

Deciphering canola–aphid interaction: a review on the role of hostplant nutrients and phenolic compounds[☆]

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Received 20 November 2025 – Accepted 16 February 2026

Abstract – Canola, *Brassica napus* L., is the top-ranked vegetable oil crop in the world, and its production is significantly hindered by aphids (mustard-oil bombs), which compromise the host plant defense. The prominent aphid species which infest the canola include *Brevicoryne brassicae*, *Lipaphis erysimi*, and *Myzus persicae*. They feed on tender parts of the plant and suck the cell sap that ultimately reduces the plant's vigor. Floral buds are weakened, and flowers may fall to reduce the number of potential pods, causing a significant yield loss (60%–77%). They also transmit ~20 different plant viruses in canola. Aphids sustain their populations through a consecutive biological cycle to produce multiple generations in a single cropping season. Continuous feeding by a multitude of aphids ultimately reduces plant growth and yield attributes, *i.e.*, plant height, number of siliques, seeds per silique, thousand-seed weight, and plant yield, significantly. Hostplant nutrient profile comprising macro- and micronutrients, *i.e.*, nitrogen, phosphorous, potassium, calcium, magnesium, iron, sulfur, copper, and zinc, also alters. These nutrients have a dual role in aphid–canola interaction, *i.e.*, they accomplish biological needs of aphids on one side and enhance host plant defense and yield on the other side. In addition, phenolic compounds are also important, especially myricetin, quercetin, gallic, caffeic, syringic, vanillic, ferulic, chlorogenic, *m*-coumaric, *p*-coumaric, sinapic, and cinnamic acid. Their role in plant defense and aphid reduction has been discussed. Classification, biosynthetic pathways, and the role of plant phenolics in countering aphid defense have been elaborated. Conclusively, this review delivers an inclusive framework for understanding the chemical and nutritional drivers responsible for aphid resistance and yield improvement, offering significant insights for developing pest-resilient canola cultivars.

Keywords: aphids / nutrients / phenolic compounds / phytochemistry

Résumé – Décryptage des interactions colza–pucerons : revue du rôle des nutriments de la plante hôte et des composés phénoliques. Le colza (*Brassica napus* L.) est la principale culture oléagineuse au monde, et sa production est fortement compromise par les infestations de pucerons, qui affaiblissent les mécanismes de défense de la plante hôte. Les principales espèces de pucerons infestant le colza sont *Brevicoryne brassicae*, *Lipaphis erysimi* et *Myzus persicae*. Ces insectes se nourrissent des parties tendres de la plante en aspirant la sève cellulaire, ce qui entraîne une réduction de la vigueur de la plante. Les boutons floraux sont affaiblis et les fleurs peuvent chuter, réduisant ainsi le nombre potentiel de siliques et provoquant des pertes de rendement significatives (60–77 %). Les pucerons sont également vecteurs d'environ vingt virus phytopathogènes chez le colza.

Les pucerons maintiennent leurs populations grâce à un cycle biologique continu, produisant plusieurs générations au cours d'une même saison culturale. Une alimentation continue de fortes populations de pucerons entraîne une diminution significative de la croissance de la plante et de ses composantes de rendement, notamment la hauteur des plantes, le nombre de siliques, le nombre de graines par silique, le poids de mille grains et le rendement global. Le profil nutritionnel de la plante hôte, comprenant les macro- et micronutriments tels que l'azote, le phosphore, le potassium, le calcium, le magnésium, le fer, le soufre, le cuivre et le zinc, est également modifié.

Ces nutriments jouent un rôle double dans l'interaction pucerons–colza : d'une part, ils satisfont les besoins biologiques des pucerons et, d'autre part, ils renforcent les défenses de la plante hôte et contribuent à

[☆] Contribution to the Topical Issue: “Rapeseed / Colza”.

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l'amélioration du rendement. Par ailleurs, les composés phénoliques jouent également un rôle important, en particulier la myricétine, la quercétine, ainsi que les acides gallique, caféique, syringique, vanillique, férulique, chlorogénique, m-coumarique, p-coumarique, sinapique et cinnamique. Leur rôle dans la défense des plantes et la réduction des populations de pucerons est discuté. La classification, les voies de biosynthèse et le rôle des composés phénoliques végétaux dans les mécanismes de défense contre les pucerons sont également détaillés.

En conclusion, cette revue brosse un portrait de la compréhension des facteurs chimiques et nutritionnels responsables de la résistance aux pucerons et de l'amélioration du rendement, offrant des perspectives importantes pour le développement de cultivars de colza résistants aux ravageurs.

Mots-clés : pucerons / nutriments / composés phénoliques / phytochimie

Highlights

This review reveals the “mustard-oil bomb” aphid impact on canola, delineating how aphid infestation disrupts nutrient and phenolics profiles and reduces yield attributes. It contributes to oilseed crop science by mapping nutrient and phenolic responses that strengthen plant defense for enhanced yield and improved pest resistance.

1 Introduction

Canola or rapeseed (*Brassica napus* L.) (Brassicaceae: Brassicales) is an amphidiploid dicotyledonous plant (Tsuge *et al.*, 2020; Azhar *et al.*, 2025). It is one of the most important oil-producing species in the genus *Brassica* (Esmailbegi *et al.*, 2018; Javed *et al.*, 2020, 2025a). Canola is thought to have evolved from other oil-producing members of the genus *Brassica*, *i.e.*, *B. rapa* and *B. oleracea*. Its genome comprised of AA ($2n = 20$) and CC ($2n = 18$) from two parents (Esmailbegi *et al.*, 2018; Azhar *et al.*, 2025). Plants have waxy-green broad leaves, bright yellow flowers, and elongated pods, which are botanically called ‘siliques’ (Friedt *et al.*, 2018, Javed *et al.*, 2025b-c) (Fig. 1).

Brassica genus is famous for its oil; however, mustard oil is detrimental to human health because of high contents of glucosinolates and erucic acid (Saikia *et al.*, 2018). Conversely, edible oil from *B. napus* has low levels of glucosinolates and erucic acid that make it more suitable for human consumption (Hatzig *et al.*, 2018). *Brassica napus* oil ranked third in the world to fulfill global consumption (Wolko *et al.*, 2019; Azhar *et al.*, 2025). It is 15%–16% of vegetable oil production in the world (Confortin *et al.*, 2019). It has high oil content (*i.e.*, 41%–43%) (Mahmood *et al.*, 2019), low amount of saturated fats (5%–8%) (Yousafi and Saleem, 2020), 60%–65% monounsaturated fats, and a significant amount of unsaturated fatty acids that make it important in reducing liver fat and treating cardiovascular diseases (Welter *et al.*, 2016; Chew, 2020). It has a high smoke point, which is suitable for intensive cooking (Ajmal *et al.*, 2018), margarine manufacturing, browning, and mixed vegetable servings (Chew, 2020).

Canola has an unachieved yield potential of 77.3% in developing countries (Ijaz *et al.*, 2019). The yield gap exists mainly due to crop losses caused by various chewing and

sucking insect pests (Shah *et al.*, 2019). Chewing insects include cabbage butterflies (*Pieris brassicae*), diamondback moths (*Plutella xylostella*), semiloopers (*Trichoplusia* spp.), and mustard sawflies (*Athalia lugens*). Sucking insect pests are comprised of aphids (*Brevicoryne brassicae*, *Lipaphis erysimi*, and *Myzus persicae*) (Mpumi *et al.*, 2020; Javed *et al.*, 2025a–g). Canola aphids (Aphididae: Hemiptera) are the major and the most destructive insect pests of *B. napus* (Nasab *et al.*, 2019; Ahmed *et al.*, 2020; Javed *et al.*, 2025d–g). They are hosted on a range of *Brassica* plants, specifically cabbage, rapeseed, mustard, cauliflower, turnip, broccoli, kale, and Brussels sprouts (Nasab *et al.*, 2019; Razmjou *et al.*, 2019; Javed *et al.*, 2022). They feed on leaves, stems, and blooms to cause heavy yield losses through leaf twisting, flower falling, and pod shattering (Gill *et al.*, 2024).

A grave attack by aphids can cause a yield loss of 60%–77% in *B. napus* (Aslam *et al.*, 2011; Javed *et al.*, 2025c). They could reduce the seed production by 9%–77% and oil content up to 11% (Mousavi, 2017). Aphids are also a vector of about 20 plant viruses, specifically cauliflower mosaic, radish mosaic, mustard mosaic, broccoli necrotic yellows, lettuce mosaic, turnip crinkle, turnip rosette, turnip yellow mosaic, and radish yellow edge virus. Through rapid reproduction, aphids defeat the plant defense, *i.e.*, the glucosinolates-myrosinase system, for which they are also called mustard oil bombs (Ahmed *et al.*, 2018; Ahmed *et al.*, 2020). They sequester glucosinates from plants and keep them separate from their body myrosinase system, and when any predator tries to feed on aphid bodies by biting, the glucosinolates get mixed with myrosinase, causing a release of toxic chemicals with a pungent odor to damage and repel the predator like a bomb (Javed *et al.*, 2022). Aphids are also developing insecticide resistance at a rapid pace, which is making them globally important in canola cultivation (Ahmad and Akhtar, 2013; Kirkland *et al.*, 2023).

