Exploiting *Cynara cardunculus* L. allelopathy for weed control

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Abstract

Allelopathy involves both the positive or detrimental, direct or indirect effects of one plant on target organisms through the release of secondary metabolites into the environment. This biological phenomenon can be manipulated by extracting the allelochemicals, most of which are water-soluble compounds, for the control of weeds. Recently, much attention has been given to the allelopathic effects of *Cynara cardunculus* L. extracts. From the recent research emerged that: 1) *C. cardunculus* allelopathy is variety and genotype dependent, with cultivated and wild cardoon showing greater allelopathic activity than the globe artichoke; 2) organic solvents are more effective than aqueous extracts in suppressing target weeds; 3) dried leaves and spring period (April) are the optimal plant material and harvest time, respectively, to enhance the allelopathic potential of *C. cardunculus* extracts; 4) sesquiterpene lactones and polyphenols are the primary chemical classes of allelochemicals in *C. cardunculus*; 5) in the field, cultivating *C. cardunculus* effectively reduces the soil weed seed bank and alters weed communities. Further efforts on *C. cardunculus* allelopathy are still required to identify the allelopathy-involved traits and transfer the genes into improved genotypes, as well as to maximize its allelopathic potential. This knowledge can play an important role for developing plant-based bioherbicides and promoting sustainable weed management in agroecosystems.

Keywords: allelopathy, allelochemicals, polyphenols, sesquiterpene lactones, globe artichoke, cardoon

WHAT IS ALLELOPATHY?

The term allelopathy, deriving from the Greek words *allelon* ("of each other") and *pathos* ("to suffer"), was coined in 1937 by Hans Molisch to indicate any biochemical interactions between all types of plants. Under a biological point of view, it is a form of amensalism, an association between organisms for which one is inhibited and the other is unaffected (Scavo et al., 2018a). The International Allelopathy Society refers to allelopathy as "any processes involving secondary metabolites produced by plants, microorganisms, viruses and fungi that influence the growth and the development of agricultural and biological systems (excluding animals), including positive and negative effects" (Torres et al., 1996). These secondary metabolites released into the environment are named allelochemicals, which are defined as "non-nutritional chemicals produced by one organism (plants, microorganisms, viruses and fungi) that affects the growth, health, behaviour or population biology of other species" (Whittaker and Feeny, 1971). Allelochemicals belong to a wide range of chemical classes, but for simplicity they are commonly grouped into three main categories: polyphenols, terpenoids and other compounds such as alkaloids and cyanogenic glycosides (Scavo et al., 2018a). Plants can release allelochemicals through root exudation, volatilization from living plant parts, leaching from aboveground parts or decomposition from plant litter. The concentration of allelochemicals into plant tissues may vary according to genotype, plant part or presence/absence of a stress factor (Scavo et al., 2018a). About the first two factors, it is well known that allelochemicals' amount differ between varieties of the same species and between plant organs. For instance, studying the allelopathic potential (in terms of phytotoxicity

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against weeds) of different durum wheat landraces, Scavo et al. (2022a) recently found that 'Timilia' and 'Russello' have the highest potential and that that ear extracts, compared to root and stem ones, are the most active. Concerning the latter factor, according to the "stress hypothesis of allelopathy" (Reigosa and Pedrol, 2002), donor plants under biotic or abiotic stress synthesize a higher amount of allelochemicals and, at the same time, stress target plants are more sensitive to allelochemicals.

Allelopathy is nowadays recognized by the scientific community as a multidisciplinary science involving skills from agronomy, organic chemistry, biology, plant physiology, microbiology, etc. Under an agroecological approach, which is the main focus of this review, allelopathy is studied in terms of phytotoxicity for the sustainable management of weeds in agroecosystems. Several agronomic techniques involving allelopathic mechanisms can be used for weed management: use of plant extracts alone (as bioherbicides) or in combination with synthetic herbicides, intercropping or cover cropping with allelopathic plant species, mulching or green manuring with plant residues from allelopathic species and inclusion of allelopathic plants into crop rotation schemes (Scavo and Mauromicale, 2021; Jabran et al., 2015). Of course, these effects are more effective when combined within an integrated weed management strategy (Scavo and Mauromicale, 2020).

