

# The allelochemical potential of an invasive ornamental plant, the Indian blanket flower (*Gaillardia pulchella* Foug.)

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## Abstract

Global spread of invasive plant species threatens biodiversity significantly, with a particularly high presence of invasives in the Asteraceae family. This is partly due to their wide use as ornamental plants and their rapid reproduction and allelopathy. The Indian blanket flower (*Gaillardia pulchella*) is a native North American species widely used as an ornamental plant and has become invasive in other countries. Although it contains bioactive compounds, its allelopathic impact on other plants has been largely unexplored. We conducted in vitro tests on oilseed rape (*Brassica napus*) germination and early growth to assess blanket flower's allelopathy. Seeds were exposed to aqueous extracts at three different concentrations (10%, 20%, and 40%). The 40% extract significantly inhibited germination during the treatment. All three concentrations inhibited root growth, with the 40% treatment showing this effect from the second day. In contrast, the extracts promoted significantly shoot elongation. Fresh weight of seedlings was not affected by the extract, but the 10% treatment resulted in higher mass. These findings provide evidence of blanket flower's allelopathic effects, shedding light on its invasive potential.

## KEYWORDS

allelopathy, biological invasion, extracts, *Gaillardia pulchella*, ornamental plant

## 1 | INTRODUCTION

In recent times, the number of invasive plant species that pose the greatest threat to biological diversity shows a continuous increase due to globalization (Seebens et al., 2017). Species frequently used as ornamental plants

in gardens often represent a significant source of invasive species. Due to their decorative nature, human involvement provides them with the opportunity to establish and spread to new, distant habitats (Montagnani et al., 2022; van Kleunen et al., 2018).

Among the members of the Asteraceae family, there is a notorious proportion of adventive species (Pyšek, 1998). The reason behind this is partly the fact that many of these species are used as ornamental plants (Araújo et al., 2021).

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On the other hand, a more detailed examination of invasive species within the family has revealed that they possess several biological characteristics that can confer advantages in successful invasive processes over native species. These include high reproductive rates, specialized dispersal mechanisms (Yan et al., 2016), and a diversity of metabolic compounds. The latter is responsible for strongly inhibiting or hindering the germination and growth of native and competing plant species in the new habitat through allelopathic effects (Araújo et al., 2021; Pyšek & Richardson, 2008). This is because over the course of evolution, species living in close proximity have successfully adapted to each other's metabolic byproducts, whereas a "foreign" species arriving from a distant location is more likely to contain compounds to which native plants could be more sensitive (Callaway & Aschehoug, 2000).

The Indian blanket flower (*Gaillardia pulchella* Foug.), belonging to the Asteraceae family, is a native annual or short-lived perennial plant species in North America. Its original distribution includes the southwestern grasslands of the United States and the Gulf Coast region. It prefers sunny, dry areas and can establish itself in disturbed habitats (Stoutamire, 1977). Due to its decorative flowering, ease of cultivation, and ability to grow in various soil types, it has become a popular ornamental plant worldwide (Hammond et al., 2007; Wiersema and León, 2013). As a result, *G. pulchella* currently occurs in much of the United States beyond its original range (Hammond et al., 2007). It has become naturalized in Macaronesia, South Africa, China, East Asia, Southeast and Southwest Europe, the Pacific Islands, and the Caribbean region. In Europe, especially in Central Europe, it exhibits invasive behavior (Hansen, 1976; Wiersema & León, 2013). In Hungary, in sandy, dry habitats and on open surfaces, particularly in the protected Kolon Lake area, it has appeared in increasing numbers and abundance in recent years (Bakacsy et al., 2023; Cseceserits et al., 2022; Molnár et al., 2019; Simon, 2000).

Numerous previous studies have reported on the biologically active compounds of *G. pulchella* and their effects. For instance, certain substances such as sesquiterpene lactones have been identified to have cytotoxic effects (Inayama et al., 1984; Kupchan et al., 1966). Furthermore, Tsay et al. (2004) demonstrated that extracts and root exudates of blanket flower cause the death of plant-parasitic nematodes. In their study on a related species, *Gaillardia aristata*, Süle et al. (2023) suggested the undiscovered role of its allelopathy in the success of its naturalization and invasion into natural vegetation.

Surprisingly, despite the potential invasiveness of the species (and even the genus), and the diverse composition of its metabolic compounds and their effects, the allelopathic potential of blanket flower has not been tested on other plants so far. This information could provide

insights into the role of this species in invasion. Therefore, the aim of this study was to assess the allelopathic effect of the *G. pulchella* on the germination and early growth of oilseed rape (*Brassica napus*). Our hypothesis was that the extract of blanket flower would inhibit rape germination and influence the morphology of seedlings, especially the length of the primary shoot and root.