2 Biology of aphids

Canola aphids range in size from 2 to 2.5 mm. Their bodies are covered with a waxy coating in case of *B. brassicae*. It is difficult to distinguish *B. brassicae* from *L. erysimi*; however, *L. erysimi* is shorter in size (1.6 to 2.2 mm) and is without a waxy coating (Gill *et al.*, 2024). The third species, *M. persicae*, is of light green to yellowish-green color with a slightly large body. Aphids reproduce both sexually (matting followed by egg laying) and asexually (parthenogenesis) (Cibils-Stewart *et al.*, 2018) (Fig. 2a,b). Morphs that feed on *B. napus* are



Fig 1. Canola (*Brassica napus* L.) plant 75 days after sowing (photo by Muhammad Wajid Javed).

usually wingless; however, winged morphs are also produced. Cibils-Stewart *et al.* (2018) mentioned that under unfavorable ecological conditions, only wingless aphids are produced. Winged morphs appear only in cold winter and usually after sexual reproduction, which occurs during the time of migration (Fig. 2a).

In sexual reproduction, aphids hatch from the eggs and start to develop on primary hosts, *e.g.*, cabbage, collards, broccoli, cauliflower, Brussels sprouts, kale, mustard, rape, kohlrabi, and turnip (Gill *et al.*, 2024). As the contents of amino acids begin to decrease (with the maturity of plant), female forms start to develop winged morphs and begin to migrate toward secondary hosts (herbaceous plants) (Fig. 2a). Here, they develop asexually through parthenogenesis for several generations and produce wingless morphs (Awmack and Leather 2002) (Fig. 2b). There is a coincidence in the quality of primary and secondary host plants. A decrease in nitrogen in the secondary host coincides with an increase in nitrogen in the primary host. Therefore, the winged morphs are produced, which begin to migrate toward the primary host, where they will produce sexually reproducing family members (Moran, 1992). They, later on, copulate and start to lay eggs that hatch in the following year (Fig. 2a).

Biological attributes of aphids vary from species to species and crop to crop (Fig. 2c). Aslam *et al.* (2011) reported distinguished biological attributes of aphids on *B. napus* under laboratory conditions where the reproductive period of female aphids varied up to 6.25 days and fecundity (reproduction capacity) was 30.8 nymphs per female (3.85 nymphs per day). Developmental or pre-reproductive period (time required by immatures to become adults) was 12.5 days (Satar *et al.*, 2005). Longevity duration of females was 16.3 days at 15°C temperature and 35.1 days at 10°C (Soh *et al.*, 2018) (Fig. 2c). However, at 30°C, the longevity reduced to 9.8 days. Lifespan varied from 15.8 days (30°C) to 28.8 days (15°C). Similarly, the fecundity varied from 1.5 (30°C) to 47.1 (25°C) nymphs per female (Satar *et al.*, 2005). Time to complete one generation was recorded as 11.3 days at 30°C and 22.6 days at 15°C, respectively. First instar needed 18.5 days to

become an adult at 10°C and 5.05 days at 30°C, respectively (Soh *et al.*, 2018). Aphids failed to become adults at higher temperatures, *i.e.*, 35°C. Aslam *et al.* (2011) reported three instars of aphids, while Soh *et al.* (2018) mentioned four instars before reaching the adult stage (Fig. 2c).

3 Implications of aphids for growth and yield

During feeding, aphids inject toxic saliva into plants (Javed *et al.*, 2020; 2022; Gill *et al.*, 2024; Javed *et al.*, 2025d). In response to this, growth and yield attributes begin to alter in the hostplant (Khan *et al.*, 2015; Javed *et al.*, 2025c,d), which is of key significance to understanding canola–aphid interaction in a dynamic ecosystem. Canola aphids cause significant losses in growth and yield attributes of *B. napus* by infesting the plants at various stages (Khan *et al.*, 2015; Razaq *et al.*, 2016; Javed *et al.*, 2025e), which, more specifically, include flowering, blooming, and pod formation (Fig. 3). There is a significant decrease in plant height, number of siliques (pods), number of seeds per silique, thousand-seed weight, oil content, and yield per unit area in infested plants. Razaq *et al.* (2011) reported a yield loss of up to 75.06% in *B. napus*, 77.25% in *B. juncea*, and 81.86% in *B. carinata* due to aphid infestation in late-sown brassica in a field environment. Under screen house conditions, 23.65 to 62.15% yield loss was recorded in different genotypes of *B. napus* (Khan *et al.*, 2015). Furthermore, the percentage recovery of oil from seeds (*i.e.*, oil content) and its quality were also affected, with Mousavi (2017) recording an 11% reduction in oil content.

4 Nutrient responses

Plants need 14 nutrient elements for growth improvement and yield enhancement (White and Brown, 2010). These nutrients are macronutrients (required in larger amounts: 1000 to 10000 mg kg⁻¹ of leaf dry weight). They include nitrogen (N), potassium (K), and phosphorous (P) as primary macronutrients, while calcium (Ca), magnesium (Mg), and sulfur (S) as secondary macronutrients. They are efficiently mobile inside plant's vascular area, except for Ca. Others are micronutrients (required in 0.1 to 100 mg kg⁻¹) like iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), boron (B), and chlorine (Cl) (Kirkby, 2012).

Hostplant nutrients have a dual role in aphid–canola interaction. Growth of aphids as well as plants improves when nutrient contents begin to increase (Rowntree *et al.*, 2010). Nutrients are not only essential for plant productivity but also important for aphid performance (Bala *et al.*, 2018). Aphids feed on the hostplant primarily to get a balanced amount of nutrients. However, feeding of aphids reduces hostplant nutrient contents. Riedell *et al.* (2007) reported a 25% reduction in Ca and Mg while challenged by aphids. Aphid infestation also restricts the translocation of micronutrients, *e.g.*, Cu, Fe, and Zn (Khattab, 2007; Javed *et al.*, 2025d). These nutrients fuel the needs of reproduction, growth, and development of aphids (Behmer, 2009). Therefore, it is important to know about the functions of various nutrients in aphids and plant bodies in order to decipher their relative role in plant defense.

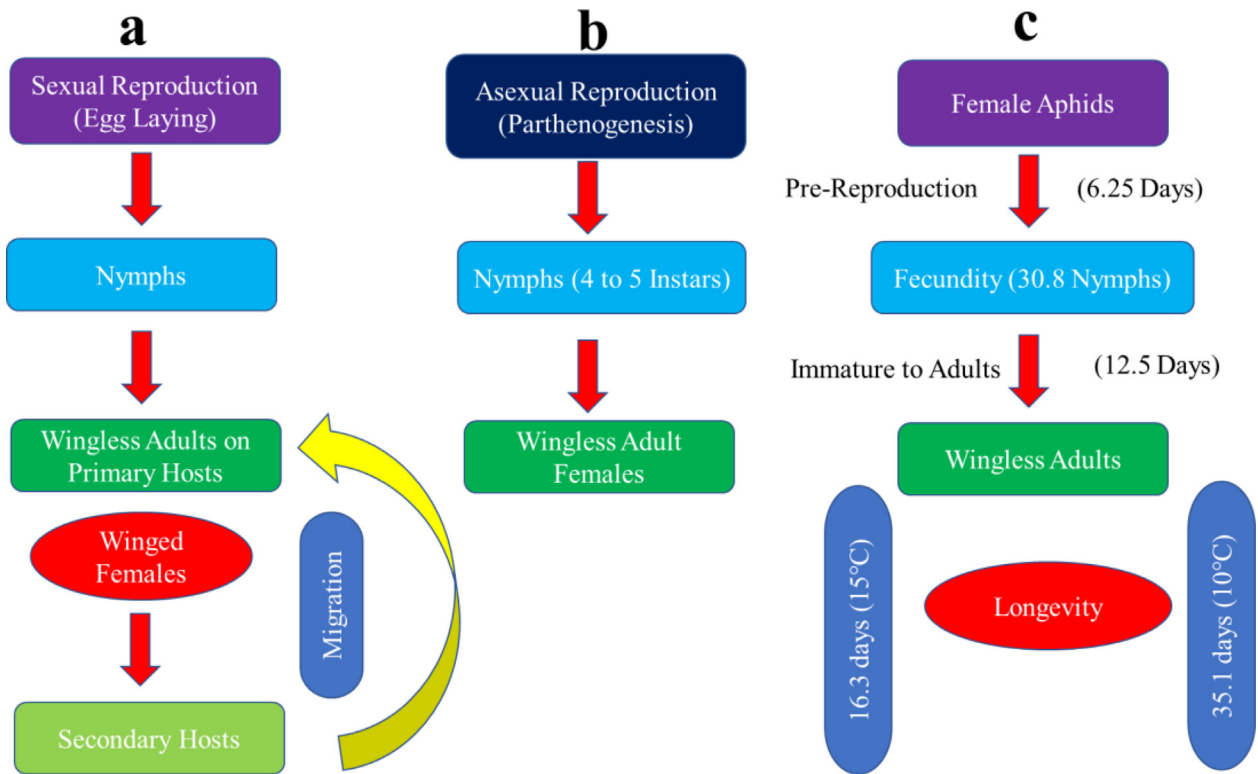


Fig. 2. (a) Sexual mode of reproduction, (b) asexual mode of reproduction, and (c) general biology of aphids in canola.