C. CARDUNCULUS: TAXONOMY, DIFFUSION AND USES

Many plants species, both wild and cultivated, herbaceous or woody, show allelopathic properties in natural conditions. In the recent years, *Cynara cardunculus* L., like many other Asteraceae members (Chon and Nelson, 2010), has been investigated for its allelopathic activity. Following Fiori's classification, already confirmed by genetic studies (Lanteri et al., 2012; Mauro et al., 2009), this species comprises three cross-pollinated and cross-compatible botanical varieties (Rottemberg and Zohary, 1996): the progenitor wild cardoon [*C. cardunculus* L. var. *sylvestris* (Lamk) Fiori] along with the domesticated forms, the globe artichoke [*C. cardunculus* L. var. *scolymus* (L.) Fiori] and the cultivated cardoon (*C. cardunculus* L. var. *altilis* DC.).

The globe artichoke is cultivated worldwide across 116,350 ha giving a total annual production of $1{,}470\times10^3$ Mg (FAOSTAT, 2023). About 80% of the world's globe artichoke harvested areas is located in the Mediterranean basin, although other countries such as Peru, Argentina and China are significantly increasing their production in the last decade (Pesce and Mauromicale, 2019). Italy is the leading producer, with 38,450 ha yielding an annual production of 376,280 Mg, followed by Egypt, which produces 315,407 Mg from 17,140 ha (FAOSTAT, 2023). No official information about cultivated cardoon's economic importance is available, but it known that most of its cultivated area is concentrated in southern European countries such as Greece, Italy, Portugal, Spain and France. The wild cardoon is distributed in the western-central part of Europe, in the Canary Islands and in Madeira (Pandino and Mauromicale, 2020). Its presence is reported also in the Americas.

C. cardunculus is an herbaceous perennial plant that well adapts to Mediterranean climatic conditions, characterized by hot dry summers and low rainfall levels (~500 mm year^{-1}), mainly concentrated in the autumn-winter period. In this context, it is grown not only for food purposes, but it shows also a high potential as a multi-purpose crop (Pandino and Mauromicale, 2020). Alternative uses of *C. cardunculus* include the production of biomass for energy, the production of biomethane, biodiesel, bioethanol and oil, the production of pulp and paper, the use as vegetable rennet and ornamental plant, and, more recently, the extraction of phytochemicals with many biological activities (Gominho et al., 2018; Mauromicale et al., 2019). Moreover, seed-propagated cultivars are gaining in popularity for their high biomass and seed production (Mazzeo et al., 2020).

C. CARDUNCULUS ALLELOCHEMICALS FOR WEED CONTROL

Allelochemicals in *C. cardunculus* have been studied since 2014 in wild cardoon (Rial et al., 2014) and their identification is being in progress. Although the wild cardoon and leaves are respectively the botanical variety and the plant organ mostly investigated for allelopathic purposes, the globe artichoke and other plant parts are also under investigation in the recent years with the aim of valorising the plant residues after harvest. The identification, isolation, purification and extraction of *C. cardunculus* allelochemicals is a topic of interest for industrial, pharmaceutical and cosmetic applications (Mandim et al., 2023; Restuccia et al., 2020). Major *C. cardunculus* allelochemicals belong to two main chemical classes: polyphenols and sesquiterpene lactones (STL) (Figure 1).

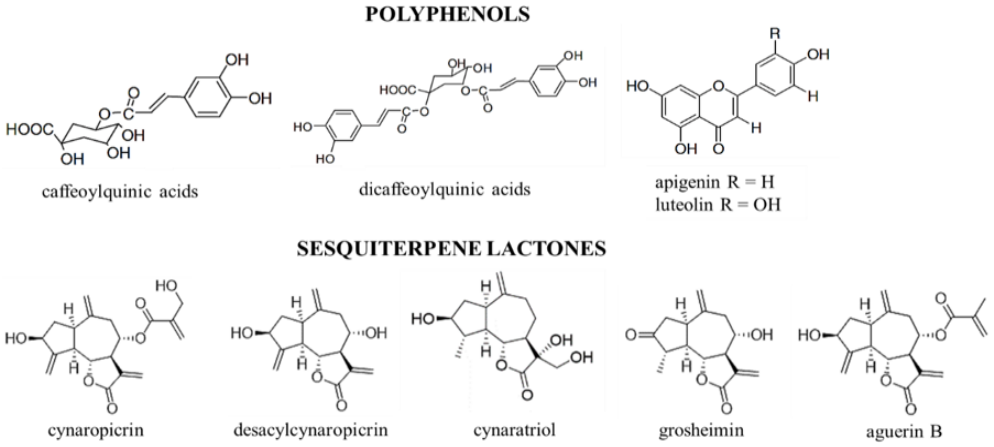

Figure 1. Main *Cynara cardunculus* allelochemicals isolated from leaves.