## 2 | MATERIALS AND METHODS

### 2.1 | Preparation of plant material and treatments

In order to test the allelopathic effect of the Indian blanket flower, we investigated its impact on the germination of test plant seeds and subsequent seedling development under in vitro conditions using a solution derived from *G. pulchella*.

For the study, mature specimens of the invasive species were collected from the Kolon Lake area in June 2022. The entire plant (roots, leafy shoots, and flowers) was collected. Collection was carried out away from agricultural or nearby areas to avoid potential misleading effects from herbicide treatment. After collection, the plant material was dried in the dark at room temperature and then processed into coarse fragments (0.5–1 cm). Raw extracts were prepared for treatments, where 20 g of dried plant material was mixed with 200 mL of sterilized distilled water, left to stand at room temperature for a day, and then filtered through filter paper.

As the test plant, oilseed rape (*B. napus* L. cv. GK Gabriella) was used. For in vitro systems, 25–25 surface-sterilized oilseed rape seeds were placed on two layers of filter paper in 9-cm-diameter Petri dishes. For the control, the filter papers were moistened with 5–5 mL of purified and sterilized distilled water. For the treatments with blanket flower extract, crude extract was diluted with sterilized distilled water to create three different concentrations: 10%, 20%, and 40%. Then the filter papers were moistened with 5 mL each of the three concentration solutions. Allelopathic bioassay studies have very diverse methodology considering the extract preparation and other parameters. However, the in vitro bioassay test we used is generally applicable to numerous plant species with various life forms, making its evaluation more straightforward (Szabó, 2000).

Petri dishes were then sealed with foil and placed in a greenhouse for 6 days (the day of placement is taken as day 0) under controlled conditions. The greenhouse settings were as follows: photosynthetic photocurrent density was  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$  (white LED 5700 K), far-red addition (PSI, Drásov, Czech Republic), day/night photoperiod was 12/12 h, day/night temperature was 24/22°C, and relative humidity was 55%–60%.

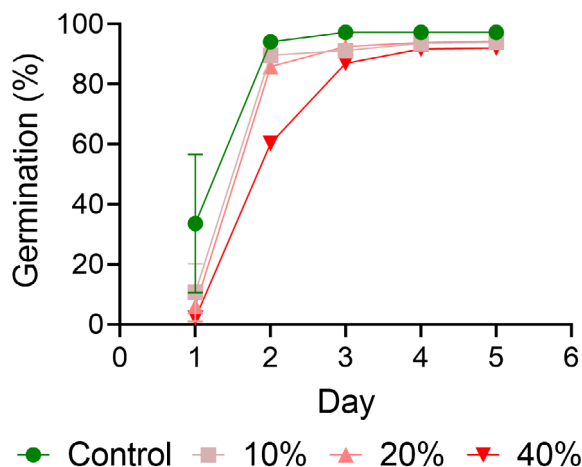
From the first day of germination onward (for 5 days), the seedlings were scanned daily using a Canon EOS 700D camera. The captured images were analyzed using Fiji (ImageJ) software (Schindelin et al., 2012): germination percentage, shoot and root lengths (cm), and the mass of germinated plants (mg FW) were measured on the last day.

## 2.2 | Statistical analysis

The presented data represent the average values of three independent experiments, each with five replicates, to test for the allelopathic effect of blanket flower extract. Statistical analysis was performed using GraphPad Prism for Windows version 8.0.1.244 (GraphPad Software, La Jolla, CA, USA). The normal distribution of the data was tested using the Shapiro–Wilk test. Statistically significant differences were determined using one-way ANOVA followed by Tukey's test for normally distributed data and the Kruskal–Wallis test for non-normally distributed data. Results were considered significant at  $p \leq 0.05$ .