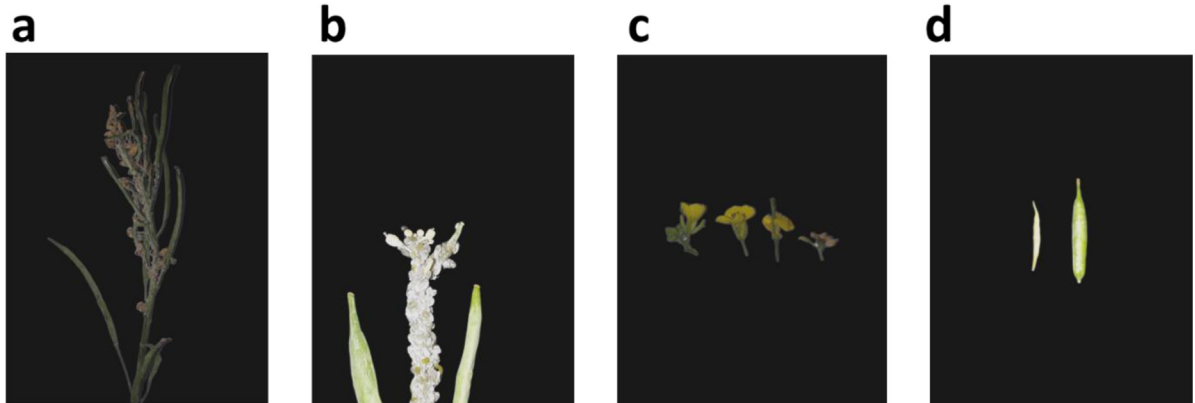


Fig 3. Infested and non-infested parts of canola (*Brassica napus*). (a) Aphid-infested inflorescence, (b) aphid-infested pods, (c) a non-infested flower on the left and infested flowers on right side, and (d) aphid-infested pods on the left and a non-infested pod on the right side. Photo courtesy by Muhammad Wajid Javed.

4.1 Role of nutrients for aphids

Nutrients, especially N, P, and K, along with Ca, Mg, Si, and S, are among the most important ingredients to determine plant defense against insect pests. Insects usually show preference for macronutrients compared to the micronutrients, as indicated in the salt experiment (Trumper and Simpson, 1993). The same is true for aphids. Awmack and Leather (2002) say that nitrogen is one of the fundamental nutrients to determine the fecundity of aphids. Equally, potassium is one of the two important minerals in insects working to regulate cell homeostasis by $\text{Na}^{2+}/\text{K}^{+}$ pumps. At resting potential, a

relatively high amount of K and a low amount of Na are present in the cell. Therefore, K is important in a number of active transport mechanisms in insects (Walter and Difonzo, 2014). Any imbalance between these two can cause paralysis or death of insects. Consequently, K is an essential nutrient in aphid hemolymph (Blow and Dougla, 2019). Being plant feeders, aphids consume a large amount of K^{+} , and any imbalance can injure aphid biological fitness (Javed *et al.*, 2022) (Fig. 4).

Ca is the second most important neurotransmitter in insects and controls the nervous system and functioning of muscles. Ca is a major component of eggshell, and aphids need it at the time of oviposition. Otherwise, Ca remains stored in the form of

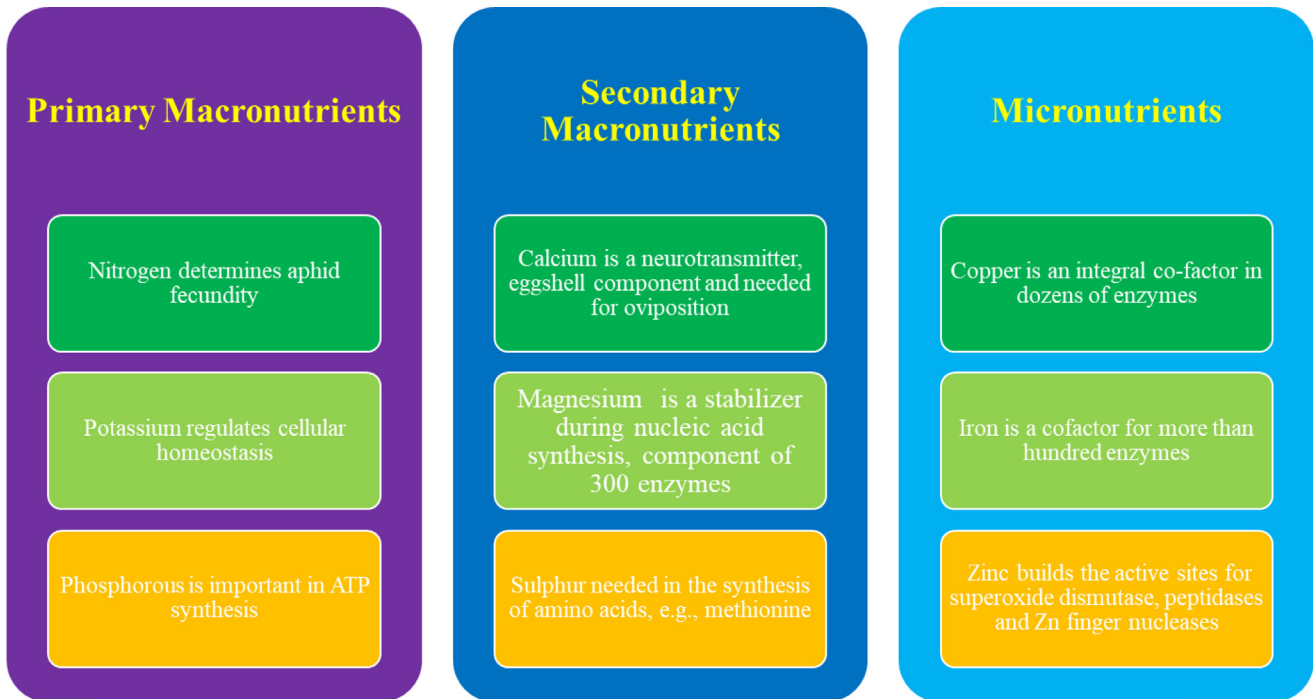


Fig 4. Role of primary and secondary macronutrients along with micronutrients for aphids.

spherites in the Malpighian region (Dow, 2017). On the other hand, Mg functions as a stabilizer for polyphosphates, *i.e.*, MgATP. Polyphosphates play their role during the synthesis of nucleic acids (DNA and RNA). Mg is also an integral component of about 300 enzymes. When the content of Mg increases in an insect's diet, Mg concentrates in the form of tubular stones in Malpighian tubules and may cause hypermagnesemia (Hofmann *et al.*, 2010). Mg is also present in insect mitochondria to play its role in cell energetics (Dow, 2017) (Fig. 4).

Cu is an integral cofactor in a dozen enzymes; therefore, any imbalance in Cu can injure the aphid nervous system (Hwang *et al.*, 2014). The dMTF-1 is an important metal-sensing transcriptional factor in insects to tolerate and resist excessive Cu accumulation (Chen *et al.*, 2008). Similarly, Fe is also a cofactor for more than a hundred enzymes. It is highly toxic in comparison to other metallic ions. It is a key player in producing oxidative stress. Excessive Fe in the diet can cause hemotoxicity in aphids. Similarly, Zn is an important component in enzymatic reactions as it builds the active sites of a number of enzymes (*e.g.*, superoxide dismutase, peptidases, carbonic anhydrase, and Zn finger nucleases—DNA binding proteins) (Carrasco-Rando *et al.*, 2016). Both excess and deficiency of Zn are lethal for aphids (Dow, 2017).

Aphids survive better on plants with high N contents (Tao and Hunter, 2012); however, excessive feeding reduces its contents in plants. Due to the attack of *B. brassicae*, the uptake of nutrients is disturbed in plants. Khattab (2007) recorded a noticeable reduction in the uptake of P and Mg along with K and Ca in plants. Riedell *et al.* (2007) recorded a decrease in leaf N, Ca, and Mg due to infestation of different species of aphids (*Schizaphis graminum*, *Diuraphis noxia*, and *Rhopalosiphum padi*) on wheat and oat. Fe improves aphid reproduction, whereas Ca increases growth and decreases death rates. Ca is also an important secondary messenger and

an integral component of eggshells (Dow, 2017). In addition, micronutrients (*e.g.*, Cu, Fe, and Zn) are important in the maintenance of aphid homeostasis and intracellular symbioses (Behmer, 2009). Moreover, Zn is an important trace element to improve fecundity, growth, and physiological performance of aphids (*M. persicae*) (Alizamani *et al.*, 2020) (Fig. 4). A review of the most recent studies on canola–aphid interaction with respect to nutrient impacts on aphids has also been tabulated (Table 1).

4.2 Role of nutrients for plants

In plants, nutrients are an important determinant of the yield and quality of produce. Nutrients are performing several functions in plants to specify plant growth stage where aphid infestation may cause significant damage (Fig. 5). Uchida (2000) delineated the role of nutrients in plants as follows (Fig. 6):

Canola plants take up nitrogen (N) either in the form of nitrate (NO_3^-) or ammonium (NH_4^+) ions. N is the fundamental constituent of amino acids, which are the building blocks of proteins (Okumoto and Pilot, 2011). Amino acids play their role in building cell protoplasm, which is the fundamental area of cell division. In this way, N helps in the growth and development of plants (Javed *et al.*, 2025g). It is also an important element of enzymes in photosynthesis and respiration. Moreover, it is an integral constituent of chlorophyll and several vitamins. Nitrogen also increases the weight and quality of plant dry matter and seed proteins (Carlisle *et al.*, 2012). Its deficiency or denaturation may cause reduction in growth due to disruption in cell division (Javed *et al.*, 2025a). Aphid-infested, nitrogen-deficient plants show a pale yellow color, which begins from the leaf tips in canola (Khattab, 2007). Later on, chlorosis appears, leading to

Table 1. Recent studies on nutrients in aphid-canola interaction along with their major findings.

