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# What Do Cross-Range Germination, Growth, and Interaction Studies Reveal about the Behaviour of an Expansive Plant Species?

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**Abstract:** Understanding the invasion potential of any plant species is crucial for early detection in habitat conservation, particularly when observing their expansion within their native region. As a test species, we utilised *Allium ursinum* L., a dominant clonal species in early spring forest floors. We compared the species' germination capacity in native (Hungarian) and non-native (North American) soils, its seedling growth, and competing performances with two co-occurring dominant species, *Melica uniflora* Retz. and *Carex pilosa* Scop., in ten soil types and three soil compositions, respectively. Additionally, the competitive interactions of *A. ursinum* with *Convallaria majalis* L., a species already introduced in North America, were assessed under three moisture conditions. The results revealed that *A. ursinum* exhibited enhanced germination in non-native soils, while its shoot growth was most vigorous in control soil. When grown in soils with different co-dominant species, *A. ursinum* seedlings exhibited varying growth rates, significantly influenced by solar radiation intensity. *A. ursinum* shoots displayed superior growth in soil collected from *C. pilosa* stands compared to soil originating from its own stands. Notably, *A. ursinum* effectively competed against *C. majalis* in moderate soil moisture conditions. Furthermore, increasing sand content improved the competitive ability of *A. ursinum* against *C. pilosa* and *M. uniflora*. Based on our findings, *A. ursinum* possesses an invasion potential for particular North American habitats. However, the extent of its potential is dependent upon soil and climatic conditions. Under medium moisture regime, *A. ursinum* might outcompete the already established *C. majalis* from its habitats. Additionally, it can potentially displace native species with comparable ecological characteristics, such as *C. pilosa* and *M. uniflora*, especially in loose soils. Similar cross-range seed germination, growth, and paired competition experiments with potential competitor species are highly recommended as these can not only elucidate its native range expansion but also various growth scenarios for its agricultural cultivation.

**Keywords:** biotic interactions; germination and growth profiles; Relative Interaction Index; invasion; competition; solar radiations; co-existing species

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## 1. Introduction

The roles of plant community compositions are usually determined by coevolved interactions of long-term associated native species [1–3]. Abiotic factors can alter the plant–plant interactions that have evolved in natural ecosystems since they can modify the competitive relationships within a system [4–6]. The manifestation of this alteration can initially be observed as a transformation in the dominant structure of plant communities [5,7,8]. Changes in the dominance structure can also occur due to the introduction of a novel and highly competitive plant species, which can then impact the coexistence of species through the exclusion of weaker competitors or by imposing constraints on similar species [9–15]. Therefore, it is necessary to investigate the probability of the establishment of a dominant species in the potential recipient ecosystem [16–20]. Due to human activities' direct and indirect consequences, many plant species have become naturalised in new geographic ranges by establishing self-sustaining populations [21–23]. A subset of these naturalised species became invasive by spreading across considerable distances [24,25] and posing a potential threat to native biodiversity and ecosystem functioning [26–28]. The spread of invasive plants is associated with a significant change in host community composition, and its impact varies as per the characteristics of the invaders and the invasibility of the host community [29–34]. The invasive properties of a plant species are determined by its ability to germinate successfully and how well it can compete against co-occurring species [23]. Among these invasive proprieties, clonal growth form is considered one of the most essential traits of successful invaders, enabling them to spread across numerous disturbed habitats [35–37]. Also, the ease of seed dispersal is key for effectively establishing an introduced alien species, e.g., for agricultural purposes [38–40], but little is known about the early-stage establishment of dominant species. Understanding the invasion potential of dominant plant species is incredibly important if we want to prevent the adverse outcomes of their accidental or intentional introductions. Interspecific interaction experiments' role and importance in understanding community dynamics have been primarily underestimated [41,42]. These interspecific interactions further elucidate the need to understand plant–plant interactions (dominant vs. subordinate species). Along with the dominant plant species, co-dominant species' behaviour in above- and below-ground spaces can be significant when disentangling how a community is organised [41,43,44].

In our study, we chose to focus on *Allium ursinum* L. (hereafter "*A. ursinum*") based on long-term monitoring studies conducted in its native range in Germany, where its behaviour has changed over the past decades, transitioning from a species with natural fluctuations to a naturally expanding species [45,46]. *A. ursinum* is a strong competitor in wet and nutrient-rich soil conditions within its native mesic habitats [14,45–48]. This plant outcompetes its natural competitors in the herb layer and can destroy the herbaceous plant community diversity by often forming monodominant stands [14,47,49–51]. Due to its high nutritional and pharmaceutical value [52–55], there have been several attempts to bring wild *A. ursinum* into agricultural production in its native range, i.e., in Europe [56–60] and outside of its native range like in India [61,62], and Russia, etc. [63]. Still, there is a significant amount of work to be conducted in this regard.

Evidently, *A. ursinum* can spread intrusively in native populations; it is assumed to be an aggressive invasive species in a new habitat. This led us to investigate its germination potential in a similar climatic zone in the northern United States. Interspecific competition with other dominant species in its native range can determine the spread of such species since these species play a fundamental role in maintaining the structure and diversity of the given plant communities [14,15]. Presumably, in its non-native range, where different dominant species with similar community characteristics exist, *A. ursinum* would have a competitive advantage there. Such competitive interactions, however, should be tested in the laboratory setting so that the impacts of the abiotic conditions and plant–plant interaction effects can be established first, as various soil properties have been reported to affect its growth, flowering, and overall nectar production [53,64,65]. *Convallaria majalis* L. (hereafter '*C. majalis*') is a native species found in the European forest floors. The similar leaf morphology of *C. majalis* and *A. ursinum* frequently leads to confusion between these two species, and due to the similarities in their life strategies, both might lead to competition in their natural habitats [66]. *C. majalis* has already escaped from cultivation and established new habitats where it has been naturalised in several states of the U.S. and Canada [67]. Hence, the question arises: under what abiotic conditions does *A. ursinum* have a chance of defeating *C. majalis* and which areas are potentially threatened if *A. ursinum* is introduced? A previous field experiment on *A. ursinum* revealed that the strongest competitors in its native plant community were *Carex pilosa* (hereafter, '*C. pilosa*') and *Melica uniflora* Retz. (hereafter '*M. uniflora*'), which are clonal and maintain biodiverse-rich herb layers, but *A. ursinum* was able to disrupt this community hierarchy [14].

In our research, the initial objective was to explore the cross-range germination of commercially available *A. ursinum* seeds in North American soils, as opposed to their germination in Hungarian soils. The main aim was to assess the species' ability to germinate effectively in soils from a novel geographic range that may have unique soil biota and chemical composition.

Secondly, we aimed to examine the effect of native soils collected under it and its native competitors on the growth of *A. ursinum* seedlings in response to direct solar radiation. We expected that more nutrient-rich soils would support more vigorous *A. ursinum* growth and that the effects of sunlight would significantly impact growth intensity.

Thirdly, the effects of soil texture and water supply were assessed on the plant–plant interactions between *A. ursinum* and its co-dominant plant species. The aim was to determine under what soil texture and water conditions *A. ursinum* can achieve greater competitiveness than its natural competitors.

By addressing these research questions, we aimed to gain a deeper understanding of the ecological factors influencing the growth and spread of *A. ursinum* and draw attention to the potential invasive behaviour of the species even within its native range. These efforts can facilitate the development of future conservation management strategies, aiming to regulate the plant's potential spread while preserving native plant communities. Considering that *A. ursinum* can be cultivated in various floral and environmental settings across Europe and other temperate regions, including the United States, we have strived to create a model that can be evaluated through applied research in specific habitat conditions.

