Camelina sativa as an Allelopathic Potential Cover Crop

Subjects: Anatomy & Morphology

Contributor: Martina Ghidoli, Michele Pesenti, Federico Colombo, Fabio Francesco Nocito, Roberto Pilu, Fabrizio Araniti

Camelina sativa, known for its high oil content and adaptability to diverse climatic conditions, exhibits allelopathic potential by releasing chemical compounds that inhibit weed growth. The crop's vigorous growth and canopy architecture contribute to effective weed suppression, reducing the prevalence and spread of associated pathogens. Furthermore, the chemical compounds released by camelina through the solubilization of compounds from leaves by rain, root exudation, or deriving from microbial-mediated decay of camelina's tissues interfere with the growth of neighbouring plants, indicating allelopathic interactions. The isolation and identification of benzylamine and glucosinolates as allelochemicals in camelina highlight their role in plant–plant interactions.

Keywords: Camelina sativa ; cover crop ; allelopathy

1. Introduction

Allelopathy is the ability of plants to release chemicals that affect the growth and development of other plants. These chemicals can be released into the soil or air and may affect neighbouring plants' germination, growth, or reproduction [1]. The allelopathic potential of crops has been recognized for many years. There is growing interest in using allelopathic crops for weed management since they can reduce the need for synthetic commercial herbicides, which can have negative environmental and health impacts, promote sustainable agriculture by reducing weed pressure and improving soil health, and be cost-effective for farmers, as they may not need to purchase and apply herbicides [1]. Depending on their activity, allelopathic crops can be classified into direct and indirect. Direct allelopathic crops release allelopathic compounds that directly affect the growth and development of weeds. Indirect allelopathic crops release allelopathic compounds that stimulate the growth and development of beneficial microorganisms, suppressing the growth of weeds [2]. The use of allelopathic crops is a promising strategy for managing herbicide-resistant weeds, even without a detailed understanding of the underlying mechanisms. While understanding the allelopathic effects and optimizing their application is important, mechanistic aspects are also crucial to the success of such initiatives. A greater understanding of plant–plant communication, recognition, and the potential non-target effects of allelochemicals, would elevate allelopathic plants from blunt tools for weed control to intelligent components of an integrated weed management program [3]. However, using allelopathic crops for weed management also has some challenges. First, the effectiveness of allelopathic crops may be influenced by environmental factors, such as soil moisture and temperature, which can affect the release and activity of allelopathic compounds [4][5][6][7]. Moreover, the development of allelopathic cash crops has also to satisfy the demand for high yields. Agriculture has traditionally prioritized breeding for yield improvement over other traits, so any form of weed suppression must consider its net effect on productivity, given that reduced yield in a weed-free environment can be compensated by the yield benefit provided by effective weed suppression. For example, Kong et al. [8] bred allelopathic rice cultivars that were high-yielding and weed-suppressive, but further research is needed to characterize the trade-offs related to yield and plant defence [9]. Genetic engineering techniques offer a sophisticated but largely underappreciated approach to developing allelopathic crops for weed management [1]. Recent efforts to identify genetic regions involved in sorgoleone biosynthesis in sorghum [10] pave the way for future up-regulation of these genes for a more significant allelopathic effect. There is also evidence that cytochrome P-450 monooxygenases play a role in allelochemical synthesis in various plant species, including sorghum [11] and benzoxazinoid allelochemical biosynthesis in cereals [12], indicating some consistency between species in their genetic tools for allelochemical synthesis. Specific genes involved in allelochemical biosynthesis can also be edited for examination or upregulation of specific compounds in the pathway [1]. Another approach to using allelopathic species for weed suppression is to apply them as cover or intercrops in rotation with a less weed-suppressive cash crop [13]. Recently, besides cereals, huge attention has been paid to brassicaceous species as cover crops with allelopathic activity [14][15][16][17]. The Brassicaceae family, or the mustard family, is a diverse group of plants that includes 375 genera and over 3200 species [17]. This family is known for its economic importance, as many members are cultivated as food crops or for their medicinal properties [18][19][20]. In addition, the Brassicaceae family is known for its allelopathic potential, particularly related to the presence of glucosinolates [17]. Glucosinolates are a class of sulfur-containing compounds found in high concentrations in many members of the Brassicaceae family. When the plant tissues are damaged by herbivores or mechanical stress, glucosinolates are hydrolyzed by the enzyme myrosinase, producing a variety of breakdown products, including isothiocyanates, nitriles, and thiocyanates [21]. The breakdown products of glucosinolates have been shown to have allelopathic effects on neighbouring plants [22][23]. For example, isothiocyanates have been shown to inhibit the germination and growth of various plant species, including lettuce and velvetleaf [24][25][26]. In addition, isothiocyanates have been shown to inhibit the growth of specific soilborne pathogens [27][28][29]. The Brassicaceae family includes several species that are known for their allelopathic potential, including *Brassica napus* (oilseed rape), *Brassica juncea* (Indian mustard), and *Sinapis alba* (white mustard). These species have been shown to release allelopathic compounds that inhibit the growth and development of weeds, and they are being investigated as potential allelopathic crops for weed management [30][31][32][33]. Research has shown that allelopathic crops, including those in the Brassicaceae family, can effectively reduce weed growth and suppress weed seed production. For example, one study found that using allelopathic cover crops, including *Brassica napus*, reduced weed biomass by 50–90% compared with a fallow control. Another study found that the use of *Brassica juncea* as a cover crop reduced the density and biomass of certain weed species by over 80%.