Nutrient studied	Research findings	Authors
Soil drenching and foliar treatments of potassium silicate were studied in augmentation with <i>Chrysoperla carnea</i> to manage different species of aphids on canola.	Soil drenching application of potassium silicate followed by <i>C. carnea</i> augmentation was the most effective treatment to reduce aphid population over foliar treatments.	Abbas <i>et al.</i> (2026)
Silicon and ammonium sulfate were studied at 0, 25, and 50 kg ha ⁻¹ dose rate and were evaluated against <i>B. brassicae</i> under field conditions.	Silicon 50 kg ha ⁻¹ reduced the most of aphid population and improved phenolic constituents (flavonoids, phenolic, hydroxybenzoic, and hydroxy cinnamic acids) and canola yield.	Javed <i>et al.</i> (2025b)
0.5 and 1 mM of salicylic and citric acid were applied in association with silicon and ammonium sulfate at 0, 25, and 50 kg ha ⁻¹ dose rates against <i>B. brassicae</i> on canola.	The 50 kg silicon was most effective followed by 25 kg silicon and ammonium sulfate to reduce aphid reproduction, improve crop yield, total phenolics, and economic benefits	Javed <i>et al.</i> (2025c)
Two different formulations of sulfur, <i>i.e.</i> , elemental and bio, were studied independently and in combination with compost against <i>B. brassicae</i> on canola in single and split doses.	Split doses were more useful than single-dose treatments. Mixture of bio sulfur with compost was found to be more useful than the others to improve plant growth and phenolics. Three flavonoids, six hydroxycinnamic acids, and five phenolic acids were activated.	Javed <i>et al.</i> (2025d)
Ammonium sulfate and silicon were studied for improvement in seed yield and nutrient profile against <i>B. brassicae</i> on canola.	Both nutrients improved pest resistance at a 25 kg dose; however, silicon 50 kg was most efficient. Ammonium sulfate 50 kg improved nitrogen, phosphorus, sulfur, and copper, while silicon 50 kg enhanced potassium, calcium, magnesium, iron, silicon, and zinc contents.	Javed <i>et al.</i> (2025e)
The 0.4% foliar treatments of silicic acid were studied against <i>L. erysimi</i> population, gas exchange, and yield responses of rapeseed.	Application of silicic acid significantly reduced the aphid population, improved seed yield, silique per plant, and gas exchange parameters over the control treatments.	Karthik <i>et al.</i> (2024a)
Foliar treatments of silicic acid were examined against <i>L. erysimi</i> biological parameters and defense enzymes in rapeseed.	The 0.4% silicic acid reduced nymph development, adult longevity, and fecundity. Defensive enzymes were increased, including phenylalanine ammonia-lyase, polyphenol oxidase, and peroxidase.	Karthik <i>et al.</i> (2024b)
Nitrogen, phosphorous, and potassium were applied in association with abscisic acid on canola against <i>B. brassicae</i> .	Combination of abscisic acid and fertilizer nutrients induced the antibiosis and antixenosis resistance against <i>B. brassicae</i> along with the enhancement of polyphenol oxidases, peroxidase, phenylalanine ammonia-lyase, phenolics, and glucosinolates.	Dehghan <i>et al.</i> (2023)
Silicon, ammonium sulfate, elemental sulfur, bio sulfur, and compost were investigated against the biological fitness attributes of <i>B. brassicae</i> under greenhouse conditions.	The 25 and 50 kg of silicon were more effective than ammonium sulfate treatments. Likewise, combined use of sulfur formulations with compost was more effective than individual uses to disturb the aphid effective fecundity, intrinsic rate of increase, relative growth rates, reproduction time, nymph survival and Kaplan–Meier functions, and progeny development.	Javed <i>et al.</i> (2022)

defoliation. In aphid-infested plants, a higher rate of nitrogen removal from apical shoots is a major cause of yield reduction (Girousse *et al.* 2005; Javed *et al.*, 2025e).

Plants take phosphorous (P) in the form of orthophosphate as either HPO₄²⁻ or H₂PO₄⁻ ions (Shen *et al.*, 2011). P has a major role in the energy transfer mechanism through adenosine

phosphates (AMP, ADP, and ATP) during photosynthesis and respiration. It is also a vital element of DNA and RNA. It is needed in higher amounts in developing apices of shoots and roots (Shen *et al.*, 2011). P helps in root development, flowering, and seed formation (Javed *et al.*, 2025a). Deficiency of P slows down crop maturity and produces substandard seeds

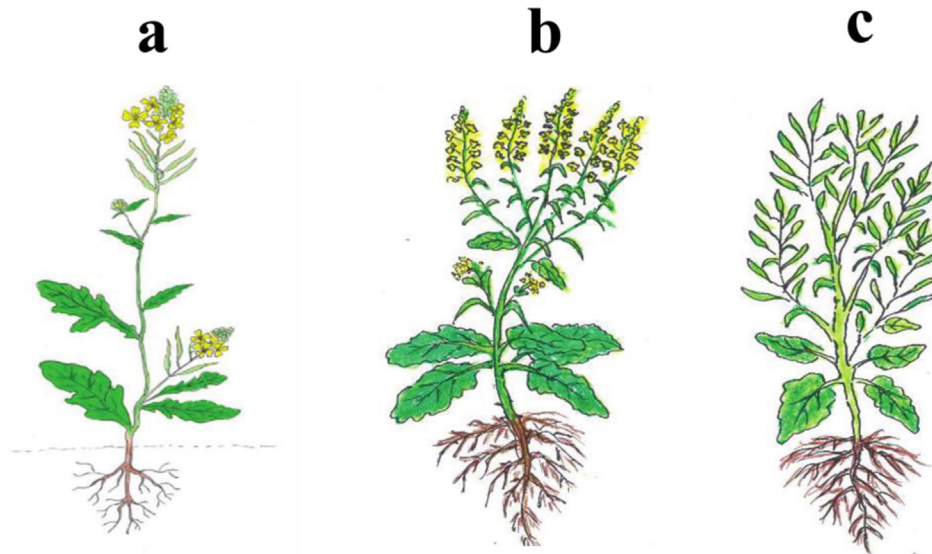


Fig 5. Nutrient flux-mediated growth stages of canola where aphids can cause significant damage. (a) Flowering, (b) blooming, and (c) pod formation.

with low oil contents (Bharose *et al.*, 2011; Javed *et al.*, 2025c). It is a relatively mobile nutrient in plants, and its deficiency produces a dark to blue-green or purple color in plants (Uchida, 2000).

Potassium (K) is available to plants in the form of K^+ ions. It is an important enzymatic activator and is vital in the growth and metabolism of canola (Myers and Gratton, 2006; Javed *et al.*, 2025e). It helps the plants to regulate water consumption by controlling the opening and closing of stomata. During photosynthesis, K manages the electrical charge balance at the site of ATP synthesis. It also assists in translocation of sugars from roots to fruits (Safar-Noori *et al.*, 2018). K also increases the size of the seed and improves the quality of plant produce (Javed *et al.*, 2025c). Its deficiency can cause marginal scorching (chlorosis at the leaf margin) in older leaves. Deficiency of K can also cause stunted growth in canola (Uchida, 2000; Javed *et al.*, 2025e). K-deficient plants have weaker stems and are susceptible to lodging and aphid attacks (Myers and Gratton, 2006; Javed *et al.*, 2025b).

Plants take calcium (Ca) in the form of Ca^{2+} ions. Ca has a prominent role in cell wall synthesis, plasticity, and cell division by regulating plasma membrane permeability. It also plays an important role in the activation of enzymes during protein synthesis and carbohydrate movement (Kirkby, 2012). Ca readily links itself to sulfate, anions, and organic acids. Its combination with organic acids neutralizes them to reduce organic acid toxicity (Uchida, 2000). Ca is important in seed production (*e.g.*, groundnut), and it improves plant yield indirectly by decreasing soil acidity, *e.g.*, liming of soil (Estefan *et al.*, 2013). It also works in maintaining the integrity of cell wall and regulates Na^+/K^+ pumps. It prevents translocation of Na^+ and Cl^- ions in plants to avoid salinity stress (Syeed *et al.*, 2011). Ca is almost immobile and does not translocate in plants. Therefore, its deficiency first appears on younger parts of plants and leaf tips (Kirkby, 2012). The emerging apices of roots and leaves become brown and die, later on. Deficiency of Ca can produce weak stems. Younger leaves may stick together at the margins, which may tear apart

when leaves start to grow. Floral buds may fall prematurely (Uchida, 2000; Javed *et al.*, 2025b).

Magnesium (Mg) absorbed in the form of Mg^{2+} ions in plants. Mg, being the cofactor of different enzymes, activates the phosphorylation process (the fundamental step in energy generation) (Uchida, 2000). It helps in the translocation of carbohydrates in plants and maintains stability of DNA and RNA. It is a mobile nutrient and is a vital component of plant chlorophyll. Mg deficiency usually produces interveinal chlorosis that first appears on older leaves (Kirkby, 2012). *B. napus* may show an orange-yellow color in leaves with green veins. Mg deficiency can appear more quickly in acidic soils or soils receiving high quantities of K or Ca fertilizers (Estefan *et al.*, 2013). Mg-deficient conditions may produce oxidative stress in plants by lowering CO_2 assimilation (Uchida, 2000).