Our findings can provide valuable insights into the species' ecological behaviour and invasive potential, enabling the management of issues arising from its cultivation and the development of effective defense strategies.

## 2. Materials and Methods

### 2.1. Study Plants

*Allium ursinum* L., commonly known as 'bear garlic' of Amaryllidaceae [68] family, is an early spring clonal and bulbous geophyte that grows climate-zonally on moist, well-drained, humus and nutrient-rich soils in mesophilic deciduous and mixed forests [47,48,51,69–71]. Furthermore, it spreads intrazonally throughout riparian forests with an additional water supply or even in treeless wet habitats (e.g., [72,73]). Its spread is limited by the fact that there is significant evaporation through its large leaf surface, which makes it a stenohydric, moisture-demanding plant species [74]. At the same time, it has high nutrient demands, especially in its reproductive phase, which is why its lifespan is approximately a decade. Its short life cycle is offset by clonal spread and significant seed production [48,70]. It germinates in the fall but is a light-demanding plant from the seedling stage by spring. When forests completely leaf out and light availability decreases, *A. ursinum* recovers nutrients from their leaves and slowly recedes into their bulbs by summer [48,49,70]. *A. ursinum* is a species with a competitive strategy [48,75,76], and it is a character species of the Fagetalia syntaxonomic group [75–77].

*Convallaria majalis* L., also called the 'lily of the valley' of the Asparagaceae family [68], is a spring clonal geophyte with a relatively thick rhizome, which can survive on slightly drier, well-drained, humus and nutrient-poor soils [78], compared to *A. ursinum*. It is climate-zonally dominant, mainly in mesophilic deciduous forests and mixed and coniferous forests [79]. Although its leaves are similar in size and shape to *A. ursinum*, they evaporate less, making them more drought-tolerant than *A. ursinum*. Its nutrient requirements are more moderate, and its growth is much slower than *A. ursinum*. While *C. majalis* has an early juvenile stage that lasts six months and a juvenile stage that lasts one to two years, during which time it grows its rhizomes and subsequently its shoots [78], its lifespan as a clonal plant can reach up to 670 years [80] and the arrangement of the ramets is genetically driven [81]. It is more shade-tolerant than *A. ursinum* because its leaves develop in the spring in moderately shaded forests, and they only wither in the fall. When competing with summer aspect species, its leaves can be damaged by direct irradiation in summer. *C. majalis* has a generalist strategy [76] and syntaxonomically is a broader Querco-Fagetea species [75,76].

*Carex pilosa* Scop. the 'hairy sedge' of the Cyperaceae family [68] is a thin rhizome-forming geophytic-hemicryptophyte [82] sedge with extensive clonal growth. The plant has deciduous leaves on reproductive shoots with long, overwintering leaves at the base [83]. It is more drought tolerant than *A. ursinum* but also tolerates a wide range of soil moisture regimes, from dry to wet, and its nutrient requirements are also lower [84–86]. *C. pilosa* has more more continental distribution than *A. ursinum*. It is a dominant species in beech and hornbeam-oak grasslands of European temperate deciduous forests. Further, it occurs in mixed forests [87,88] and in the forest steppes of the Southeast European part of Ukraine and Russia [89]. *C. pilosa* is a hemisciophyte or moderate sciophyte [82] with a competitive strategy [76] and syntaxonomically a Fagetalia, Carpinion character species [75–77].

*Melica uniflora* Retz., commonly known as 'wood Melick' of the Poaceae family [68], is a thin-rhizome forming proto-hemicryptophyte [72], which is a loose tussocky grass with shoots that die off in the fall. Its distribution is similar to *A. ursinum* but can also be found in the Mediterranean and Asia Minor. It is a dominant grassland constituent of deciduous forests but is also common in mixed forests and forest steppes. It has lower nutrient requirements and is more drought tolerant but does not tolerate flooding [72]. Its clonal shoots can grow even in shady habitats. *M. uniflora* has a competitive strategy [76] and is syntaxonomically a broader Querco-Fagetea species [75,76].

### 2.2. Seeds and Propagules Procurement

To minimise the genetic or climatic adaptions within seed material, *A. ursinum* seeds for all germination and growth experiments were sourced from a single commercial source based in the London, UK (https://kykeonplants.mysimplestore.com, accessed on 19 September 2023). For the competition experiments, the propagules of *A. ursinum* and co-existing species *C. pilosa* and *M. uniflora* were collected from the Mecsek Hills in an Oak-Hornbeam (*Asperulo taurinae-Carpinetum* Soó et Borhidi in Soó 1962) plant association in April 2017–2018. *C. majalis* rhizomes were also procured commercially (Pecs, HU; https://profifaiskola.com/, accessed on 19 September 2023). *A. ursinum* seedlings that were in the same developmental stage and size were selected, while in the case of *C. pilosa*, *M. uniflora* and *C. majalis* equal-sized ramets and rhizomes were used for planting (each of $\leq$5 cm with 1–2 nodes per pot). These soil-less root systems were kept wet and were immediately used for the growth and interaction experiments.

### 2.3. Growing Media Types

For the *A. ursinum* germination test in native and non-native ranges, nine soil samples were procured across the Mecsek hills (native range) and the northern part of the U.S.A. (non-native range) during the spring of 2017. In the native range, these nine soils were sampled from the *Asperulo taurinae-Carpinetum* plant community where *A. ursinum* has monotypic stands and borders the herb layer dominated by *C. pilosa* or *M. uniflora*. The monotypic stands of *A. ursinum* dominated three sampling sites, *C. pilosa* dominated another three, and the subsequent three sites were dominated by *M. uniflora*, respectively [14] *A. ursinum* shoots growth test was also conducted in these nine soils associated with these three dominant plants. The soil was collected in plastic bags at a 5–10 cm depth of 0.5 $m^2$. After large debris and litter removal, samples were stored at ~10 °C until the experimental setup [90]. Collected soil types are brown forest soils with clay illuviation (Luvisoils).

In the non-native range, similar procedures were followed for the nine soil collection sites across Montana, Idaho, and Washington, states within the U.S.A. The habitats can be characterised as coniferous forests (*Pseudotsuga menziesii* and *Pinus contorta* series) with metamorphic, sandy loam soils and bottomland hardwood forests (*Populus trichocarpa* and *Populus trichocarpa-Pinus ponderosa* communities) with alluvial soils.

For the interaction experiment with *C. majalis*, we used a commercially available universal potting soil (Pecs, HU; https://www.praktiker.hu/, accessed on 19 September 2023). For the soil mixtures of the *C. pilosa* and *M. uniflora* interaction experiments, only soil samples collected from *A. ursinum* were used by homogenising them from different habitats. There were three soil texture categories for interaction experiments with *C. pilosa* and *M. uniflora* with 0%, 25%, and 50% of the sand mixture. Potting soil was used in the control sets of germination, growth, and competition (only *A. ursinum* vs. *C. majalis*) tests, while a commercially procured (Pecs, HU; https://www.praktiker.hu/, accessed on 19 September 2023) fine river sand of nursery grade was used in sand-soil categories of *C. pilosa* and *M. uniflora* interaction experiments.

### 2.4. Cross-Range Germination Test

Before germination tests, a water-floating test for seeds and embryo dissections was performed on a random seed lot. To assess the germination vigour of *A. ursinum*, commercially procured seeds were sown into soils from each of the nine sites from the native and non-native ranges. The native range setup had ten soils: three of each *A. ursinum*, *M. uniflora*, and *C. pilosa* growing soils and with one potting soil as a control. In the non-native range, there were also nine soil sites and one potting soil control. In both ranges, each site had ten seeds with ten replications. All the setups had 40-celled seed trays (each cell/pot: 5 × 5 × 6 cm) in all experiments. The facility had to simulate the natural conditions, i.e., seed trays were kept in a growth room with the natural light source but without additional heating ($-4 \pm 2$ °C to $10 \pm 5$ °C). Double-layered jute bags were covered over trays to model the effect of natural leaf litter and avoid direct light. Soil moisture levels were monitored weekly and augmented accordingly. The number of germinated seeds ($\geq$2 mm root) was recorded at the end of the experiment, around the 10th week.