About polyphenols, *C. cardunculus* is very rich in phenolic acids, caffeoylquinic acids and flavonoids (Pandino et al., 2015). The polyphenolic profile and the amount of single compounds are genotype- and plant part-dependent, as well as crop- and post-harvest management dependent (Lombardo et al., 2017; Pandino et al., 2017; Sałata et al., 2022, 2023). Leaves are the major source of polyphenols content, particularly luteolin derivatives in globe artichoke and apigenin derivatives in wild and cultivated cardoon (Pandino et al., 2012a, b). Specifically, *C. cardunculus* phenolic allelochemicals are phenolic acids such as syringic acid, *p*-coumaric acid, myricitrin, quercetin, naringenin, etc. (Kaab et al., 2020b), caffeoylquinic and dicaffeoylquinic acids, as well as luteolin- and apigenin derivatives (Scavo et al., 2020a). The concentration of these allelochemicals can be enhanced through the application of gibberellic acid (Lombardo et al., 2022) or directly on the seedlings by inducing 24h of light and full water-supply under controlled conditions (Pandino et al., 2022).

Major *C. cardunculus* STLs with recognized allelopathic properties are cynaropicrin, deacylcynaropicrin and other cynaropicrin derivatives, cynaratriol, grosheimin and aguerin B (Rial et al., 2104, 2016). Cynaropicrin has been found as the most abundant STL in leaf extracts of the three botanical varieties, followed by cynaratriol, whereas aguerin B showed the highest concentration among the minor STLs (Scavo et al., 2019a). Also, Ramos et al. (2013) indicated in cynaropicrin the most abundant STL in the lipophilic extracts of cultivated cardoon. Concerning the botanical varieties, wild cardoon has the highest levels of total STLs, followed by cultivated cardoon and globe artichoke (Scavo et al., 2019a). The common precursor of STLs in the Asteraceae family is costunolide, and their biosynthetic pathway is regulated by three enzymes (de Kraker et al., 2002): the germacrene A synthase (GAS), the germacrene A oxidase (GAO) and the costunolide synthase (COS). Eljounaidi et al. (2014) elucidated two P450 genes from the biosynthetic pathway of *C. cardunculus* STLs: CYP71AV9 and CYP71BL5.

STUDY ON *C. CARDUNCULUS* ALLELOPATHY UNDER LABORATORY CONDITIONS

The first research about *C. cardunculus* allelopathy was carried out by the Cadiz Allelopathy Research Group in 2014 (Rial et al., 2014), in which the authors studied the allelopathic activity of wild cardoon on seed germination and seedling growth of four crops (lettuce, watercress, tomato, and onion) and two weeds (barnyardgrass and brachiaria). Through a metabolomic study involving different kinds of extractive organic solvents (dichloromethane, ethyl acetate, acetone, methanol, and water), six STLs were isolated from wild cardoon leaves, with aguerin B, grosheimin and cynaropicrin that showed the highest inhibitory activity against that target species. Two years later, the same research group evaluated the joint action of binary mixtures of three active STLs (aguerin B, grosheimin and cynaropicrin) and one nonactive compound (11,13-dihydroxy-8-desoxygrosheimin) via the wheat coleoptile bioassay (Rial et al., 2016). A total of 17 binary mixtures at different levels of inhibition (ED25, ED50, and ED75) was studied. The authors reported 25 additive effects, 7 synergistic effects and 2 antagonisms, thus demonstrating that the allelopathic effect of the ethyl acetate extract of wild cardoon is possible due to the prevalence of more additive and synergistic effects rather than antagonism. This research is of particular importance considering that in nature the allelopathic effect of a certain plant is due to the combined effect of different allelochemicals acting in synergism rather than to a single compound.