Plants take sulfur (S) in the form of sulfate SO_4^{2-} ions. It is actively involved in the biosynthesis of sulfur-based amino acids (Javed *et al.*, 2025a). Therefore, it participates in protein synthesis (Uchida, 2000). It is also important in the metabolism of vitamin B (co-enzyme A, thiamine, and biotin) (De Pascale *et al.*, 2007). It also helps in the formation of chlorophyll, protein, seeds, nodules, oil, nutrients, glucosinolates, and phenolic contents in *Brassica* spp. and canola (Rehman *et al.*, 2013; Javed *et al.*, 2025a–d). S deficiency can produce chlorosis in younger leaves, and veins show light color. Growth of the plant reduces and maturity of the crop delays. Stems become thin and show excessive stiffness. Such stems may obstruct translocation of nutrients, and plants may lodge early (Demir and Basalma, 2018; Javed *et al.*, 2025g). Its deficiency symptoms are similar to nitrogen and more prevalent in sandy soils with low organic matter (Estefan *et al.*, 2013).

Plant takes copper (Cu) as Cu^{2+} ions. It is an integral component of several photosynthetic enzymes (Uchida, 2000). Cu is also an element of plastocyanin (a chloroplast protein in electron transport chain). It contributes to the stability and synthesis of chlorophyll and other pigments in plants.

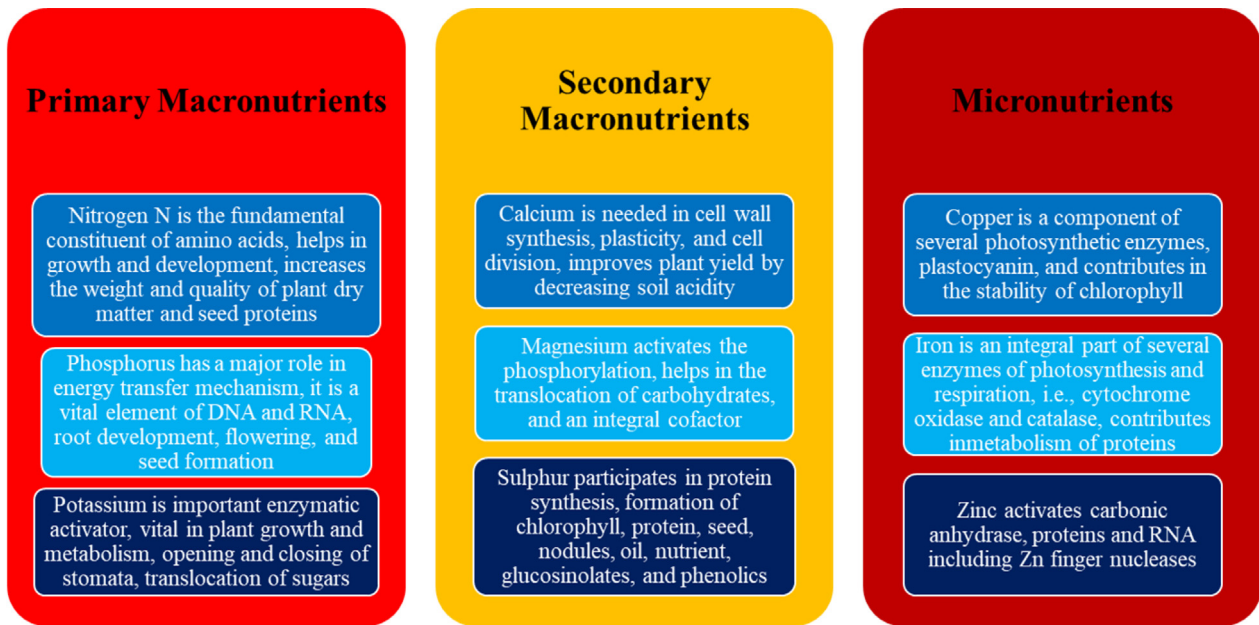


Fig 6. Categorical role of macronutrients (primary and secondary) and micronutrients for canola.

However, Cu toxicity decreases canola growth, causes distortion of new leaves, and results in loss of chlorophyll in the apical meristem (Zaheer *et al.*, 2015; Javed *et al.*, 2025a). Bleaching, defoliation, and twig dieback may occur later on. Male and female reproductive organs may become sterile (Khandekar and Leisner, 2011).

Plants take iron (Fe) either in the form of Fe^{2+} or Fe^{3+} ions. It is an important part of heme enzymes (during photosynthesis). Fe is also an integral part of several enzymes that participate in respiration, i.e., cytochrome oxidase and catalase (Uchida, 2000). Fe, as a component of ferredoxin, is required in the reduction of sulfate and nitrates. It also contributes to the metabolism of proteins (Pavlovic *et al.*, 2013). It is also involved in the biosynthesis of chlorophyll molecules. Therefore, Fe deficiency can cause interdigital chlorosis, which is more common in alkaline or excessively limed soils. Newly emerging leaves may appear white (Uchida, 2000).

Plants uptake zinc (Zn) in the form of Zn^{2+} ions (Roy and Ghosh, 2020). Zn has an important role in the formation of tryptophan (a player in the production of indole acetic acid in plants). It is important in several metabolic processes, as it is a part of different metal-containing enzymes, e.g., dehydrogenases (Uchida, 2000). It activates carbonic anhydrase enzyme, specifically. Zn is also vital in the production of protein and RNA, including Zn-finger transcription factors (Carrasco-Rando *et al.*, 2016). In *B. napus*, Zn deficiency can produce stunted plants with inter-venial chlorosis on lower, older leaves. Sometimes, chlorotic tissues may drop out from the leaf area. This may alter plant photosynthesis and growth (Uchida, 2000).

4.3 Role of nutrients in plant defense against aphids

Any alteration in nutrient contents in plants is strongly linked to plant defense and performance of aphids. Tao and Hunter (2012) showed that feeding of aphids on nutritionally deficient plants reduces aphid body mass. High activity of

aphids was noted on plants with higher nutrient contents, particularly nitrogen (Garratt *et al.*, 2010a,b). Nitrogen is one of the most important nutrients to improve the aphid performance. Most of the studies reported an improved development of herbivores under an excessive supply of nitrogen (Lu *et al.*, 2007). A few studies mentioned that nitrogen negatively affects the development of aphids on canola when applied at moderate rates (Javed *et al.*, 2025a, e). Nitrogen affects the growth of aphids by regulating the availability of amino acids (Javed *et al.*, 2022). Excessive use of nitrogen was found to reduce the contents of lignin in plants, which is the fundamental constituent of resistance against aphids (Torres-Olivar *et al.*, 2014). An adequate supply of nitrogen helps the plants to synthesize physical defense compounds, e.g., lignin and suberin, as a potent tool of aphid resistance (Wang *et al.*, 2020).

Conversely, phosphorus (P) is not a limiting factor for insect growth as nitrogen is. Due to its role in the synthesis of ATP, enzymes, and nucleic acids, phosphorus plays a diverse role in plant defense, especially against hemipterans (Singh and Sood, 2017). Equally, potassium (K) defends the plants by modulating biochemical contents, specifically amino acids, silica, and carbohydrates in plants (Imas, 2013). K, again, is an important regulator of Na/K pump to maintain homeostasis in aphids, and its imbalance affects aphids negatively (Dow, 2017; Singh and Sood, 2017).

Due to injury of aphids, the particular type of proteins called *forisome* accumulates across the wounded sieve tubes to restrict the loss of phloem (Will *et al.*, 2007). This plugging is mediated by the influx of Ca^{2+} ions. Aphids adopt an alternate mechanism for continuous flow of sap in their mouths. They increased the transcript levels of a number of Ca-binding proteins, e.g., calmodulin-binding proteins, calcium-dependent protein kinases, pinoid-binding protein, calcium-transferring ATPases, and calcium-binding calreticulin (Giordanengo *et al.*, 2010). Induction of Ca-binding proteins produces senescence in plants. *Brevicoryne brassicae* was

found to induce senescence-associated proteins in *A. thaliana* (Will *et al.*, 2007). Being an important component of insect eggshells, any imbalance in Ca can significantly affect the new offspring of aphids (Dow, 2017).

In a similar way, magnesium (Mg) also defends against insects, as it is an important stabilizer of ATPs and ADPs. An increase in the contents of Mg during feeding increases the chances of tubular stones in insects (Wessing and Zierold, 1992). Also, iron (Fe) is a cofactor of several enzymes in insects. Fe can cause damage to aphids by hemotoxicity (Graca-Souza *et al.*, 2006). Parallel to these, copper (Cu) defends the plants by damaging the nervous system of insects (Hwang *et al.*, 2014). It is also a part of several enzymes as a cofactor. Similarly, zinc (Zn) is also a critical element, and it forms the active sites of several enzymes. Excess of Zn can generate hard concretions, *e.g.*, Zn-stones in aphids and other insect pests (Killilea *et al.*, 2015).

5 Phenolic responses

Phenolics are the allelochemicals that perform various functions to defend the plants against aphids and other pests. Phenolic compounds affect the food intake, disturb the enzymatic catalysis, and delay aphid growth (Czerniewicz *et al.*, 2017; Javed *et al.*, 2025c). Vuolo *et al.* (2019) defined the phenolic compounds as one of the important anti-oxidative metabolites that are biosynthesized through the phenylpropanoid or shikimate pathway. Chemically they are composed of a benzene ring with one or several hydroxyl subunits (Tsao, 2010). They are usually derived from phenylalanine, which, in turn, is produced by the activity of phenylalanine ammonia-lyase (PAL) enzymes (Tajik *et al.*, 2019). This enzyme is induced particularly from the elicitation of phytohormones (*e.g.*, jasmonic acid), which are produced under octadecanoid pathways. Later on, they transfer the amino acids to the site of production of the secondary metabolites.