2. *Camelina sativa*: A Promising Cover Crop

Camelina sativa is an oilseed crop that has gained interest as a biofuel and food source due to its high oil content and potential health benefits, and is an annual plant belonging to the Brassicaceae family. The plant grows up to 60–120 cm in height and has a slender, branching stem covered with narrow, lanceolate leaves (**Figure 1**).

Figure 1. *Camelina sativa* at flowering stage.

The leaves are alternate, and the plant produces yellow flowers with four petals. Following pollination, the flowers develop into fruits, known as siliques, which contain small, round seeds. *Camelina sativa* is adapted to grow in temperate regions but can also tolerate a wide range of climatic conditions. It is known for its ability to grow in marginal lands with low fertility and limited water availability, making it suitable for cultivation in arid and semi-arid regions. The recommended seeding rate is approximately 10–15 kg per hectare, and the plant requires full sun exposure for optimal growth and development. *Camelina sativa* prefers well-drained soil with a pH ranging from 5.5 to 8.0, and its cultivation offers several environmental benefits. Its deep root system improves soil structure, reduces erosion, and enhances water infiltration. The crop requires fewer pesticides and fertilizers than conventional oilseed crops, reducing potential negative environmental impacts. It is a cool-season crop that can withstand frost and has a relatively short growing season of around 85–105 days [34][35][36]. One of the primary uses of *Camelina sativa* is for oil production. The plant's seeds are rich in oil, typically containing 30–45% oil content. Camelina oil is characterized by its high levels of omega-3 fatty acids, particularly alpha-linolenic acid (ALA). It is considered a valuable alternative to fish oil and can be used for human consumption, animal feed, and biodiesel production [37][38]. Beyond its economic and environmental benefits, camelina cultivation has been found to have implications for pathogen management, highlighting its potential as a sustainable and integrated pest management strategy. In fact, numerous studies have demonstrated the ability of *Camelina sativa* to suppress various plant pathogens, thereby reducing the incidence and severity of diseases. The mechanisms underlying disease suppression include direct antimicrobial properties of plant-specialized metabolites and the activation of systemic acquired resistance (SAR) and induced systemic resistance (ISR) in neighbouring plants. For example, camelina plants produce glucosinolates, which are known to exhibit fungicidal and bactericidal activities against a range of pathogens [39][40].

One of the most important biotic stresses in soybean production is soybean cyst nematode (Heterodera glycines Ichinohe, SCN), a serious pest that affects 90% of the soybean-producing areas in the U.S. [41]. A study conducted by Acharya et al. [41] found that winter camelina and brown mustard are non-hosts for SCN populations and reduced egg numbers [41].

Extensive research consistently confirms the positive effects of green manure cover crops on soil quality, especially in low-carbon or degraded soils. These advantages encompass enriching soil organic carbon content, enhancing soil structure, preventing erosion, and mitigating crop diseases [42]. Furthermore, green manures play a pivotal role in nurturing the soil's microbial community, improving nutrient availability, and fostering beneficial interactions between crop plants and microorganisms. The presence of green manures creates competition for niches, effectively curbing the proliferation of harmful microbial pathogens and ultimately resulting in increased yields of cash crops [43].