### 2.5. Growth Experiment

To assess the growth patterns of *A. ursinum* in different soils, *A. ursinum* germinated seedlings were sown in ten soils (similar to the germination test setup mentioned above: three *A. ursinum*, three *M. uniflora*, three *C. pilosa,* and one as a control with potting soil). Each soil had five seeds per pot with ten replications. All the treatment trays were subjected to the same growing conditions as in the above-mentioned soil germination test. Weeds were recorded and removed to minimise resource depletion. After the first emergent leaf, setups were transferred to an unheated hoop house facility by the following week to receive enough solar exposure. During the growth experiment, we also recorded mean solar radiation data (W/m$^2$/min) from the A.W.S., i.e., Automated Weather Station (http://joido.ttk.pte.hu, accessed on 19 September 2023) of the University of Pecs (46°04′39.9″ N 18°12′23.2″ E; a.s.l. 174 m; manufacturer: Vaisala (Vantaa, Finland; https://www.vaisala.com, accessed on 19 September 2023) and Lambrecht GmbH (Göttingen, Germany; www.lambrecht.net, accessed on 19 September 2023). As there was no micrometeorological station inside the greenhouse and A.W.S. was just next to the greenhouse, we related the energy from the solar radiation with the potential comparative growth dynamics of the test plants in ten soils. Presumably, this parameter is mainly related to the temperature and humidity conditions found in the greenhouse. From the 13th week onward, jute bags were removed to avoid the irreversible bending of young seedlings. Leaf length and width were recorded weekly. At the end of the experiment (~21st week), above-ground and below-ground biomass was harvested, dried (at 60 °C for 48 h) and weighed.

### 2.6. Interaction Experiments

*A. ursinum* thrives in well-watered and nutrient-rich soils; the alteration of these conditions was tested within the framework of an interaction experiment that included

*A. ursinum* with *C. majalis*, *C. pilosa*, and *M. uniflora*. In the interaction experiment between *C. majalis* and *A. ursinum*, we used universal potting soil as the growing media and set three watering levels. For the experiment, 45 cells of seed trays (each cell/pot: 5 × 5 × 6 cm) were filled with potting soil. Growth conditions were the following: illuminance = 70 µE /$m^2$/s; relative humidity = 60%; temperature = 22–23 °C; photo period = 12/12 h in all. The young seedlings of *A. ursinum* and rhizomes of *C. majalis* were used in the following layout: *A. ursinum* alone: 15 × 1/cell; *C. majalis* alone: 15 × 1/cell; *A. ursinum* + *C. majalis* together: 15 × 1-1/cell. To model different levels of water supply, we set three different watering regimes: 8 mL water, low moisture; 15 mL water, medium moisture; 30 mL water, high moisture. Leaf length and width were recorded for all plants weekly. The experiments were terminated when *A. ursinum* mortality reached 80% in any of the given settings.

Plants in this experiment were grown for another season to test their regeneration ability. Trays were kept in an open outdoor growth facility without additional heating with a natural light source. Soil moisture levels were monitored and augmented accordingly. A single-layered jute bag covering was used to avoid weed germination and rainwater or snowfall erosion that would lead to soil compaction. In spring 2018, trays were moved back into the growth room and kept under the above-mentioned detailed conditions. The collection method of the leaf parameters was the same as the previous year. For below-ground parameters, 'number of roots' and 'longest root length' were recorded for all plants. Above and below-ground biomass was separately weighed after drying.

The soil structures were different in the *A. ursinum* + *C. pilosa* and *A. ursinum* + *M. uniflora* interaction experiment, and the water supply was the same within the year. We used the same seed trays as in the previous interaction experiment. The 45 cells were filled with soils collected in *A. ursinum*-dominated stands from natural habitats and were homogenously mixed with sand in the following ratios: 100/0, 75/25, and 50/50. The seedlings of field-collected *A. ursinum* were transplanted into these pots with the following setup: *A. ursinum* alone 15 × 3 (1/cell) or with either competing species (*C. pilosa* or *M. uniflora*). We also planted the ramets of the competing species pairs *A. ursinum* + *C. pilosa* (15 × 3; 1/cell) and *A. ursinum* + *M. uniflora* (15 × 3; 1/cell). Greenhouse growing conditions were the same as in the case of *C. majalis*. Watering was carried out until saturation, called the 'wet state' in 2017. Leaf length and width were recorded for *A. ursinum* plants weekly. For *C. pilosa* and *M. uniflora,* we recorded the 'plant height' and 'number of leaves' at the same time as *A. ursinum*. Trays were wintered outside of the greenhouse in natural weather conditions. In spring 2018, trays were moved back into the greenhouse and kept under the above-mentioned conditions. The experiments were terminated when *A. ursinum* mortality reached 80% in any of the given settings. In 2018, the interaction experiment with the *A. ursinum* + *C. pilosa* and *A. ursinum* + *M. uniflora* pairs were retested for one season (without regeneration phase), but with a lower water supply, i.e., in the 'moist state'. Experimental and growth settings were the same as in the case of *C. majalis* in 2017. The collection method of the leaf parameters was the same as the previous year. For below-ground parameters, 'number of roots' and 'longest root length' were recorded for all plants. Above- and below-ground biomass were separately weighed after drying.

## *2.7. Data Analysis*

### 2.7.1. Germination Test

Testing the germination ability of *A. ursinum* seeds in different soils from native and non-native ranges led us to significant germination differences. First, to determine the applicability of ANOVA, the dataset was checked for the necessary requirements, namely normality and homoscedasticity. The normality test was achieved using the Shapiro–Wilks test, while the existence of homoscedasticity among datasets was determined using the Flinger–Killeen non-parametric test because of the non-normal distribution of the data, after which the Wilcoxon Sum Rank test was used to show the significant differences among the datasets.

#### 2.7.2. Growth Experiment

Growth rate profiles for ten different soils based on the maximum growth values of *A. ursinum* seedlings during a 21-week timeframe were box plotted and analysed for further insights using ANOVA and Duncan post hoc tests. Growth rates of *A. ursinum* seedlings in several soils were studied using abiotic parameters like soil type and total solar radiation per week (the sum between measurements). While neither growth rate nor solar radiation has normal distribution and homogeneity of variances (homoscedasticity), quantile normalisation was applied to the data for calculating 3-way ANOVA followed by the Duncan post hoc test. Duncan post hoc test is needed when more than two experimental setups are involved in the experiment.

#### 2.7.3. Interaction Experiments

We calculated Relative Interaction Index (Armas et al., 2004 [43]) to evaluate competition and or facilitation between our test species. This index measures the 'relative interaction intensity' in plants, with strong mathematical and statistical properties with defined limits (+1 and −1; see Section 3.3) for competition and facilitation as it uses basic arithmetical operators, which make the index quite suitable for measuring multi-species interactions at the community level.

$$\mathrm{RII} = (\mathrm{B_w} - \mathrm{B_o})/(\mathrm{B_w} + \mathrm{B_o}) \tag{1}$$

where ($\mathrm{B_o}$) is biomass or growth attained by the candidate plant species growing without inter or intraspecific interactions and ($\mathrm{B_w}$) is growth with an interaction between an opponent and dominant plant. Inter or intraspecific interactions are primarily a result of differences in their growth or biomass when grown alone vs. together with other species. Later measurements might be shorter or larger depending on the interaction type, i.e., competitive or facilitative [43]. Based on the growth values of our interacting plants, several R.I.I. profiles of *A. ursinum* alone, co-existing species alone, and *A. ursinum* together with co-existing species were calculated using this equation; later, these were box-plotted and further tested for significance using *t*-test.