In 2018, for the first time the allelopathic effects of the three botanical varieties of *C. cardunculus* (globe artichoke, wild and cultivated cardoon) were studied at two different dilutions (40% and 80%) against six cosmopolitan weed species widely diffused in Mediterranean agroecosystems (Scavo et al., 2018b). Overall, all extracts reduced by 39% seed germination on the average of the weed species, with the cultivated cardoon extract at 80% dilution that was the most active (Figure 2). An autoallelopathic effect on wild cardoon was also observed, especially by cultivated cardoon extract that allowed only 9% of seed germination. The allelopathic effects of the three *C. cardunculus* botanical varieties were also tested on the seedling growth of two weeds (*Amaranthus retroflexus* L. and *Portulaca oleracea* L.) and on the same wild cardoon (Scavo et al., 2019b). It was found that all the extracts reduced the root length of *A. retroflexus* and the hypocothyl length of *P. oleracea*. About the aboveground part length, a stimulatory effect was observed on *A. retroflexus*, while an inhibitory one on *P. oleracea*, denoting a species-specific effect (Figure 3).

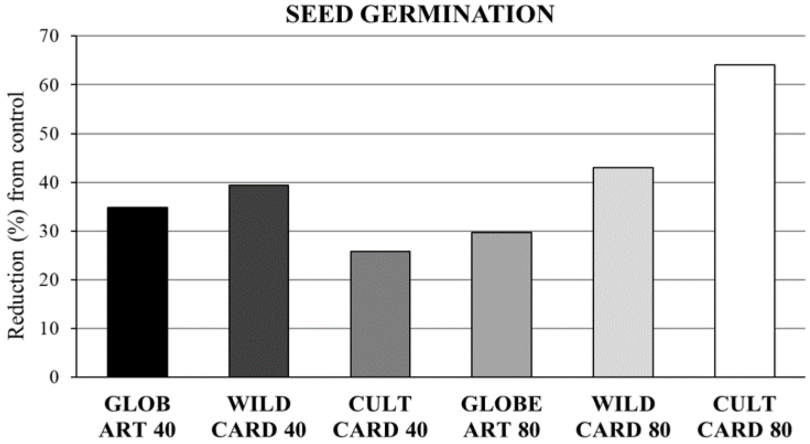

Figure 2. Allelopathic effects of the three *Cynara cardunculus* botanical varieties (GLOB ART, WILD CARD and CULT CARD) on seed germination of six common weeds. 40 and 80 indicate extract's dilution. Taken from Scavo et al. (2018b).

Given that in previous researches the cultivated cardoon extract was found to show the highest allelopathic activity, it was further investigated by Scavo et al. (2019a). In particular, the allelopathic effects of the extracts obtained from dried, lyophilized and fresh leaves treated with three different solvents (water, methanol and ethanol) were studied on two spring-summer (*A. retroflexus* and *P. oleracea*) and two-autumn-winter (*Stellaria media* (L.) Vill. and *Anagallis arvensis* L.) weeds. Interestingly, ethanolic extracts completely inhibited seed germination of the four weeds, followed – in terms of inhibitory effects – by methanol and distilled water. Lyophilized leaves were found to be the most inhibitory plant material, allowing just a 3% of seed germination on the average of the four target weeds. However, dried leaves should be preferred since they show both a significant inhibitory activity and a lower cost of preparation than lyophilisation.