Green manure and biofumigant crops are widespread in cropping rotations, aimed at maintaining or improving agricultural soil yields by preventing degradation and protecting vital ecosystem services. In recent decades, there have been significant advancements in our understanding of soil microbiomes in agriculture. The use of advanced techniques like metagenomics has enabled researchers to delve deeply into soil microbiomes, providing unprecedented insights [44]. As a result, we now recognize the crucial role of the soil microbiome in delivering essential ecosystem services that are vital for agriculture [45]. This growing awareness has spurred investigations into management practices that aim to restore, protect, and enhance soil ecosystem health, with organic amendments such as green manure being among the promising approaches. For example, brassica biofumigants release glucosinolates during their growth, which subsequently convert into toxic isothiocyanates in the soil, influencing the structure of soil microbial communities both during the biofumigant's growth and shortly after its incorporation [46][47].

Additionally, the research focused on the degradation of pure 2-propenyl glucosinolate and the effect on the soil bacterial community composition. The results obtained showed a significant impact on the bacterial community composition. Interestingly, significant alterations in the soil community due to biofumigant exudates were observed, despite the ferrosol's high clay and organic matter content. These results suggest that brassica biofumigation might be effective on ferrosols and similar soil types with high clay and organic matter content [47].

Camelina also exhibits a capacity for weed suppression (**Figure 2**); in fact, *Camelina sativa*'s vigorous growth and canopy architecture can effectively suppress weed populations, subsequently reducing the prevalence and spread of associated pathogens. However, the careful selection of cover crop species and the timing of interseeding play a crucial role in obtaining advantages while maintaining optimal sugar beet yield. In North Dakota, when camelina was interseeded during the V1–V3 growth stages of corn and the V1–V2 growth stages of soybean (*Glycine max* (L.) Merr.), there was a reduction of 14% in corn yield and 10% in soybean yield [48].

Figure 2. Camelina capacity for weed suppression.

3. *Camelina sativa*: A Potential Allelopathic Crop

The allelopathic potential of *Camelina sativa* has been widely investigated in the past. But the analytical and chemical approaches used were mainly based on targeted analysis, which strongly reduced the amount and the complexity of chemicals being characterized. Moreover, there are no available studies focused on the bio-guided fractionation of the phytocomplex of this species aimed at identifying the classes of compounds involved in the allelopathic phenomenon and/or on the phytotoxicity of the plant extracts. Therefore, despite the evidence of camelina's allelopathy, this field of research is superficially explored, and new coupled to classical approaches should be used to shed light on this phenomenon.

The first study reporting the allelopathic potential of *Camelina sativa* was published by Grummer and Beyer [49], which observed that the presence of camelina in fields cropped with linseed significantly reduced crop yield. They highlighted that this phenomenon was observable when significant rainfall was in conjunction with specific phenological stages of camelina and linseed plants, suggesting that the allelochemical release through the solubilization of compounds from leaves by rain was responsible for the phytotoxic effects observed [49][50]. After almost twenty years, a clearer understanding of this phenomenon was achieved thanks to studies on the effects of camelina's leaf lixiviates on seedlings' growth and their interaction with soil bacteria [51]. In particular, such studies demonstrated that under controlled conditions, the lixiviates collected from camelina's intact leaves were interfering with the growth of germinating *Linum usitatissimum* seedlings. Moreover, they demonstrated that gram-negative bacteria mediated these growth alterations in the camelina phyllosphere [50][51].

Successively, Lovett and Jackson [52] reported that the effects observed on linseed seedlings were also observable on several species of higher plants, and the main bacteria mediating the effects were *Enterobacter cloacae* or *Pseudomonas fluorescens*. Moreover, they highlighted that the bacterial activity rapidly produced the allelochemical involved in plant interference, which probably was an organic compound produced by degrading a more complex metabolite commonly found in plants belonging to the Brassicaceae family. The isolation and identification of this specialized metabolite involved in this plant–plant interaction were achieved only after a year when benzylamine was identified as an allelochemical influencing the association of *C. sativa* with linseed [53][54]. It was demonstrated that camelina leaves contain organic acids that support rapid bacterial growth, breaking complex organic compounds into simpler molecules. One of these compounds, benzylamine, exhibits allelopathic properties, as reported by Lovett and Duffield [53][54]. Successively, it was reported that the release of the precursor, benzyl isothiocyanate, may require damage to the leaves, and the highest concentration of allelopathic activity may occur during the senescent stage of the life cycle when bacterial populations are at their peak. Lovett reported that in Petri dishes, low benzylamine concentrations stimulated germinating linseed seedlings similar to camelina leaf washings, but higher concentrations had an inhibitory effect, as is typical of allelochemicals [55].

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