Data from germination, growth, and interaction experiments were analysed using Microsoft Office 365 suite (Version 2310 Build 16.0.16924.20054; Microsoft Corporation, Redmond, WA, USA) and R (version 4.4.0) [91].

## 3. Results

### 3.1. Germination Test

Even though there was a negligible significant difference between native Hungarian and non-native American soils (overall only), based on the Wilcoxon Sum Rank test results, significant germination differences were observed between the native Hungarian *A. ursinum* soils and the non-native American soils ($p$-value < 0.001). The median of germination in Hungarian *A. ursinum* soils was higher than in American soils (see Figure 1). Significant differences were also observed between the *A. ursinum* soils and the *C. pilosa* together with *M. uniflora* soils within native soils ($p$-value $\leq$ 0.0001; see Table 1).

**Table 1.** Result of the Wilcoxon Sum Rank test assuming that there were no significant differences between datasets ($p < 0.05$).

| Soil Type | *p*-Value |
|---|---|
| HUN vs. USA | 0.2362 |
| AU vs. USA | <0.01 |
| AU vs. CP + MU | <0.0001 |
| USA vs. CP + MU | <0.001 |

Abbreviations: HUN—Hungary; USA—United States of America; AU—*Allium ursinum*; CP—*Carex pilosa*; MU—*Melica uniflora*.

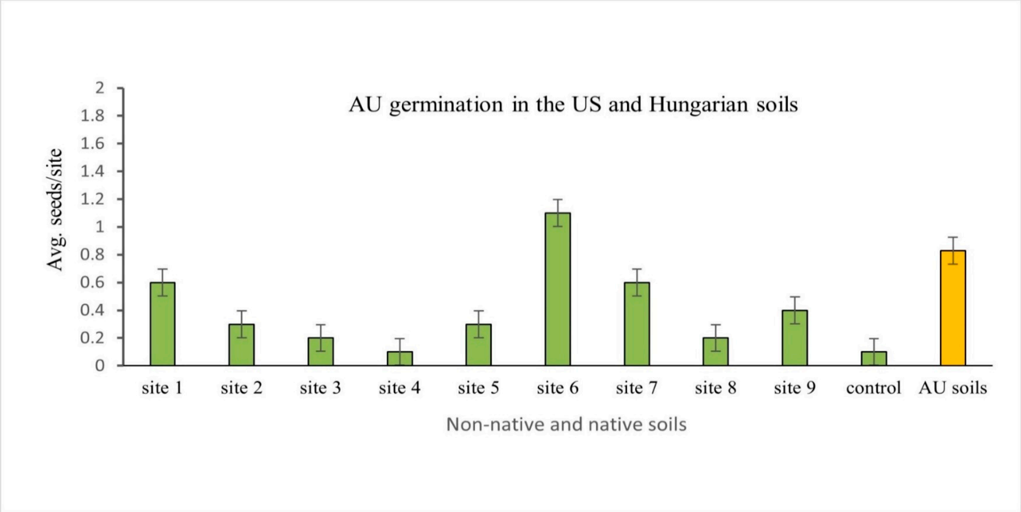

**Figure 1.** Comparative germination profile of significantly different *A. ursinum* seeds germination in non-native U.S. soils (in green) against the native Hungarian *A. ursinum* soils (in brown). Error bar represent the standard error in dataset.

Higher germination was observed in *A. ursinum* soils; the second suitable soil was considered under *M. uniflora,* and the less suitable soil for germination was the *C. pilosa* soil. The American soils also showed significant differences when compared with the native Hungarian *C. pilosa* and *M. uniflora* soils ($p$-value $< 0.001$; Table 1); however, there were differences among American soils as well (Figure 1).

### *3.2. Growth Experiment*

The initial intensive growth of *A. ursinum* shoots extends from week 6 to week 14, with another growth period occurring up to the 18th week (red line). The average growth rate of *A. ursinum* shoots shows a maximum between weeks 10 and 11, with a local maximum between weeks 16 and 19. The most intense growth from the 6 to 13th week occurs on *C. pilosa* soils (light blue line), except the control. *M. uniflora* soils show low growth intensity (green line) after a local maximum peak from the 6 to 14th week. The first growth period is shorter in the control (dark blue line), lasting until week 13. However, it only results in a local maximum, with the highest growth value among all soils occurring in the 17th week (Figure 2 and Supplementary Figure S3).

As we can see from Table 2, there were highly significant effects ($p$-value $\leq 0.001$) of measured abiotic factors such as the sum of weekly solar radiation (here, this refers to the reflected sun rays as these setups were inside a greenhouse facility). The soils (referred to as type here, which are based on the procurement site) were also highly significant ($p$-value $\leq 0.001$) with differences in their mean growth rates. Additionally, the mutual effect of the weekly amount of solar radiation and the soil type was significant on the mean growth rate of *A. ursinum* shoot growth (Table 2). As evident from Figure 3, various soils had similar growth affinity beyond their types, for example, between *A. ursinum*_3 and *M. uniflora*_2 or among *C. pilosa*_1 & 2 and *M. uniflora*_3. Further, *A. ursinum* soils had the most divergent growth profiles, while *M. uniflora* soils shared an affinity with *C. pilosa* and *A. ursinum* soils. *C. pilosa* soils were mostly the same in their growth rates, except *C. pilosa*_3 being an outlier with a similar growth profile as the control, though only under the low magnitude of solar radiation.

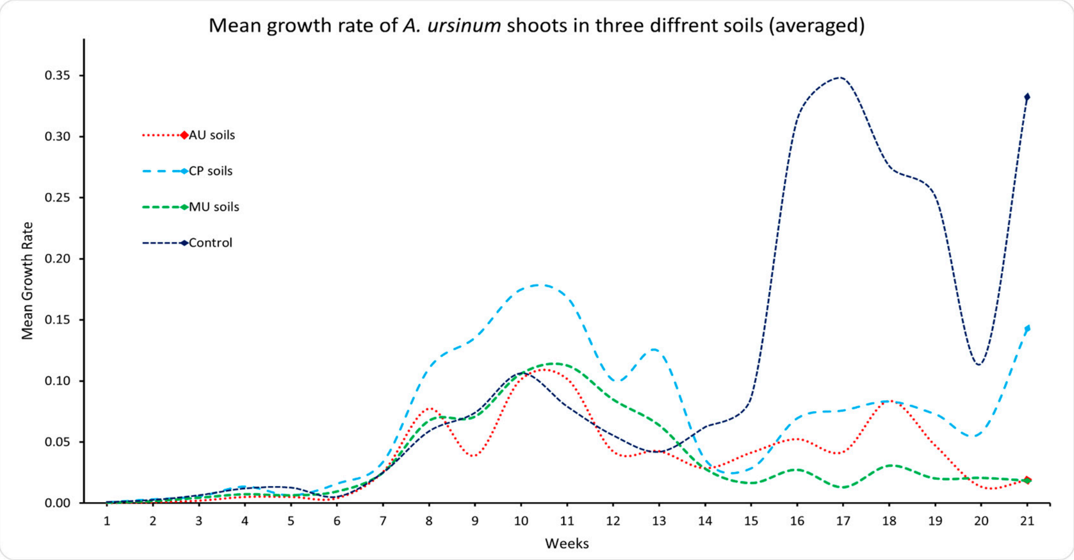

**Figure 2.** The mean growth rate of *A. ursinum* shoots for 21 weeks across different soil types. Legend: AU = *A. ursinum*; CP = *C. pilosa*; MU = *M. uniflora*.