## 3 | RESULTS

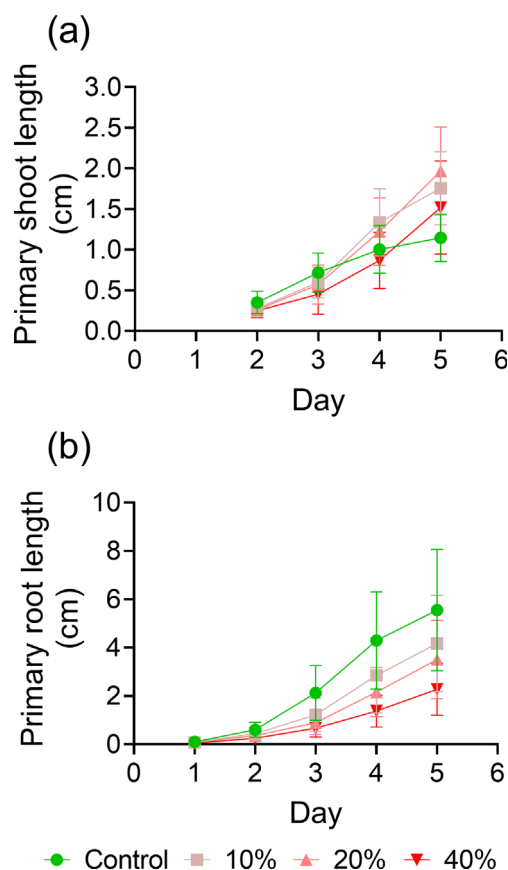
The aim of our study was to assess the potential allelopathic effect of blanket flower (*G. pulchella*) on oilseed rape. In the in vitro test, we examined the effect on the germination percentage of oilseed rape seeds over 5 days,



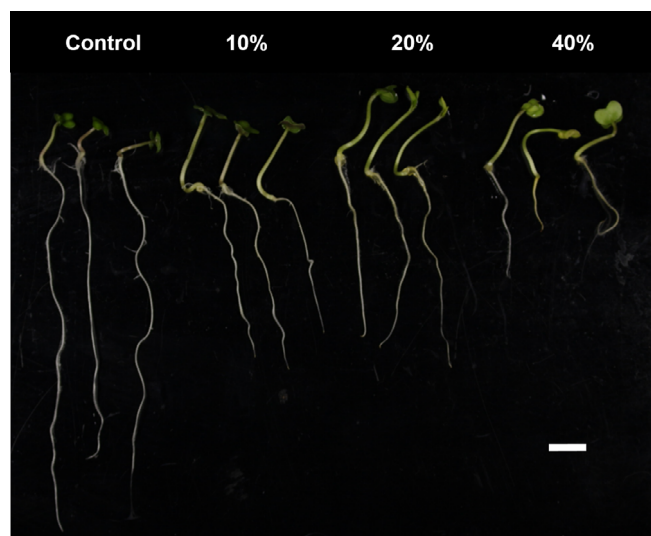
**FIGURE 1** Effect of different concentrations of aqueous extracts from *Gaillardia pulchella* on the dynamics of oilseed rape germination. Data are presented as mean  $\pm$  SD ( $n = 375$ ). Statistically significant differences were determined using one-way ANOVA followed by Tukey's test for normally distributed data and the Kruskal–Wallis test for non-normally distributed data. Results were considered significant at  $p \leq 0.05$ .

as well as the development of shoot and root lengths, and the mass of germinated seedlings.

The effect of blanket flower extracts on oilseed rape germination percentage is illustrated in Figure 1. In all treatments, seed germination began on the first day. Control seeds showed rapid germination under normal conditions, starting at 33.6% and reaching 97.3% by the third day. The germination of seeds treated with 10% and 20% extracts progressed similarly. They started at 10.6% and 6.1% on the first day, and achieved a germination percentage of 94% by the fifth day. In comparison with the control, seeds exposed to the 10% and 20% treatments showed significant inhibition of germination until the fourth day (Table S1). With the application of the 40% extract, only 2.1% of seeds germinated on the first day, followed by a slower, steady increase to 92% by the fifth day (Figure 1). When compared with the control, seeds treated with 40% blanket flower extract showed significant germination inhibition on all 5 days. Between seeds



**FIGURE 2** Effect of different concentrations of aqueous extracts from *Gaillardia pulchella* on early shoot (a) and root development (b) of oilseed rape. Data are presented as mean  $\pm$  SD ( $n = 375$ ). Statistically significant differences were determined using one-way ANOVA followed by Tukey's test for normally distributed data and the Kruskal–Wallis test for non-normally distributed data. Results were considered significant at  $p \leq 0.05$ .

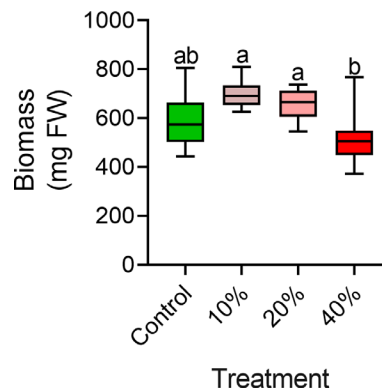


**FIGURE 3** Effect of aqueous extracts from *Gaillardia pulchella* on early development of oilseed rape seedlings compared to the control (distilled water). The applied concentrations were 10%, 20%, and 40%. The representative image shows oilseed rape seedlings at 5 days of age. Scale: 1 cm.

treated with the 10% and 40% extracts, significant differences were observed only on the first 2 days (first day  $p = 0.036$ , second day  $p < 0.001$ ; Table S1). As for the 20%- and 40%-treated seeds, significant differences in germination were only observed on the second day ( $p = 0.014$ ). On the other days and in comparison, there was no significant difference in germination percentage (Table S1).