Several studies have shown the defense role of phenolic compounds against insects or pathogens (Khoshfarman-Borji *et al.*, 2020; Javed *et al.*, 2025c–e). Besides plant defense, these chemicals provide color, scent, and other tangible properties to plants. They also contribute in indirect plant defense through alternation in host plant quality to restrain aphid development and modify host plant preference (Khoshfarman-Borji *et al.*, 2020; Javed *et al.*, 2022, 2025b–d). Kumar *et al.* (2017) showed that phenolic compounds were inversely related to aphid preference. Phenolic compounds are also the best antioxidants to relieve plants from oxidative stress (Tajik *et al.*, 2019).

5.1 Classification of phenolic compounds

Jacobo-Velázquez and Cisneros-Zevallos (2020) classified the phenolic compounds on the basis of hydroxy or methoxy subunits. Phenolic compounds have one hydroxy (4-hydroxybenzoic acid and *p*-coumaric acid), one hydroxy and one methoxy (vanillic acid and ferulic acid), one hydroxy and two methoxy groups (syringic acid and sinapic acid), and two hydroxy subunits (protocatechuic acid and caffeic acid). In Brassica, sinapic acid is the most abundant phenolic compound (Williamson and Clifford, 2010). Phenolic acids can be either

hydroxy cinnamic acid (C6-C3) or hydroxy benzoic acid (C6-C1), with at least one benzene ring in their structure (Williamson and Clifford, 2010). Chrzanowski (2012) categorized phenolic acids on the basis of the number of carbon atoms (length of the side chain), *e.g.*, benzoic, cinnamic, and phenylacetic acid.

Hydroxycinnamic acids (C6–C3) exist either in *cis* or *trans* formation with double bonds. They exist in the form of hydroxy acid condensates, mono/disaccharides (producing esters), alcohols, or amides. While hydroxybenzoic acid (C6–C1) usually comprised of ellagic, gallic, salicylic, protocatechuic, 4-hydroxybenzoic, gentisic, syringic, vanillic, and hexa-hydroxy-diphenic acids (dilactone and ellagic acid). They occur in conjugate forms (Williamson and Clifford, 2010). Formation of hydroxybenzoic acid is rather a complex process. They may be the direct product of the shikimate pathway or produced from the derivatives of cinnamic acid (Averesch and Krömer, 2018). The basic framework of vanillic acid derives from ferulic acid, whereas that of syringic acid derives from sinapic acid. Caffeic acid or *p*-hydroxybenzoic acid produces protocatechuic acid. Hydroxybenzoic acids also produce vanillic, gallic, syringic, and protocatechuic acids (Spilioti *et al.*, 2014).

Parallel to these, flavonoids are the largest group of phenolic compounds having low molecular weight, carrying 15 carbons (C6–C3–C6). They have two benzene rings (A and B), which are held together by a C3 linkage. Ring A is derived from acetate *via* the malonate pathway, whereas ring B is derived from phenylalanine by the shikimate pathway (Williamson and Clifford, 2010). In addition, the third ring, called ring C, is responsible for producing varieties in flavonoids, *e.g.*, anthocyanidin, flavonols, flavanols (catechin), flavanones, flavones, isoflavones, and flavanols.

Flavonoids are among the most important groups. They exist as glycosides with relatively stable bonds with sugars, and hence, are less bioavailable. They are yellow or red in color due to the presence of chromophores, which produce different colors in seeds, flowers, and fruits. Flavonols and flavones are red in color, whereas flavanones are either brownish or colorless (Brouillard and Dangles, 2017). They exist as polyphenols (Brouillard and Dangles, 2017). They contain more than one aromatic ring, mostly C15 (Iwashina, 2003). Flavonoids destroy free radicals, and therefore, they are important against herbivore-induced oxidative stress (Brouillard and Dangles, 2017). Around 5000 flavonoids are present in plants, and only a few of them are responsible for plant defense (Iwashina, 2003). Khan *et al.* (2011) and Javed *et al.* (2025c) found that flavonoids, especially kaempferol, quercetin, and myricetin, were indispensably reduced in *B. napus* due to *B. brassicae* infestation. Xiao *et al.* (2019) also described a significant manifestation of flavonoids in response to herbivores in Brassica. They found quercetin as a major flavonoid that exist as glycosides called rutin (Ateyyat *et al.*, 2012).

Roughly 70% of plants contain flavonoids. Other groups are anthocyanidins, proanthocyanidins, leucoanthocyanidins, flavonol, flavones, and flavan (Iwashina, 2003). Flavonols (myricetin, quercetin, kaempferol, isorhamnetin, and rutin) are among the most important class of flavonoids, which are responsible for pest resistance (Samanta *et al.*, 2011). In flavonoids, the occurrence of two OH groups contributes to antioxidant activity, while the third OH group reduces this activity (Qayyum *et al.*, 2016). Table 2 describes categories,

Table 2. Categories, sub-types, specific compounds, and the significance of major classes of phenolic compounds in canola.

Categories	Sub-types	Specific compounds	Significance
Hydroxycinnamic acids	Sinapates	Sinapic acid, sinapine, and sinapoyl glucose	Primary phenolic compounds. Sinapine (sinapoyl choline) is the key anti-nutrient.
	Ferulates	Ferulic acid and feruloyl choline	Present in cell wall, contributes to structural integrity of plants.
	Other acids	<i>p</i> -coumaric, chlorogenic, and caffeic acid	Present in seeds in minute quantity but higher in vegetative plant tissues.
Hydroxybenzoic acids	Benzoic derivatives	Syringic, salicylic, vanillic, <i>p</i> -hydroxybenzoic acids	Minor constituents; released during alkaline hydrolysis of plant tissues.
Flavonoids	Flavonols	Quercetin, isorhamnetin (glycosides), and kaempferol	Powerful antioxidants and are found in leaves and seed coats.
	Anthocyanins	Cyanidin-3-glucoside, pelargonidin	Role in pigmentation levels are usually low in yellow/brown canola.
	Flavones	Apigenin and luteolin	Present in very small quantities compared to flavonols.
Tannins	Condensed tannins	Proanthocyanidins and procyanidins (dimers and trimers)	Present in the seed coat and associated with protein digestibility issues.
Lignin and lignans	Hydrolyzable	Gallotannins	Present in negligible amount.
	Lignans	Pinoresinol, secoisolariciresinol, and lariciresinol	Phytoestrogens present in the fiber of seed meal.
	Lignin	Guaiacyl (G) and syringyl (S) units	High-molecular-weight polymers and are the component of the insoluble fibers.

specific compounds, and the significance of various phenolic compounds that exist in canola (*B. napus*).

5.2 Biosynthesis of phenolic compounds

Phenolic compounds are produced due to the transformation of benzene ring-based amino acids, *e.g.*, phenylalanine and tyrosine (Chrzanowski, 2020). Anaerobic removal of the ammonia group from phenylalanine and tyrosine in the presence of L-phenylalanine ammonia-lyase (PAL) and tyrosine ammonia lyase (TAL) produces *trans*-cinnamic acid and *p*-coumaric acid, respectively (Czerniewicz *et al.*, 2017). Later on, condensation of three acetate subunits with *p*-coumaroyl-CoA, catalyzed by chalcone synthase, produces various classes of flavonoids (*e.g.*, anthocyanins, proanthocyanidins, flavones, flavandiols, flavonols, and isoflavonoids) (Ferrer *et al.*, 2008). Products of phenylpropanoids produce ferulic acid (dehydration), caffeic acid (hydroxylation), and *p*-coumaric acid (methylation). Both free and complex formations of cinnamic acids exist in the form of *depsides* or *glycosides*. They are present in cell nucleus, cell wall, and vacuole (Czerniewicz *et al.*, 2017).

Hydroxycinnamic acid and hydroxybenzoic acid are the derivatives of non-phenolic cinnamic and benzoic acid, which are biosynthesized through the shikimate pathway from L-phenylalanine and L-tyrosine, respectively (Williamson and Clifford, 2010). Initially, L-phenylalanine and L-tyrosine undergo deamination to produce either cinnamic or *p*-coumaric acid. Later on, their benzene rings combine with hydroxyl (OH) groups (*i.e.*, hydroxylation) and methyl (CH₃) groups (*i.e.*, methylation) to produce ferulic and caffeic acid, respectively. Occasionally, the branched chain of cinnamic acid may be degraded to produce benzoic acid, which is

hydroxylated and methylated to generate protocatechuic acid and *p*-hydroxybenzoic acid (Vuolo *et al.*, 2019).

Another explanation of phenolic compound biosynthesis is based on the production of cinnamic acid from L-phenylalanine (under the action of PAL enzymes). This is the very first stage to produce phenolic compounds. Later on, cinnamic acid is changed into *p*-coumaric acid under the action of cinnamic acid 4-hydroxylase (CAH). Then *p*-coumaric acid is converted into caffeic acid and *p*-hydroxybenzoic acid (both are the derivatives of hydroxybenzoic acid). Caffeic acid is methylated to form ferulic acid. Ferulic acid is then methylated to produce sinapic acid. Later on, *o*-coumaric acid is also formed from cinnamic acid to produce salicylic acid. Salicylic acid is finally transformed into gentisic acid that, in turn, changes into *o*-pyrocatechuic acid (Fig. 7).