**Table 2.** The effects of solar radiation and soil types on the mean growth rate of *A. ursinum* shoots across ten different soils using a 3-way ANOVA test.

| | Df | Sum Sq. | Mean Sq. | F Value | Pr (>F) |
|---|---|---|---|---|---|
| Solar | 1 | $2.415 \times 10^{12}$ | $2.415 \times 10^{12}$ | 119.365 | <0.001 |
| Soil Type | 9 | $7.684 \times 10^{12}$ | $8.538 \times 10^{11}$ | 42.206 | <0.001 |
| Solar: Soil Type | 9 | $3.246 \times 10^{12}$ | $3.607 \times 10^{11}$ | 17.831 | <0.001 |

Solar = sum of solar radiation between weekly measurements (Wm$^{-2}$).

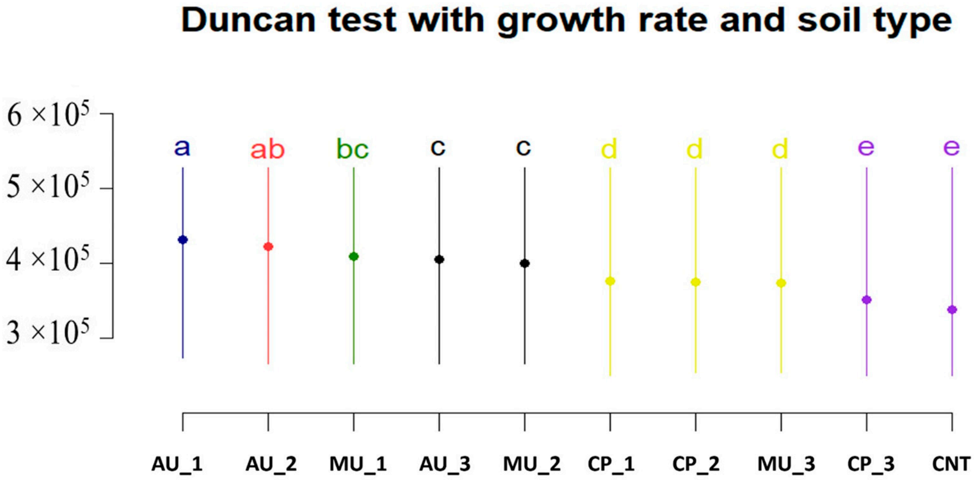

**Figure 3.** Duncan post hoc test for growth rate and soil origin type showing which soil origin had a similar effect on *A. ursinum* growth rate in response to total solar radiation, y-axis: quantile-normalised values of growth rate (order of magnitude similar to the values of the sum of solar radiation. Abbreviations: AU—*A. ursinum*; CP—*C. pilosa*; MU—*M. uniflora*; CNT—Control; 1/2/3—site name. Different letters (a, b, c, d, e) above the symbols refer to significant differences ($p < 0.05$) between the effect of soil origins on growth rates.

### *3.3. Interaction Experiments*

### 3.3.1. Competition between *A. ursinum* and *C. majalis* under Three Moisture Categories (Figure 4)

The presence of *C. majalis* did not impact the *A. ursinum* shoots in any moisture category, as their average R.I.I. value was around zero. However, in the presence of *A. ursinum*, the *C. majalis* shoots suffered a significant disadvantage in all moisture categories (F = 22.99, df = 5, $p < 0.001$). These results indicate different competitive behaviours in the low (F = 8.04, df = 5, $p < 0.001$), medium (F = 48.5, df = 5, $p < 0.001$), and high (F = 4.53, df = 5, $p < 0.01$) moisture categories based on the one-way analysis of variance (see Supplementary Table S1). During the second year of regeneration, the *A. ursinum* shoots showed no change in the case of the low moisture category. In contrast, significant advantages were observed in the medium moisture category, while they were disadvantaged in the case of high water supply.

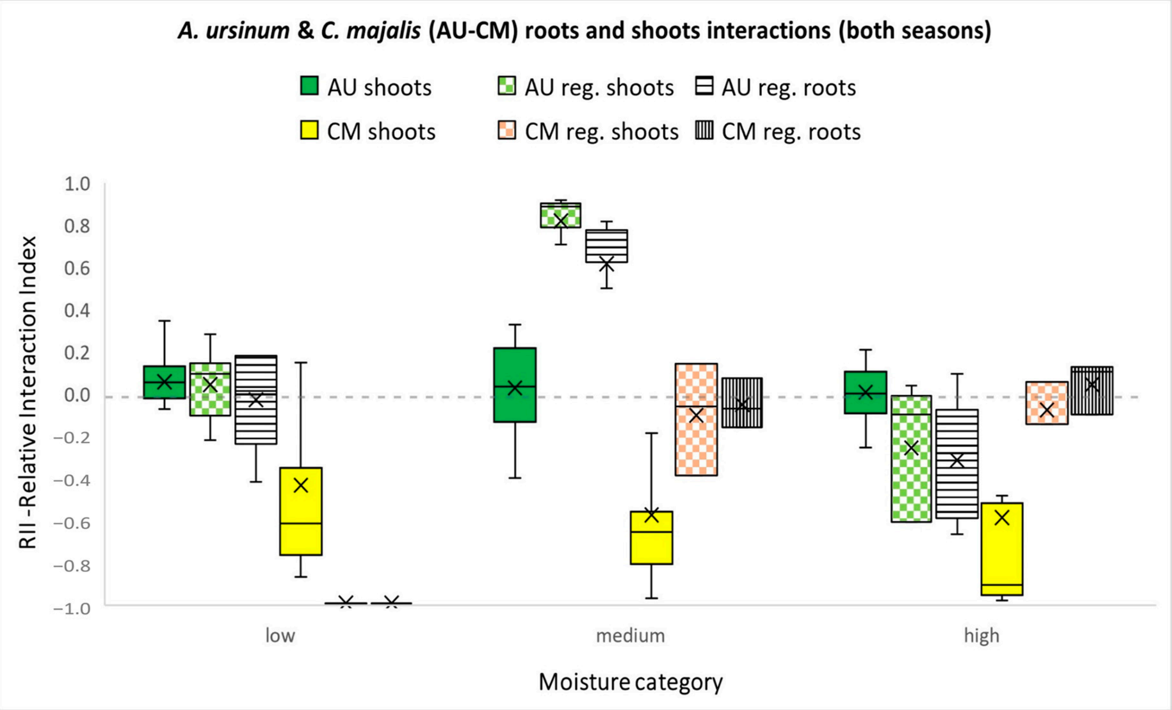

**Figure 4.** Cross categories box-plots of R.I.I. (Relative Interaction Index) values based on shoots (Total Leaf Area) and roots (Numbers of Roots) of *A. ursinum* and *C. majalis* in three moisture categories. The values above the zeroth fainted dotted line are positive R.I.I. values signifying facilitation, while below this are negative R.I.I. values indicating competition. Both seasons' mean (2017–2018) regenerated plants were harvested by the following spring season. 'x' indicates the mean R.I.I. values in all the box plots. Abbreviations: AU—*A. ursinum*; CM—*C. majalis*; reg.—regenerated.

