2017), powdery mildew caused by Erysiphe cruciferarum ( Gunasinghe et al., 2013), charcoal rot caused by Macrophomina phaseolina ( Tande et al., 2015), and root rot caused by Fusarium species ( Okello et al., 2018). Some of these pathogens are generalists, which may affect subsequent rotational crops ( Okello et al., 2018). Like other brassicas, carinata is susceptible to insect pests, including cabbage looper Trichoplusia ni, diamond back moth Plutella xylostella, spotted cucumber beetle Diabrotica undecimpunctata, turnip aphid Lipaphis pseudobrassicae, yellow margined leaf beetle Microtheca ochroloma and Pieris rapae ( Baldwin et al., 2021). There is a limited number of studies that quantified the effects of weeds on carinata seed yield. One study in North Dakota reported a 16% yield reduction when weeds were not controlled (Hossain et al., 2018). Although carinata forms a competitive canopy (Gesch et al., 2015) against weeds, an integrated weed management strategy that employs cultural, mechanical practices and the use of herbicides is prudent for profitable production. Managing plant populations by optimizing seeding rate and row spacing along with optimal fertilizer application can reduce the impact of weeds. Pendimethalin and S-metolachlor can be used for preemergence weed control, while broadleaf and grass control can be achieved using clopyralid and clethodim (Leon et al., 2017). Carinata is not invasive or likely to become a weed in subsequent crops. Flumioxazin, acifluorfen, bentazon, and carfentrazone can be used to control volunteer carinata in rotational crops (Leon et al., 2017). The prevalence of wild radish (Raphanus raphanistrum) in the Southeast United States can reduce yield and harvest quality through resource competition and contamination of harvested carinata seeds. Increasing cropping system diversity by planting carinata in a 3-year crop rotation may reduce insect pests, diseases, and weed pressure in rotational crops like canola (San Martin, et al., 2019). Carinata’s vigorous growth and broad leaves smother weeds. Weed biomass decreased by 67% as the seeding rate increased from 50 to 300 seeds m⁻² (Hossain et al., 2018). Planting in narrow rows (no more than 36 cm and preferably 19 cm) and using high seeding rates (>5.6 kg ha⁻¹) will favor rapid canopy closure and weed suppression (www.sparc-cap.org/resources/factsheets/carinata).

5.5  Seed quality

Carinata has 39% and 61% long-chain (C14–C18) and very-long-chain (>C19) fatty acids, respectively. Of these, 6%, 31%, and 62% are saturated, polyunsaturated, and monounsaturated fatty acids, respectively (Seepaul et al., 2020). Oil concentration responds to nutrient management, particularly N application rates. An increase in N application rates resulted in a decrease in oil content, and an increase in protein content as oil and protein concentrations are inversely related (Hossain et al., 2018, 2019; Johnson et al., 2013; Kumar et al., 2020; Pan et al., 2012; Seepaul et al., 2020; Seepaul, Small, Mulvaney, et al., 2019; Verma et al., 2018). Oil concentration decreased at a rate of 0.26 g kg⁻¹ for every kg increase in nitrogen application per hectare (Alberti et al., 2019). Nitrogen application rates, split management of N, or N source did not affect the concentration of fatty acids (Seepaul et al., 2020). Oil concentration increased with seeding rate in one study (Hossain et al., 2018) but did not differ in others (Mulvaney et al., 2019; Pan et al., 2012) and did not respond to row spacing (Mulvaney et al., 2019) or irrigation (Verma et al., 2018). Plants grown at lower seeding rates generally have greater nitrogen uptake than those from higher seeding rates, which may negatively affect oil concentration (Harker, O’Donovan, Smith, et al., 2015; Harker, O’Donovan, Turkington, et al., 2015; 2012). Except for nitrogen management, carinata seed and oil yields can be optimized through agronomic manipulations with little or no effect on seed oil, protein, and fatty acid concentrations.

Glucosinolates are often concentrated in the leaves and roots during early stages of development and reallocated to the seeds at maturity (Bellostas et al., 2004; Jørgensen et al., 2015). Carinata shoots comprise mostly of aliphatic GSLs with roots containing aliphatic and aromatic GSLs
at about a 1:1 ratio and ranged from 8 to 25 μmol g\(^{-1}\) of total GSLs (Kirkegaard & Sarwar, 1998). Seeds contain about 80 μmol g\(^{-1}\) of GSLs comprising mainly of sinigrin, but can be as high as 160 μmol g\(^{-1}\) (Marquez-Lema et al., 2008; Mnzava & Olsson, 1990; Seepaul et al., 2020; Seepaul, Small, Mulvaney, et al., 2019). After oil extraction, carinata seed meal can be used as supplemental protein for animal feed since it contains up to 53.5% crude protein, 76% of which are rumen degradable protein (Ban et al., 2017; Paula et al., 2019). However, carinata meal must contain less than 2.0% erucic acid and less than 30 μmol g\(^{-1}\) of GSLs like sinigrin due to their detrimental effects on the health of animals by reducing palatability and interfering with iodine uptake (Nega & Woldes, 2018; Tripathi & Mishra, 2007). Therefore, carinata meal is restricted to 10% of the total diet or 0.3% of body weight per day (Paula et al., 2019; Schulmeister et al., 2019). The seed meal containing high GSL levels (44–168 μmol g\(^{-1}\)) can be used as a soil amendment due to its biofumigant properties to suppress pest and disease activity (Gimsing & Kirkegaard, 2009; Mazzola & Manici, 2012; Pattison et al., 2006).