5.3 Mode of action of phenolic compounds against aphids

Phenolic acid and polyphenol oxidases (PPO) are naturally present in plants in isolated organelles. When the tissue is damaged due to aphid puncture, the phenolics and their detoxifying enzymes encounter each other to elicit a potent phenolic defense response (Altunkaya and Gökmen, 2009). Brassica phenolics produce hostplant defense against aphids through antibiosis, antixenosis, and anti-symbiosis (Javed *et al.*, 2020, 2025e). Chrzanowski *et al.* (2012) and Javed *et al.* (2025c) described the antibiotic mechanism of phenolic compounds against aphids through reduction in development, survival, and reproduction fitness. Infestation of aphids increases the synthesis of amino acid peptides (*e.g.*, systemin) to elicit plant lipase in cell membrane to liberate linolenic acid.

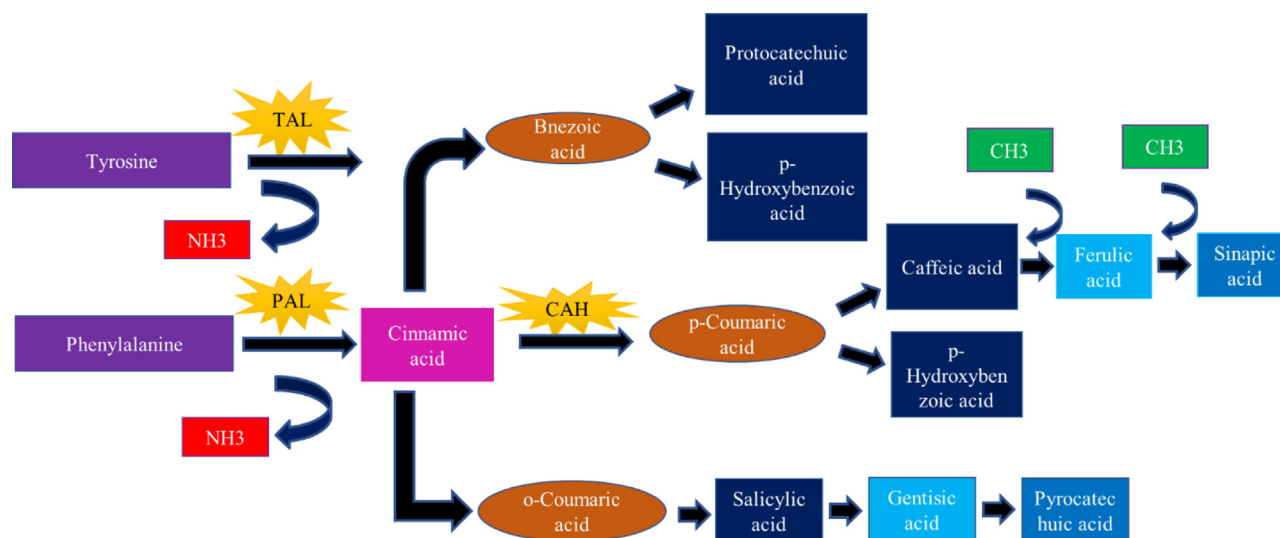


Fig 7. Biosynthesis of hydroxybenzoic and hydroxycinnamic acid from amino acids tyrosine and phenylalanine, using tyrosine ammonia lyase (TAL), L-phenylalanine ammonia-lyase (PAL), and cinnamic acid 4-hydroxylase (CAH) enzymes. NH_3 and CH_3 show deamination and methylation, respectively. Figure courtesy by Muhammad Wajid Javed.

The linolenic acid induces jasmonic acid pathway to produce proteinase inhibitor, peroxidase, and polyphenol oxidase (Vuolo *et al.*, 2019).

These oxidizing enzymes act on plant phenolics to form quinones and reactive oxygen species. Quinones, when ingested by the aphids, work as anti-nutritional proteins to reduce nutrient intake and food digestion (Dampc *et al.*, 2020; Javed *et al.*, 2025b, f). The proteinase inhibitors attach themselves to aphid digestive enzymes in the midgut, therefore affecting food digestion. Phenolics may also inflict injuries to aphid midgut by the mechanism of oxidative stress. They freely bind with *thiols* inside midgut epithelium to decrease the availability of non-protein *thiols* and vitamin C (ascorbic acid).

Similarly, flavonoid, *e.g.*, quercetin, interferes in the insect molting by reducing the expression of ecdysone receptor (EcR) genes (Oberdörster *et al.*, 2001). Besides these, flavonoids and phenolic acids (vanillic, ferulic, and 4-hydroxybenzoic acids) have been recorded to suppress the acetylcholinesterase enzyme, which is responsible for molting in rice weevils (Maazoun *et al.*, 2019). Flavonoids, *e.g.*, taxifolin is documented to reduce glutathione S-transferase expression (insecticide detoxifying enzyme in insects) (Wang *et al.*, 2016).

Phenolic compounds also cause antixenosis. They make the plant a less preferable host and reduce food palatability (Chrzanowski *et al.*, 2012). Dreyer and Jones (1981) reported dihydrochalcones (flavonoids), as an effective deterrent for aphids (*e.g.*, *S. graminum* and *M. persicae*). Phenolics may change the plant morphological attributes (wax, hairiness, and color) or discharge deterrent volatile compounds (Vendramim and Guzzo, 2012), which ultimately result in reduced host colonization. However, if the aphids have still been able to colonize the plants, phenolics may trigger a hypersensitive response using peroxidase enzymes to lignify plant tissues. This lignification appears as a strong physical barrier against aphid stylets. In addition, peroxidase transforms chlorogenic acid to chloroquinone, which attaches to the amino acids to decrease their availability (Appel, 2017).

Anti-symbiosis is another mechanism of phenolic defense to reduce aphid populations (Czerniewicz *et al.*, 2017; Javed *et al.*, 2025a–e). Czerniewicz *et al.* (2017) demonstrated that an increase in the contents of various phenolics negatively correlated with the population of aphids (*S. avenae*) in wheat. Phenolics may affect pre-reduction time, fertility, and population growth of aphids (Gantner *et al.*, 2019). In the same way, flavonoids (quercetin and myricetin) cause endocrine toxicity in aphids. Both quercetin and myricetin, in the presence of Fe^{3+} , enhances the production of OH radicals from hydrogen peroxide at pH 4.7. Quercetin and myricetin may also cause DNA damage in aphids (Ateyyat *et al.*, 2012). Quercetin causes DNA damage through the production of hydrogen peroxide (Sosa *et al.*, 2000).

Therefore, to counter the phenolic defense, aphids detoxify the phenolic compounds and transform them into non-toxic derivatives using salivary sheath enzymes (peroxidases, phenoloxidases, and pectinases) (Cherqui and Tjallingii, 2000). In short, plant triggers the phenolic defense in response to aphid feeding. Simultaneously, aphid tries to counter the defense by synthesizing peroxidase and polyphenol oxidase to oxidize phenolics into less toxic compounds (Xiao *et al.*, 2019; Dampc *et al.*, 2020). Table 3 highlights major studies on recent findings in aphid-phenolic interactions in canola.

5.4 Functions of plant phenolic compounds

The mentioned functions of phenolic compounds are referred from PubChem (<https://pubchem.ncbi.nlm.nih.gov/>).

Myricetin is an efficient inhibitor of cyclooxygenase-1, which is responsible for preventing neoplasm or tumor. It is an important plant metabolite, an antioxidant, a hypoglycemic agent, and a food component. Quercetin is an anti-cancer agent, a chief bioflavonoid in human food, an antioxidant and antibacterial agent. It prohibits cell cycle at G1 phase and efficiently inhibits heat shock proteins. This also inhibits

Table 3. Recent studies on aphid-phenolic interactions in canola.

Phenolics studied	Research findings	Authors
<i>Aphis gossypii</i> adaptive divergence was studied on different leguminous hosts in association with defense chemicals.	Aphids fed more on cowpeas with excessive salivation and 75% more honeydew secretions, while the converse happened on hyacinth, probably due to higher phenolics.	Pan <i>et al.</i> (2026)
Plant secondary metabolites, particularly phenolics, were investigated for resistance against aphids.	Aphid population is reduced due to enzymatic actions, antioxidant defense activations, behavioral alterations, and suppression of digestion, and host defense signaling causes antibiosis and antixenosis.	Farhan <i>et al.</i> (2025)
Phenolic compounds were studied in canola through reverse phase (RP)-HPLC in response to <i>B. brassicae</i> infestation and sulfur treatments in contaminated soils.	Quercetin, ferulic, gallic, caffeic, chlorogenic, <i>m</i> -coumaric, sinapic, syringic, vanillic, ferulic, <i>p</i> -coumaric, and cinnamic acids were activated.	Javed <i>et al.</i> (2025)
Phenolic profile in canola was studied against <i>B. brassicae</i> infestation in response to silicon and ammonium sulfate treatments.	Myricetin, chlorogenic, gallic, <i>m</i> -coumaric, <i>p</i> -coumaric, and sinapic acids were activated in response to silicon treatment, whereas quercetin, sinapic, and syringic acids were elicited due to ammonium sulfate in the AS 50 kg ha ⁻¹ treatment.	Javed <i>et al.</i> (2025)
RP-HPLC profile of phenolic compounds was estimated against <i>B. brassicae</i> on canola under the treatments of salicylic and citric acid biostimulants.	The 1 mM salicylic acid enhanced gallic, cinnamic, <i>m</i> -coumaric, and <i>p</i> -coumaric acids, while 1 mM citric acid accumulated myricetin, quercetin, caffeic, syringic, chlorogenic, vanillic, ferulic, and sinapic acids. Salicylic acid, being a phenolic compound, significantly reduced the aphid abundance.	Javed <i>et al.</i> (2025)
Plant secondary metabolites, specifically phenolics, were reviewed for their types, insecticidal activities, and mechanisms of action.	Both simple (hydroxybenzoic acids, phenolic acids, and catechols) and complex phenolics (tannins, lignins, tannic acid, and flavonoids) were important against Brassica aphids, <i>e.g.</i> , <i>L. erysimi pseudobrassicae</i> and <i>M. persicae</i> , to reduce aphid populations through aphicidal, repellent, and induction of plant volatiles.	Farhan <i>et al.</i> (2024)
Shoot metabolome of <i>B. nigra</i> was studied against different aphid species in response of nematode infection	Aphid survival was reduced where hydroxycinnamic acid, glucosinolates, and salicylic acid-2-O-β-d-glucoside were dominant.	Pajar <i>et al.</i> (2024)
Total phenolics were assessed against <i>B. brassicae</i> under the elicitation treatments of salicylic acid, chitosan, and gamma-aminobutyric acid treatments.	Combination of salicylic and gamma-aminobutyric acids provided the highest total phenolic content against cabbage aphids and reduced their population.	Shahrokhi <i>et al.</i> (2024)
Phenolic responses against <i>B. brassicae</i> on canola were examined under fertilizer and abscisic acid treatments.	Fertilizers and abscisic acid produced strong antibiosis and antixenosis against <i>B. brassicae</i> through the elicitation of total phenolic compounds and phenol-based enzymes, particularly polyphenol oxidases and phenylalanine ammonia-lyase.	Dehghan <i>et al.</i> (2023)
Phenolic- and glucosinolate-based pest resistance against aphids and other insect complexes was assessed in different accessions of <i>B. carinata</i> .	Accessions having high levels of phenolics and glucosinolates were resistant against aphids and other pests.	Zhou <i>et al.</i> (2022)