On the other hand, *C. majalis* regeneration was unsuccessful in the low moisture category, resulting in all the plant deaths (R.I.I. values −1.0). However, in the medium- and high-water supply categories, the shoots of the plants were able to regenerate, reducing their disadvantage compared to the previous year, but they remained in the negative range. The behaviour of the roots of *A. ursinum* and *C. majalis* during the regeneration year was similar to that of the shoots. However, the latter's roots slid into the positive range in the case of high water supply.

### 3.3.2. Competition between *A. ursinum* and *C. pilosa* in a Wet Environment (Figure 5)

In the first year of the experiment, there was no competition between *A. ursinum* and *C. pilosa* at zero sand content. However, the *C. pilosa* shoots were at a disadvantage at a quarter of sand content, while the *A. ursinum* roots gained an advantage (by −0.2 mean

R.I.I. value). At half sand content, *C. pilosa* was destroyed. In the following regeneration year, the competition increased as irrigation decreased. The zero-sand content became disadvantageous for *A. ursinum* shoots (−0.2 average R.I.I. value), while *C. pilosa* still showed no reaction. The R.I.I. values of the regenerated roots were around zero for both *A. ursinum* and *C. pilosa*. At a quarter sand content, the disadvantage of *A. ursinum* shoots increased, with the average values of the roots slipping into the negative range. The disadvantage of *C. pilosa* shoots was accompanied by a low average R.I.I. value of the roots (−0.4), indicating a significant disadvantage. Half of the sand content favoured the regeneration of *A. ursinum* shoots, with a slightly positive value of mean R.I.I. around 0.1 and an even higher R.I.I. median of 0.35. However, the shoots (−0.7 RII value) and roots (−0.65 RII value) of *C. pilosa* could not withstand the increased sand content. Overall, high sand content was advantageous for *A. ursinum* in the competition, while increasing sand content linearly reduced the competitiveness of *C. pilosa* shoots and roots.

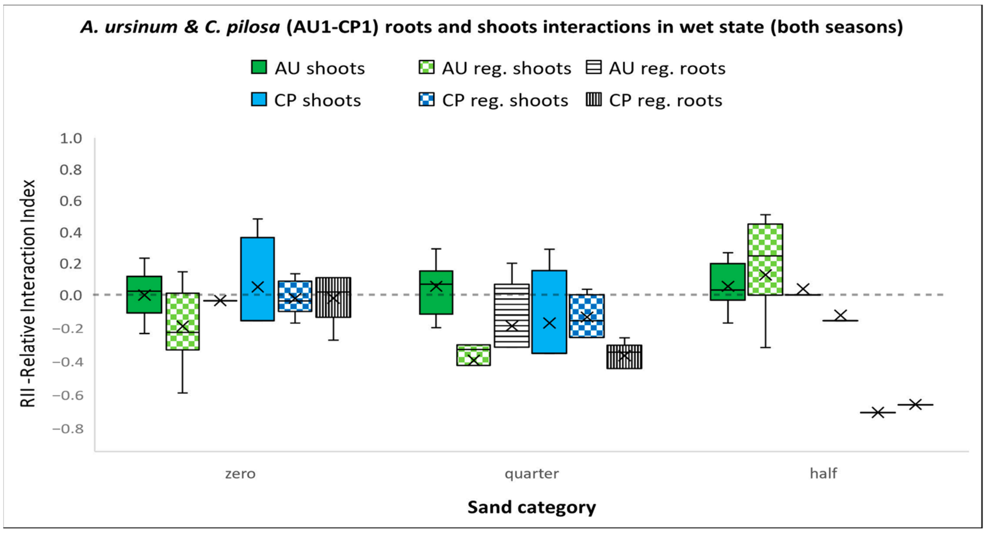

**Figure 5.** Cross categories box-plots of R.I.I. (Relative Interaction Index) values based on shoots (Total Leaf Area) and roots (Numbers of Roots) of *A. ursinum* and *C. pilosa* in three sand categories. Values above the zeroth fainted dotted line are positive R.I.I. values signifying facilitation, while below this are negative R.I.I. values indicating competition. 'Wet state', denoted with number 1, is water-saturated soils, and 'both seasons' means regenerated plants were harvested by the next spring season (2017–2018). 'x' indicates the mean R.I.I. values in all the box plots. Abbreviations: AU—*A. ursinum*; CP—*C. pilosa*; reg.—regenerated.

### 3.3.3. Competition between *A. ursinum* and *M. uniflora* in a Wet Environment (Figure 6)

In the first year of the experiment, in the presence of *M. uniflora*, *A. ursinum* shoots developed better in all soil texture categories, with primarily positive R.I.I. values (around +0.1) with increasing sand content. On the other hand, the shoots of *M. uniflora* were at a disadvantage with increasing sand content, with increasingly negative average R.I.I. values (−0.1, −0.3, and −0.5). Further, overall, *A. ursinum* interaction effects were significantly (F = 8.47, df = 3, $p < 0.001$) competitive (all R.I.I. values < 0) on *C. pilosa* roots and shoots across all soil compositions (see supplementary file/table). In the following regeneration year, the regeneration of *A. ursinum* shoots became more extreme in all soil structure categories. In addition, the *A. ursinum* shoots were significantly disadvantaged (with a < 0 R.I.I. value) in the case of quarter sand content. The *M. uniflora* shoots behaved similarly to the previous year, only in the case of zero sand content. In the case of increasing sand content, they were at an increasing disadvantage due to their shoots' regeneration and roots' development. Overall, *A. ursinum* proved to be a stronger competitor, while the competitiveness of *M. uniflora* decreased as the proportion of sand increased.

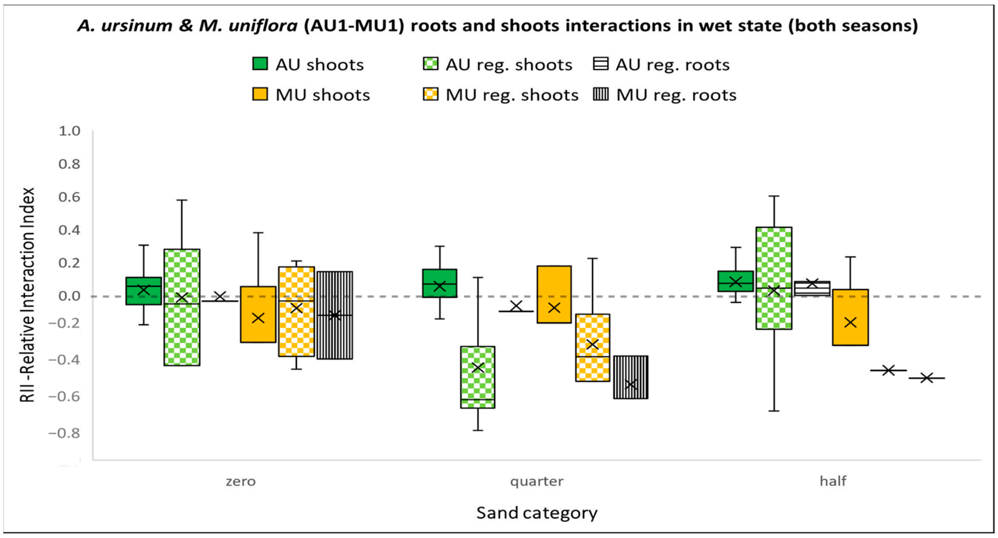

**Figure 6.** Cross categories box-plots of R.I.I. (Relative Interaction Index) values based on shoots (Total Leaf Area) and roots (Numbers of Roots) of *A. ursinum* and *M. uniflora* in three sand categories. Values above the zeroth fainted dotted line are positive R.I.I. values signifying facilitation, while below this are negative R.I.I. values indicating competition. 'Wet state', denoted with number 1, is water-saturated soils, and 'both seasons' means regenerated plants were harvested by the next spring season (2017–2018). 'x' indicates the mean R.I.I. values in all the box plots. Abbreviations: AU—*A. ursinum*; MU—*M. uniflora*; reg.—regenerated.