## 6 CURRENT STATE OF CROP IMPROVEMENT

Successful oilseed crop improvement involves developing varieties with a higher yield, better oil quality, and resistance to various biotic and abiotic stresses. This requires access to phenotypically and genotypically diverse germplasm from existing germplasm resources and wild genotypes, which can broaden the genetic base by identifying and incorporating desirable traits into the existing varieties.

### 6.1 Carinata as a desirable donor for interspecific hybridization

Carinata possesses several desirable traits like tolerance to abiotic stress (heat, salt, and metal toxicity; Gugel et al., 1990; Iretelli & Navari-izzo, 2008; Mafakheri & Kordrostami, 2020), resistance to various biotic stresses (blackleg disease, stem rot, white rust, alternaria black spot, powdery mildew, and aphids; Chavan & Kamble, 2014; Gebre-Medhin & Mulatu, 1992; Gugel et al., 1990; Mehta, 2014; Navabi et al., 2010; Sharma et al., 2017; Tonguc & Griffiths, 2004; Yitbarek, 1992), pod shattering resistance and relatively large seed size (Getinet et al., 1996; Thakur et al., 2019), which makes it a desirable donor for various interspecific hybridization programs for the improvement of related species. Traits like late maturity, long and profuse vegetative growth, tall plant stature, low oil content, high erucic acid content, low harvest index, and unattractive seed coat color are major constraints for its adoption as an oilseed crop for edible purposes (Thakur et al., 2019). Interspecific crosses between carinata (female) and B. juncea (male) resulted in the successful production of F1 progeny in different studies (Getinet et al., 1997; Ghosh-Dastidar & Varma, 1999; La Mura et al., 2010; Rahman, 1976). Similar reports of successful hybridization between different Brassicaceae members like carinata (female) and B. napus (male; Fernandez-Escobar et al., 1988; Getinet et al., 1997; La Mura et al., 2010; Niemann et al., 2012); carinata (female) and B. nigra (male; Chang et al., 2011; Mizushima, 1950); carinata (female) and B. oleracea (male; Chang et al., 2011; Rahman, 2001, 2004); carinata (female) and B. rapa (male; Choudhary et al., 2000; Jiang et al., 2007; La Mura et al., 2010; Liu et al., 2009; Rahman, 2001, 2002, 2004; Struss et al., 1991; Struss et al., 1992) are available.

In some cases, hybridization between allotetraploid (carinata, napus, and B. juncea) and diploid (B. nigra, B. rapa, and B. oleracea) brassica species have resulted in the formation of nonviable seeds due to pre- (Diederichsen & Sacristan, 1994) and post-fertilization barriers (Nishiyama et al., 1991). Doubled haploid methods, ovary and ovule culture, embryo culture, and protoplast fusion techniques have been utilized to overcome post-zygotic interspecific incompatibility barriers for these crosses (Diederichsen & Sacristan, 1994). Ovary and ovule culture (Sabharwal & Doležel, 1993) and protoplast fusion (Klima et al., 2009) technique resulted in the production of viable F1 seeds between carinata and napus. Protoplast fusion between black rot-resistant carinata accession PI 199947 and susceptible rapid cycling B. oleracea breeding line followed by backcross to B. oleracea resulted in the generation of resistant varieties (Tonguç et al., 2003). Similarly, embryo culture between carinata and B. oleracea (Rahman, 2004; Sharma et al., 2017; Tonguc & Griffiths, 2004) and carinata and B. rapa (Busso et al., 1987; Meng et al., 1998; Quiros et al., 1985; Rahman, 2004) resulted in the production of successful F1 hybrids.