The trend in the development of primary shoot lengths of seedlings was as follows: Under control conditions, seedlings maintained significantly longer primary shoot lengths until the third day ( $p < 0.001$ ) compared with treated seedlings (Figure 2a). Interestingly, starting from the fourth day of germination, a significant elongation of shoot lengths was observed in seedlings treated with 10% and 20% extracts ( $p < 0.001$ ). The shoot lengths of seedlings treated with the 40% extract remained shorter than that of the control until the fifth day ( $p < 0.001$ ), only exceeding the control's length on that day (Figure 2a). Notably, significant differences were observed among treated seedlings from the third day, particularly noticeable between the two lower concentrations (10% and 20%) and the higher concentration (40%) (Table S2).

Blanket flower extract significantly inhibited the primary root growth of seedlings in a concentration-dependent manner compared with the control (Figure 2b). On the first day of germination, there were no differences in shoots between seedlings treated with different concentrations, except between the control and the 40% treatment



**FIGURE 4** Effect of different concentrations of aqueous extracts from *Gaillardia pulchella* on the biomass of oilseed rape at the end of the treatment. Data are presented as mean  $\pm$  SD ( $n = 375$ ). Different letters indicate significant differences among treatment values analyzed using Tukey's test for normally distributed data and the Kruskal–Wallis test for non-normally distributed data. Results were considered significant at  $p \leq 0.05$ .

( $p = 0.006$ ; Table S3). Following this, significant differences in the development of primary root lengths were found between the control and all treated seedlings ( $p < 0.001$ ). Throughout the observation period, seedlings grown under control conditions had the longest primary root, followed by the 10% treatment, then the 20% treatment, and finally the 40% treatment (Figure 2b).

Overall, treated plants exhibited a phenotype characterized by longer primary shoot lengths and shorter primary root lengths compared with control seedlings, as illustrated in Figure 3.

Blanket flower extract did not significantly affect the fresh weight of seedlings. A significant difference was only observed between the masses of seedlings treated with 10% and 20% extracts and those treated with the 40% extract ( $p = 0.001$  and  $p = 0.004$ ) (Figure 4 and Table S4). However, a trend emerges, with the highest mass belonging to seedlings treated with the 10% extract, followed by the 20% treatment and control seedlings. The lowest mass was associated with seedlings treated with the 40% extract (Figure 4).

## 4 | DISCUSSION

In this study, the allelopathic effect of *G. pulchella* was tested on the germination and early development of *B. napus*. We hypothesized that the allelopathic effect of blanket flower could play an important role behind its competitive ability and invasive tendency. The results demonstrated a significant impact of blanket flower extracts on oilseed rape germination and growth. Lower concentrations of blanket flower extracts (10% and 20%)

resulted in slower germination during the first 2 days, while the higher concentration (40%) nearly completely inhibited germination on the first day. The differences between concentrations were most significant in the initial days (Figure 1). During the initial days, there were no differences in the applied concentrations, but later, the lower concentrations (10% and 20%) allowed the roots to grow longer than in the case of the higher concentration (40%) (Figures 2a and 3). Regarding shoot length, slower growth was observed in the lower concentrations (10% and 20%) during the first 3 days, but on the fourth day, the shoot lengths significantly increased and reached or exceeded those of the control group. In the case of the higher concentration (40%), shoot lengths were generally shorter throughout the observed period (Figures 2b and 3). The different concentrations of the extract influenced germination percentages and plant morphology to varying extents.