### 3.3.4. Competition between *A. ursinum* and *C. pilosa* in Moist Environments (Figure 7)

Both species showed a negative competitive interaction in all three soil compositions. The different sand ratios reduced the competitiveness of both species, although the *A. ursinum* was less affected than its fellow competitor, i.e., *C. pilosa* here.

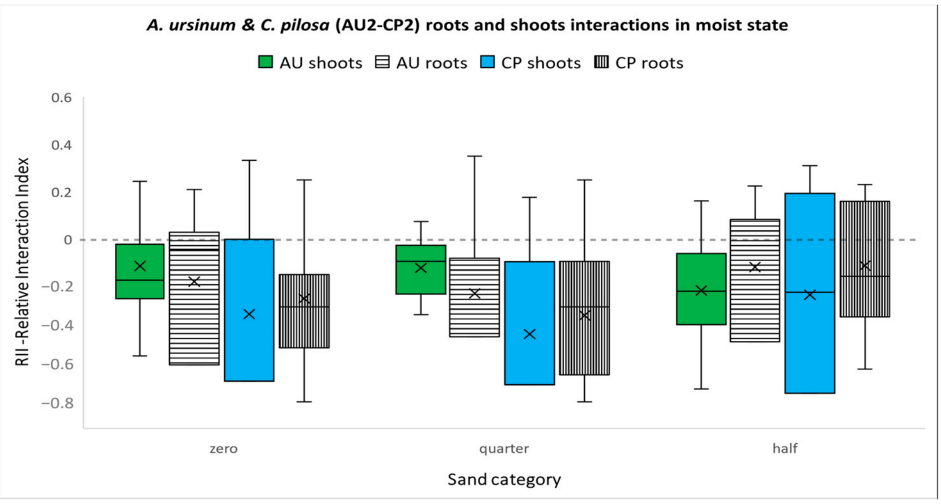

**Figure 7.** Cross categories box-plots of R.I.I. (Relative Interaction Index) values based on shoots (Total Leaf Area) and roots (Numbers of Roots) of *A. ursinum* and *C. pilosa* in three sand categories. Values above the zeroth fainted dotted line are positive R.I.I. values signifying facilitation, while below this are negative R.I.I. values indicating competition. 'Moist state', denoted with number 2, is moderately water-saturated soils. 'x' indicates the mean R.I.I. values in all the box plots. Abbreviations: AU—*A. ursinum*; CP—*C. pilosa*.

### 3.3.5. Competition between *A. ursinum* and *M. uniflora* in a Moist Environment (Figure 8)

In the case of zero sand and the presence of *M. uniflora*, the *A. ursinum* shoots suffered a significant disadvantage, but the roots did not. *M. uniflora* shoots and roots were better developed (F = 6.04, df = 3, $p \leq 0.001$). All of the R.I.I. values of *M. uniflora* roots fell into the positive range. At quarter sand content, the *A. ursinum* shoots are still at a disadvantage, but the extent of this is decreasing, and the roots are already slightly better developed. The shoots and roots of *M. uniflora* developed better than in the case of zero sand content. In the case of half sand content, the *A. ursinum* shoots are no longer at a disadvantage, and the roots behave similarly to when they were at a quarter sand content. On the other hand, the *M. uniflora* shoots are at a disadvantage in the presence of *A. ursinum*, with an average R.I.I. value of −0.2, and the advantage of the roots also disappears. However, they are not yet at a disadvantage. Overall, the increasing sand content is advantageous for *A. ursinum* and disadvantageous for *M. uniflora* in the competition (F = 6.04, df = 3, $p = 0.00062$; see supplementary file/table).

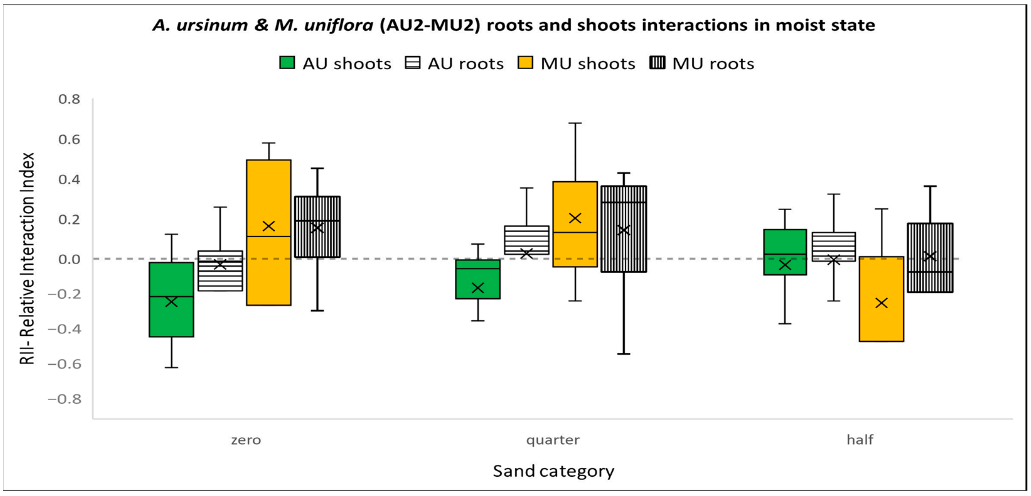

**Figure 8.** Cross categories box-plots of R.I.I. (Relative Interaction Index) values based on shoots (Total Leaf Area) and roots (Numbers of Roots) of *A. ursinum* and *M. uniflora* in three sand categories. Values above the zeroth fainted dotted line are positive R.I.I. values signifying facilitation, while below this are negative R.I.I. values indicating competition. 'Moist state', denoted with number 2, is moderately water-saturated soils. 'x' indicates the mean R.I.I. values in all the box plots. Abbreviations: AU—*A. ursinum*; MU—*M. uniflora*.

## 4. Discussion

### *4.1. Cross-Range Germination Test*

Our cross-range germination study demonstrated that *A. ursinum* can germinate in several American soils more effectively than in Hungarian soils. Here, we found a significant difference in the germination between *A. ursinum* soils and those collected from areas dominated by co-existing species in its native range. However, based on our earlier soil analyses, we reported that there were no major significant differences in the abiotic soil parameters like pH or moisture content of soils collected from *A. ursinum* dominated areas and those dominated by co-existing species (cf. Kaushik et al., 2021 [14]; see supplementary file). This suggests that there might be other more likely biotic effects behind the different cross-range germination capacities, such as allelopathy. The strong allelopathic effect of *A. ursinum* on other species has already been demonstrated [92], but further research is needed to understand how it affects its own seedlings or how the allelopathic substances of competitors influence the germination capacity of bear's garlic. Moreover, we would speculate the likelihood of *A. ursinum* invasion in American soils; as a clonal propagator, it has demonstrated a successful establishment of an early stage of invasion, i.e., germination [23,36,37].

### 4.2. Growth Experiment

In our growth experiment, the growth period showed a close correlation with the intensity of solar radiation, confirming what many authors have already found [93–96]. However, differences in the magnitude of growth may arise from variations in the capacity of the soil to supply nutrients to the plants (see Supplementary File).