### 6.2 Oil quality, quantity, and secondary metabolites

The development of genotypes with high erucic acid content in brassica species is an important research area due to its high demand for various industrial applications (Taylor et al., 1995). Velasco et al. (1998) used ethyl-methane sulfonate (EMS) to increase the erucic acid content in carinata line C-101. It led to an increase of the erucic acid content of M4 generation lines to 52.2%–59.3% compared to 39.0%–47.6% in parental lines. Velasco et al. (1995) also used EMS to develop low erucic acid (5%–10%) containing carinata lines fit for edible purposes. Carinata breeding programs have also reported the development of varieties with very low erucic acid
content ranging from 0% to 2% suitable for edible purposes and high erucic acid-containing varieties (up to 50%) suitable for industrial application (Alonso et al., 1991; Fernandez-Escobar et al., 1988; Getinet et al., 1996; Jadhav et al., 2005).

The development of transgenic lines in carinata is an other strategic approach to increase erucic acid (C-22:1) and nervonic acid (C-24:1) content. Minimal efforts have been made to develop transgenic lines with improved erucic and nervonic acid content in carinata. Jadhav et al. (2005) used two approaches, that is, co-suppression and antisense repression of the FAD2 gene in carinata, to decrease the production of polyunsaturated C-18 fatty acids and increase of erucic acid and VLCFA (very long-chain fatty acid) content. This study resulted in an increased proportion of erucic acid content by 12%–27% for co-suppressed and 5%–19% for anti-sense repression transgenic lines. While the VLCFA content increased by 6%–15% and 5%–19% for co-suppressed and antisense repression transgenic lines of carinata, respectively. Mietkiewska et al. (2008) used 3′-UTR of the FAD2 gene to form an intron-spliced hairpin RNA (ihp RNA) to silence the FAD2 gene, which led to an increase of 16% and 10% in oleic acid and erucic acid content, respectively, in carinata. They also used a second construct containing ihp RNA targeted to the endogenous FAD2 gene of carinata along with heterologous Crambe abyssinica FAE gene with seed-specific napin promoter to increase erucic acid production by 16%. Reports of varieties with increased nervonic acid, 5,13-docosadienoic acid, 5-eicosenoic acid, eicosapentaenoic acid contents to meet various industrial, biofuel, and nutritional needs are also available in carinata (Chang et al., 2009; Jadhav et al., 2005; Taylor et al., 2010). The mean value of different oil quality traits of carinata has been provided in Table 4.

6.3 | Breeding targets

The development of disease-tolerant or resistant carinata lines is important for higher yield and oil content. Tonguc and Griffiths (2004) evaluated 54 carinata accessions from the USDA collection for resistance against race 4 of Xanthomonas campestris pv. campestris (Xcc) causing black rot disease in other brassica species. Out of the 54 accessions of carinata tested, two accessions (A 19182 and A 19183) did not exhibit any symptoms, while three accessions (PI 199947, PI 199949, and PI 194256) segregated for resistance to Xcc. The National Gene Bank of India (NBPGR) at New Delhi contains two registered varieties (IC 443624 and IC 544702) resistant to white rust disease. The gene bank also has one variety each, which is registered for tolerance to Alternaria blight (IC 305114), resistance to white rust and leaf and stag head stage (IC 523914), good yielding (IC 296346), and resistance to pod shattering and lodging (IC 555215). Efforts are being made to develop herbicide-tolerant lines of carinata against Group 2 and Group 4 herbicides like dicamba (3,6-dichloro-2-methoxybenzoic acid) at Agriculture and Agri-Food, Canada. They have developed two tolerant lines UF-S2 and UF-S3, which will be tested for their herbicide tolerance at a field trial in Uruguay by Nuseed (http://westerngrains.com/projects/developing-unique-herbicide-tolerant-brassica-carinata-and-brassica-juncea-germplasm/). The development of early-maturing varieties of carinata has been reported from some parts of the world. The NBPGR at New Delhi has one registered early-maturing variety (IC 467732) of carinata in their collection. The gene bank also contains three registered varieties of carinata (IC 555215, EC 223405, and IC 199711), which are yellow seeded. Generally, yellow seeded carinata lines produce heavier seeds (+0.4 g) with higher oil (+2.3%), protein (+2.1%), and lower crude fiber (−1.2%) content than brown seeded lines (Getinet et al., 2004).

### Table 4 Mean value of seed quality traits of commercial carinata variety Avanza 641 grown in north Florida (adapted and modified from Mulvaney et al., 2019). The mean represents the average of 128–304 samples from four site-years. SEM is the standard error of the mean.