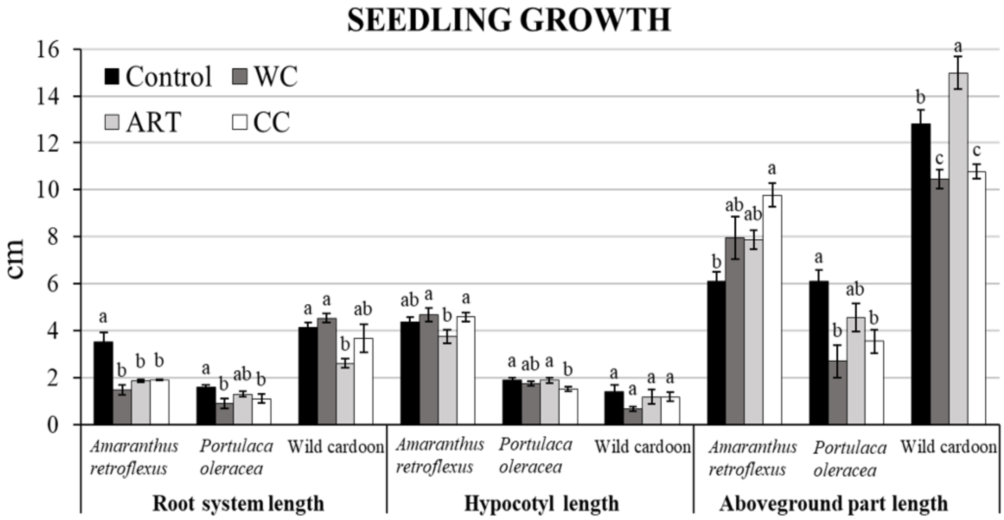

Figure 3. Allelopathic effects of the three *Cynara cardunculus* botanical varieties on the seedling growth of *Amaranthus retroflexus* and *Portulaca oleracea*. WC: wild cardoon; ART: globe artichoke; CC: cultivated cardoon. Taken from Scavo et al. (2019b).

An important step forward in *C. cardunculus* allelopathy was the research jointly performed by Cadiz and Catania allelopathy research groups (Scavo et al., 2019c), which selected the most efficient extraction method of *C. cardunculus* allelochemicals. Basically, different extractive solvents and concentrations were compared. The ethyl acetate and the ethanolic extracts showed the highest inhibition activity both on wheat coleoptile elongation and target weeds, and root length was the most affected parameter. In addition, the aqueous extract was separated into two fractions for a better detection of allelochemicals. Four compounds were isolated from the alcoholic fraction of the aqueous extract (4 STLs and the lignan pinoresinol), and three of them were described in cultivated cardoon for the first time. Applying the stress hypothesis of allelopathy described by Reigosa and Pedrol (2002) on cultivated cardoon, it was found that light stress (caused by 60% shading through the erection of a black polyethylene net) significantly increased the amount of STLs in spring-harvested leaves, especially in cynaratriol and cynaropicrin derivitives, and that this increase was corroborated by the enhancement of cardoon allelopathic activity (Scavo et al., 2020b).

Kaab et al. (2020a) investigated the specific modes of actions of *C. cardunculus* extracts by evaluating two physiological parameters (fluorescence and electrical conductivity) and two oxidative stresses (melondialdehyde and hydrogen peroxide) in *Trifolium incarnatum* L. The observed symptoms on *T. incarnatum* were leaf necrosis, chloroses and electrolyte leakage, which led to disturbance in the electron transport chain in photosynthetic system and consequently to an increase in ROS production and a decrease of ATP levels.

The study of Kaab et al. (2020b) was aimed to assess the phytotoxic activity of 10 crude extracts obtained from different wild Tunisian plants against three target weeds (*T. incarnatum*, *Silybum marianum* (L.) Gaertn. and *Phalaris minor* Retz.). The authors indicated that wild cardoon methanolic extract had the highest inhibitory activity against seed germination and seedling growth Nevertheless, the authors proposed a new formulation for a bioherbicide based on wild cardoon allelochemicals for post-emergence application to improve the penetretion of allelochemicals through epicuticular waxes. They reported that this formulation showed the same herbicidal activity as the standard industrial bioherbicide containing pelargonic acid. In addition to the previous research, in the study of Mejías et al.

(2022) three *C. cardunculus* STLs (aguerin B, grosheimin and cynaropicrin) have been encapsulated with lithocolic acid in core/shell nanotubes. Encapsulation of STLs in nanotubes gave better results than the same nonencapsulated compounds in terms of phytotoxicity against three target weeds.

STUDY ON *C. CARDUNCULUS* ALLELOPATHY UNDER FIELD CONDITIONS

The allelopathic activity of *C. cardunculus* in open field conditions has still been little investigated. In the work of Scavo et al. (2019d), the authors studied the effects resulting from the repeated cultivation in two different areas with globe artichoke, cultivated and wild cardoon on the quali/quantitative composition of the soil weed seedbank. In one location, the repeated cultivation for three consecutive years of globe artichoke and cultivated cardoon respectively halved and decreased by a third the number of weeds in the soil compared to a faba bean/wheat rotation; the same results were corroborated in the other location, compared to an olive grove. Moreover, from the soil DNA extraction, the DGGE analysis revealed that the presence of cultivated cardoon had a negative influence toward *Bacillus subtilis*, while on the other, a positive one toward the beneficial soil bacteria *Pseudomonas putida* and *Azospirillum brasilense*. Therefore, *C. cardunculus* allelopathy not only decreased the weed soil seedbank, but stimulated also the presence of beneficial soil bacteria (Figure 4). In this regard, it should be also reminded that allelochemicals interact with the physical, chemical and biological soil characteristics that, in turn, influence their retention and transport into the soil (Scavo et al., 2019e). Altogether, this complex process affects the level of phytotoxicity of allelochemicals into the soil.