lipoxygenase and cyclooxygenase pathways to restrict inflammatory agents. Quercetin also serves as an important scavenger of radicals.

Gallic acid is an astringent (constricts the skin), an antioxidant, an inhibitor of cyclooxygenase-2, an important plant metabolite, an antineoplastic agent, a human xenobiotic, and an inducer of apoptosis. Syringic acid is an important plant metabolite, which is derived from gallic acid. Vanillic acid is

also an important plant metabolite and flavoring agent. It is an intermediary product of the biotransformation of ferulic acid to vanillin.

Caffeic acid is an orally bioavailable plant metabolite with anti-oxidative, anti-inflammatory, and anti-cancer properties. It averts free radical-mediated DNA damage. Its *trans* form is more abundant, but *cis* structure is also present in plants. It is an inhibitor of lipoxygenase and glutathione transferase.

Chlorogenic acid is a product of *trans*-caffeic acid and quinic acid. This is an intermediate metabolic product during the synthesis of lignin. It is actually a tannin.

Ferulic acid also existed in *cis* and *trans* structures. It is an antioxidant, a plant metabolite, an anti-inflammatory agent, an apoptosis inhibitor, a human xenobiotic, and a MALDI (matrix-assisted laser desorption/ionization) matrix material. Coumaric acid is present in *ortho*, *meta*, and *para* formations. It is also an anti-inflammatory, antimicrobial, anticancer, and antioxidant agent. It reduces peroxidation of lipids with antioxidant and antimicrobial properties. Sinapic acid is also an important antibacterial, anti-inflammatory, anti-mutagenic, anti-glycemic, anticancer, and neuroprotective agent.

5.5 Role of phenolic compounds in plant defense against aphid

Studies have described the role of phenolic defense during aphid feeding, which is regulated by PAL enzymes (Smith and Boyko, 2007). Phenolic compounds that work against aphids may comprise myricetin and quercetin (flavonoid), gallic acid, syringic acid, and vanillic acid (hydroxybenzoic acid), along with caffeic acid, chlorogenic acid, ferulic acid, *m*-coumaric acid, *p*-coumaric acid, sinapic acid, and *trans*-4-hydroxy-3-methoxy cinnamic acid (hydroxycinnamic acid) (Chrzanowski and Leszczyński, 2008; Czerniewicz *et al.*, 2017; Gantner *et al.*, 2019). Ciepiela and Chrzanowski (2001) recorded higher contents of ferulic acid in aphid-resistant winter triticale. Aphid biological fitness was also affected negatively due to different phenolic acids.

Here, *p*-coumaric acid reduced the number of *S. avenae* nymphs (Chrzanowski, 2012). Chrzanowski (2012) also recorded a noticeable decrease in fecundity and population growth when *S. avenae* fed on caffeic acid-treated plants. Cabrera *et al.* (1995) also noticed that feeding of aphids could activate the plant phenolic defense and could increase the contents of caffeic acid to reduce the survival of aphids. Gantner *et al.* (2019) also reported a smaller number of aphids (*Myzocallis coryli*) on hazel cultivars having higher contents of gallic, chlorogenic, and caffeic acid.

Chrzanowski and Leszczyński (2008) also showed that wheat plants with higher levels of ferulic and *o*-coumaric acid usually had lower populations of aphids. However, Gantner *et al.* (2019) presented a contradictory finding and showed that higher ferulic acid may not make the plant resistant to aphids. Czerniewicz *et al.* (2017) showed that the contents of caffeic, *o*-coumaric, *p*-coumaric, and chlorogenic acid increased in response to aphid feeding, but levels of ferulic acid remained unchanged. A few important phenolic acids, *e.g.*, chlorogenic acid, *p*-hydroxybenzoic acid, and (+)-catechin influenced the migratory flight of aphids (*R. padi*) from bird cherry-oats toward triticale and orchard grasses (Czerniewicz *et al.*, 2011).

In flavonoids, quercetin and its derived form (rutin) are the most important group of flavonols that work against aphids. Tosh *et al.* (2003) reported a number of negative effects of quercetin on insect pests. Ateyyat *et al.* (2012) also found a significant decline in aphid population (*Eriosoma lanigerum*) in response to quercetin, rutin (a derivative of quercetin), and naringin. Sosa *et al.* (2000) found quercetin to reduce larval growth in *Tenebrio molitor*.

Łukasik and Goławska (2013) showed that phenolics (quercetin) also prolonged the pre-reproductive period and developmental time of aphids (*S. avenae* and *R. padi*). Higher mortalities were reported on plants having higher contents of phenolics. On the other hand, lower contents of quercetin reduced the ingestion, while higher contents blocked the feeding of aphids. Łukasik and Goławska (2013) also demonstrated negative effects of phenolics (luteolin and genistein) on feeding of aphids (*Acyrtosiphon pisum*). Similarly, Łukasik *et al.* (2017) showed the negative impacts of quercetin on aphids (*A. pisum*) on Fabaceous plants.

6 Prospects and applications of the nutrients and phenolics for canola development

The future of protecting canola crops relies on leveraging interaction between plant nutrition and phenolic chemistry. Instead of depending solely on heavy sprays of pesticides, researchers are looking at how we can fuel a plant's internal security system. By fine-tuning the nutrients we provide—specifically sulfur, potassium, and silicon—we aren't just making the plant grow faster; we are effectively turning the switch on for the plant's ability to produce phenolic compounds. These phenolics, which include substances like ferulic, chlorogenic, caffeic, coumaric, and sinapic acids, act as a multi-layered defense. They lignified the plant's cell walls, making it physically harder for aphids to pierce the tissue, and they turned the plant's sap into an indigestible, bitter, unappealing food that stunts the pests' ability to survive.

The real prospect here is moving toward a “bottom-up” defense-mediated strategy. By using metabolic engineering or precision nutrient application, a canola plant's defense could be optimized against aphids. This shift is not just about plant health; it is about a more sustainable way toward canola production. When a plant can defend itself through activation of its own built-in defense, we reduce our dependence on synthetic chemicals, protecting the environment while ensuring that canola remains a high-yielding crop for the future.

7 Conclusion

Both aphids and canola have developed an intricate pattern of relation that is dynamic in a continuously evolving environment. Aphids feed on canola plants and cause severe damage. However, hostplant nutrients and phenolic compounds in canola play a vital role for plant defense against aphids. Aphids require nutrients for biochemical and biological needs, while plants require them for growth, yield, and sustainable vigor. Both macro- and micronutrients are essential for aphids as well as canola growth, having different roles and functions in both organisms. On similar lines, the role of phenolic compounds is also pivotal in aphid–canola interaction, where phenolic compounds play an interactive role of defense, plant vigor improvement, and aphid management. Instead of a single line of defense, phenolic compounds target aphids with a multilayered defense: they strengthen the plant's tissues to make them physically harder to feed, they make the

sap into a less digestible component, and they even release plant volatiles that produce an antixenotic response in aphids. By focusing on these, we can breed “smarter” canola varieties that are naturally resilient and consume less pesticides and provide crop produce.

Acknowledgments

The author acknowledges the critical comments and review by Dr. Lewis J. Wilson, CSIRO, Australia to improve the quality of this manuscript.

Funding

No funding was received for this publication.

Conflicts of interest

The author has no conflict of interest to declare related to this publication.

Author contribution statement

Muhammad Wajid Javed conceptualized, collected the data, wrote, and reviewed the manuscript.

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Cite this article as: Muhammad Wajid Javed. 2026. Deciphering canola- aphid interaction: A review on the role of hostplant nutrients and phenolic compounds. *OCL* 33: 13. <https://doi.org/10.1051/ocl/2026006>