| Trait                  | Mean   | SEM  |
|------------------------|--------|------|
| Oil concentration, %   | 39.7   | 0.2  |
| Protein in seed, %     | 31.6   | 0.2  |
| Glucosinolates, µmol g⁻¹ | 92.9  | 1    |
| Saturated fatty acids, % | 6.2  | 0    |
| Monounsaturated fatty acids, % | 57.2 | 0.1  |
| Polynsaturated fatty acids, % | 35.9 | 0.1  |
| Long-chain fatty acids, % with chain length 14–18 C | 49.8 | 0.2  |
| Very long-chain fatty acids, % with chain length >19 C | 52.7 | 0.2  |
| Iodine value           | 113.7  | 0.1  |
| Other fatty acids in seed, % | 0.6  | 0    |
| C16:0 (palmitic acid), % | 3.4   | 0    |
| C16:1 (palmitoleic acid), % | 0.2  | 0    |
| C18:1 (oleic acid), %   | 12.7   | 0.1  |
| C18:0 (stearic acid), % | 1.1    | 0    |
| C18:2 (linoleic acid), % | 18.3  | 0.1  |
| C18:3 (linolenic acid), % | 12.9  | 0.1  |
| C20:0 (arachidic acid), % | 0.8   | 0    |
| C20:1 (eicosenoic acid), % | 8.6   | 0.1  |
| C16:0 (eicosadienoic acid), % | 1.4  | 0.1  |
| C22:0 (behenic acid), % | 0.5    | 0    |
| C22:1 (erucic acid), %  | 36.4   | 0.1  |
| C22:2 (docosadienoic acid), % | 0.5  | 0    |
| C24:0 (lignoceric acid), % | 0.3   | 0    |
| C24:1 (nervonic acid), % | 1.4    | 0    |
Carinata is widely adaptable to diverse growing regions, cropping systems, and management regimes with demonstrated potential to be grown on the continents of Asia, Africa, North America, South America, Europe, and Australia either as a spring or winter crop in double-cropped systems. Carinata is a biocomponent platform for fuel, meal, and co-products (McVety et al., 2016; Schulmeister et al., 2019; Taylor et al., 2010) shown to increase farmer incomes and provide ecosystem goods and services (Basili & Rossi, 2018; Christ et al., 2020). Producers need to connect the ancillary value of growing carinata in their rotation with their entire cropping system. Further, quantifying and valuing the ecosystem goods and services and providing economic incentives to grow a commodity crop with significant cover crop benefits can aid in adoption.

Adopting carinata in double-cropping systems would require continuing research to integrate crop biology with agronomy, to understand growth and development and its interaction with agricultural inputs and management. Such research results would enhance the productivity of carinata in diverse cropping systems when planted either as a spring or winter crop. Improving carinata productivity requires genetic improvement in agronomic traits and the development of best management practices to optimize the crop in diverse rotations. Current carinata lines have low genetic diversity (Khedikar et al., 2020); therefore, research should focus on developing genomic resources to characterize genetic diversity to aid marker–trait associations for agronomic traits (Thakur et al., 2019). Reducing the growth cycle length by 2–3 weeks with minimal yield penalty and improving freeze tolerance at the vegetative and bolting stages can increase adoption as a winter crop. Improving resource use efficiency (nutrients and water) of carinata may lead to sustainable yields over a broader range of environmental conditions. Production on marginal lands, especially in arid and semiarid regions, can enhance the crop’s ecological value as demonstrated in Italy (Basili & Rossi, 2018; Cardone et al., 2002, 2003). With increasing acreages under cultivation, the probability of pests and diseases increases; therefore, identifying resistance to pests and diseases common within potential growing regions and developing integrated control methods are necessary. Improvements in oil profiles and VLCFA concentrations, such as nervonic acid, can lead to the development of novel biomolecules. Adaptable and yield-stable carinata varieties would require best management practices for sustainable production. These include refining recommendations for optimal rotation sequences, tillage practices, planting date, seed rate, row spacing, fertilizer application, pest control, and harvest management of spring- and winter-planted carinata in different growing regions.

Scaling up commercial production to produce advanced renewables in the United States must fit within the contextual framework of the USDA Agriculture Innovation Agenda benchmarks to increase productivity by 40%, reduce carbon footprint by 50%, reduce nutrient loss by 30%, and increase biofuel feedstock production and biofuel production efficiency by 2050 (https://www.usda.gov/aia). Fitting carinata into this framework requires developing a regional bioeconomy with infrastructure and logistics to grow, transport, crush, convert, distribute, and use oil, meal, and co-products close to where the crop is grown to minimize carbon footprint and to improve the environmental sustainability of biofuel production systems.

ACKNOWLEDGMENTS
This research was funded by USDA-NIFA Bioenergy Coordinated Agricultural Projects Grant # 2016-11231 (Southeast Partnership for Advanced Renewables from Carinata). Our sincere thanks to Ms. Sapna Rawat, University of Delhi, for sketching the growth stages of carinata.

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

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article, as no new data were created or analyzed in this review of the literature.

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How to cite this article: Seepaul R, Kumar S, Iboyi JE, et al. *Brassica carinata*: Biology and agronomy as a biofuel crop. *GCB Bioenergy*. 2021;13:582–599. https://doi.org/10.1111/gcbb.12804