The maximum growth exhibited by seedlings grown in control soil can be explained by their excellent nutrient-supplying ability, which manifests when the root system is already sufficiently developed. However, growth starting later in other soils may be due to the lack of mycorrhizal colonisation, which exists as part of the natural biota of soils and can provide an initial advantage to seedlings. The development of *A. ursinum* mycorrhiza was found to be inversely proportional and dynamically variable over time when compared to the nutrient-supplying capacity of the plant's soil [97]. Additionally, in closed stands, the soils (i.e., habitat type), light availability, and the dominance of *A. ursinum* also had a significant effect on the diversity and abundance of root mycorrhiza [90,98,99]. The decomposition of *A. ursinum* leaves results in a substantial nitrogen surplus [100], thereby contributing to the enhancement of soil nutrient levels [101,102], with microbial activity playing a pivotal role as the primary catalyst [103].

In contrast to *A. ursinum*, the leaves of *C. pilosa* decompose slowly and are partly evergreen, so they do not provide a significant nutrient surplus. Nevertheless, seedlings grew more vigorously in this soil. This leaf decomposition phenomenon is interesting because, in the monodominant stands of *A. ursinum*, the positive effect of maternal plants on seedlings was demonstrated [47]. However, this support was not evident when fully developed *A. ursinum* plants surrounded the seedlings. Based on the above, it can be hypothesised that the allelopathic compounds produced by *A. ursinum* may not only affect co-existing species but, at high concentrations, promote self-selection and the maintenance of an appropriate distance from maternal plants. Surviving seedlings may benefit from maternal plants whose large leaves create a favourable environment by maintaining a higher humidity [47]. Our study suggests that *A. ursinum* grows more effectively on *C. pilosa* dominated soils compared to *M. uniflora* soils, which could result from differences in their nutrient supply capacities.

### 4.3. Interaction Experiments

In the interaction experiments conducted on nutrient-rich soils (*A. ursinum* + *C. majalis*), it is presumed that *C. majalis* shoots were significantly disadvantaged in all moisture categories because *A. ursinum* seedlings already had leaves and roots that could immediately grow, while *C. majalis* had to develop these first from the rhizome, which requires more time [78]. The amount of water supplied did not appear to affect competition in the first year. However, in the next season, their interaction was more even as both plants sprouted from their respective perennating organs (bulbs and rhizomes, respectively). However, due to continued illumination, *C. majalis* could continue to photosynthesise even after *A. ursinum* had retreated into its bulb. The different strategies of the two species determined the outcome of the second year's competition, where the effects of water supply were more apparent and significant. Under low moisture conditions, which occurred during the summer months, *C. majalis* could not regenerate. Under favourable conditions with medium moisture, *A. ursinum* was most competitive and clocked a growth sprint with its abundant nutrient supply [48]. This reflects that under favourable medium water supply conditions, the nutrient utilisation ability of *A. ursinum* is better than that of *C. majalis*. The slower-growing, lower-nutrient-demanding, but much more water-tolerant *C. majalis* [104,105] outperforms *A. ursinum* under high water conditions. Our results suggest that the cultivation of *A. ursinum* may pose challenges as the absence of shading could make competition of light-demanding weeds more competitive. However, in the shaded forests adjacent to the cultivated areas, there is a possibility for the invasion of *A. ursinum* in a relatively narrow, moderately watered range.

The current study provides a comprehensive exploration of the competitive interactions between *A. ursinum* + *C. pilosa* and *A. ursinum* + *M. uniflora*, considering three distinct soil compositions and two varying watering regimes. The study investigates the effects of increasing sand content, which alters soil texture and has a direct impact on nutrient content, soil aeration and porosity, water penetration, and drainage. The modifications to these factors ultimately influence the outcomes of species competition.

In the experiment, the abundant irrigation intended to simulate water supply in *A. ursinum*-dominated riparian forests [69,74,106]. Both *C. pilosa* and *M. uniflora*, found in similar habitats [107], were negatively affected by the increasing sand content, particularly regarding water impact. Consequently, *A. ursinum* gained an initial advantage, enabling it to outcompete other species more quickly in the subsequent year. Our results indicate that increasing the sand content did not provide *C. pilosa* and *M. uniflora* with a competitive advantage against *A. ursinum*. The early leafing out of *A. ursinum* put it ahead in the competition, giving it a distinct edge [47,48]. Detached *C. pilosa* and *M. uniflora* ramets were self-sufficient, not requiring leaf development like *C. majalis*. This led to a more balanced competitive situation in the first year with *A. ursinum* seedlings. These results indicate that the competition dynamics were influenced by the natural habitat preferences of *M. uniflora* and *C. pilosa* [85,108,109]. Factors such as climatic tolerance and shade adaptation contributed to the competitive abilities of the species [89,110]. Additionally, the outcome of growth and interaction experiments was dependent on the initial size of the propagules [79,111]. The availability of water and nutrients post-detachment played a critical role in the results of the experiments, emphasising the significance of the optimal shoot-to-root ratio [112].

Furthermore, *C. pilosa* was a stronger competitor than *M. uniflora*. These findings reveal the significance of soil composition and early leafing out in determining species success and competition. The study provides a detailed understanding of the complex interactions between soil composition, watering regimes, and species competition that impact species dynamics in a natural environment.

## 5. Conclusive Remarks

The outcome of the growth and interaction experiments consistently relied on the initial size of selected propagules, including seeds, bulbs, ramets, or rhizomes. Notably, co-existing species with significant biomass demonstrated varying growth patterns, suggesting the influence of the propagule type's initial size, particularly in the context of rhizome nodes and root production [79,111]. In the field experiment, *A. ursinum* exhibited a tendency to form a monotypic stand in the long term, mainly thriving in more humid conditions that supported an extended lifespan (e.g., *A. ursinum* + *C. majalis*; in high moisture conditions) [47,48,69]. The high mortality during the regeneration phase highlighted the potential vulnerability of *A. ursinum* due to the lack of protective leaf litter cover, leaving buds susceptible to frost damage [113]. Incorporating physically integrated rhizome fragments with parent plants might help alleviate the competitive effects of *A. ursinum*-like species [114,115], thereby promoting more balanced coexistence in the herb layer, a crucial consideration for sustainable agricultural practices.

To gain deeper insights and projections, further research is recommended, mainly focusing on the potential agricultural benefits and risks associated with *A. ursinum* cultivation. Due to the germination responses in non-native soil types, the species could significantly spread and monopolise favourable habitats while adversely affecting the pre-existing species dynamics in the herb layer of American temperate forests. Also, its aggressive growth patterns and the potential to monopolise favourable habitats underscore the need for vigilant management strategies to prevent its uncontrolled spread and the subsequent disruption of native plant communities in agricultural settings. Additionally, expanding the interaction experiments to include more species paired with *A. ursinum* could shed light on effective intercropping strategies that promote beneficial coexistence while mitigating potential agricultural risks [116]. A proactive approach, such as Early

Detection and Rapid Response (EDRR), is crucial in curbing the potential spread and adverse effects of introduced invasive species [39,40,117], emphasising the significance of preventive measures as the primary defense against invasion in agricultural landscapes.

**Supplementary Materials:** Supplementary files are accessible here: https://doi.org/10.5281/zenodo.6483485, accessed on 19 September 2023. Reference [118] is cited in the supplementary materials.

**Author Contributions:** Research conceptualisation, R.W.P. and T.M.; sample design and methodology, R.W.P. and T.M.; investigation and data collection, K.K., R.W.P. and T.M.; resources, T.M. and R.W.P.; data analysis and interpretation, K.S.-T., R.W.P., T.M., K.K. and K.R.; writing—original draft preparation, K.K.; writing—review and editing, T.M., K.R., R.W.P., K.S.-T. and R.R.; supervision, R.W.P. and T.M.; project administration, K.K., T.M. and R.W.P.; funding acquisition, R.W.P., R.R. and K.K. All authors have read and agreed to the published version of the manuscript.

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