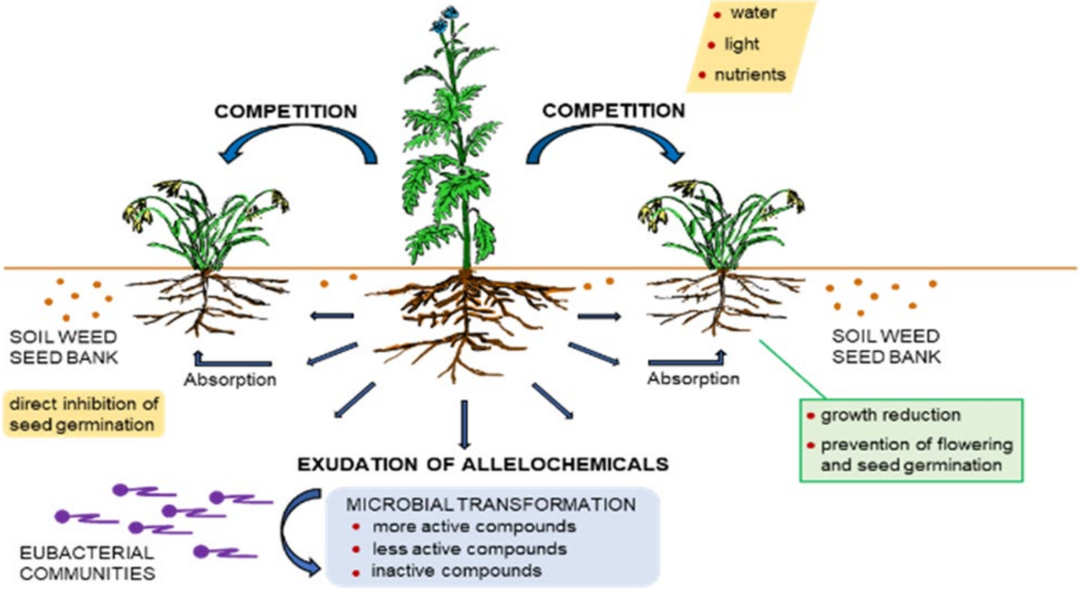

Figure 4. Phytotoxic effects of *Cynara cardunculus* in the field. Both competition and allelopathy are involved in this process, the latter also mediated by soil microorganisms. Taken from Scavo et al. (2019d).

Uddin et al. (2020) studied the invasive ability of wild cardoon, evaluating whether co-occurring native *Juncus pallidus* R.Br. and non-native *Lolium rigidum* Gaud. species may evolve tolerance to the allelochemicals induced by wild cardoon in Australian fields. After growing the test species in pots filled with collected invaded and uninvaded rhizosphere soil of wild cardoon, the authors found a higher total phenolic content and a lower pH in the invaded rhizosphere than the uninvaded one. Furthermore, they reported a high reduction of seed germination and seedling growth in the invaded rhizosphere of wild cardoon, but little effect on non-native grass species, meaning that *L. rigidum* coevolved tolerance to *C. cardunculus* allelochemicals.

CONCLUSIONS

The following conclusions can be drawn from this review:

- *C. cardunculus* allelopathy varies largely among botanical varieties, with cardoon forms showing a greater allelopathic potential than globe artichoke;
- Major *C. cardunculus* allelochemicals are sesquiterpene lactones and polyphenols;
- The most efficient extraction procedure for *C. cardunculus* allelochemicals involves the use of ethanol or ethyl acetate as extractive solvents and dried leaves as plant material;
- The amount of *C. cardunculus* allelochemicals can be increased by inducing plant stress such as shading;
- *C. cardunculus* leaf extracts show marked allelopathic effects on both autumn-winter and spring-summers weeds;
- The allelopathic effects of *C. cardunculus* are also visible under field conditions through the reduction of the soil weed seedbank and by a chemical advantage for its invasive capacity.

The allelopathic potential of *C. cardunculus* may be manipulated for sustainable weed management purposes such as its inclusion into crop rotation schemes, the use of its plant residues as dead mulch and the possible production of bioherbicides. Further research is however still needed to better understand *C. cardunculus* allelopathy, especially in field conditions.

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