Simmons (2005) tested the competitive effectiveness of *G. pulchella* against the invasive bastard cabbage *Rapistrum rugosum* (L.) All. in its native habitat. Blanket flower caused a 72% reduction in above-ground productivity of *R. rugosum* at the highest sowing rate, without significantly suppressing native species. Although our study did not directly test the allelopathic effect of *G. pulchella* on mature plants, our results indirectly support Simmons (2005) observations. One of our findings suggests a delayed allelopathic effect of blanket flower on seed germination (Figure 1). Additionally, it aligns with our observation that the allelopathic impact of blanket flower extract led to an increase in primary shoot elongation and inhibited primary root elongation, even at lower concentrations (Figures 2 and 3). Roots serve to anchor plants in the soil and facilitate nutrient and water uptake, thus fundamentally influencing plant productivity and survival (Jackson et al., 1996). In a dry or semi-arid environment, such as native and invasive habitats of blanket flower (North American prairies and Pannonian sand grasslands), if root systems do not reach sufficient depth to access moisture due to allelopathy, the growth of the plant community may be compromised. Moreover, in sandy soils, precipitation can leach active compounds deeper into the soil, making allelopathic effects more pronounced in drier conditions (Fekete, 1981). These expressed effects could provide a competitive advantage to blanket flower. Interestingly, Csiszár et al. (2013) only found a similar allelopathic effect to ours in the case of *Conyza canadensis* (L.) Cronq. among the eight invasive Asteraceae species they examined. This increased shoot growth can also result from suppression of the root. Saved energy by root suppression may be allocated into the upper-ground part of the test plant.

From the study by Csiszár et al. (2013), it can be observed that the allelopathy of invasive Asteraceae species generally negatively affects the germination, shoot, and root growth of the test plant *Sinapis alba* L. The most significant inhibitory effect on the root growth of the test plant was exerted by the Asteraceae species included in the study. This aligns with the strong root growth inhibition observed in blanket flower extract used in the present study. Kupchan et al. (1966) and Inayama et al. (1984) reported cytotoxic effects of certain compounds from *G. pulchella*, which could be responsible for inhibiting root growth in plants. However, further investigations are needed to substantiate this claim. Bais et al. (2003) supported this assumption by observing that allelochemicals (such as [−]-catechin) from *Centaurea maculosa* Lam. induced reactive oxygen species (ROS) waves at the root meristem of *Arabidopsis thaliana* under in vitro conditions, ultimately leading to root system decay.

The results of this study indicate that lower concentrations of blanket flower extracts led to an increase in seedling mass compared to the higher concentration, and to a somewhat insignificant extent compared to the control (Figure 4). This outcome aligns closely with the findings of Bakacsy et al. (2022), who tested the effect of *Juncus compressus* purified extracts on *A. thaliana* seedlings. They found that juncusol increased the biomass of test plants in the applied lower concentrations (0.1 and 0.5 mM) compared with the control, with no significant difference observed in the higher-concentration treatment. Lopes et al. (2022) present the potential allelopathic effects of Asteraceae species as agricultural bioherbicide. Therefore, it may be worth considering testing the purified active ingredients of blanket flower in the future. Moreover, Tsay et al. (2004) demonstrated that blanket flower extract and root exudates lead to the mortality of plant-parasitic nematodes. Consequently, Tsay et al. (2004) suggest planting blanket flower as a rotational crop, intercropping it with other species, or incorporating its parts into the soil for controlling plant-parasitic nematodes (e.g., *Meloidogyne incognita*). However, due to the invasive nature of the species, we recommend planting blanket flower and other *Gaillardia* species as ornamentals in crop rotations or for grassland restoration only within their native habitat. Despite the fact that *G. pulchella* in its original habitat did not cause the decline of the other native species, it is advisable to approach with caution, as Simmons (2005) points out. The study by Guller et al. (2022) reinforces that overplanting native species also hinders the reestablishment of the original state of native communities in the long run.

Future research can expand the understanding of allelopathic effects of blanket flower in various directions. It would be interesting to investigate the intraspecific allelopathic effects on the species, which, for

example, had a facilitating effect on the germination of its own seeds in the case of *Rumex obtusifolius* L. (Ohsaki et al., 2020). It is worth exploring the role of environmental variables and the influence of other plant species. Furthermore, for a deeper understanding of the ecological role and spread mechanisms of *G. pulchella*, long-term ecological observations and field studies may also be necessary.

## 5 | CONCLUSION

The results provide evidence that the allelopathic effect of *G. pulchella* significantly impacts the early development of oilseed rape. Plant shoot and root growth are sensitive to the presence and concentration of the chemical compounds of blanket flower. These in vitro results suggest that the allelopathic effect of blanket flower may contribute to the competition and invasion ability of other plant species. The allelopathic effect of the species may affect plant competition and biodiversity, especially in areas of *G. pulchella* invasion. The results are also of wider importance in terms of plant ecology and agricultural practice, and thus open many additional research directions in the field of species invasion and allelopathy.

## AUTHOR CONTRIBUTIONS

László Bakacsy: Conceptualization, methodology, experimental design, investigation, reviewing and editing, supervision. Krisztina Napsugár Nagy and Luca Viktória Kardos: Investigation, data curation, formal analysis, writing—original draft preparation. Zsófia Orbán: Collecting plant materials, discussion, revision. The final manuscript has been read and approved by all authors.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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