European Journal of Agronomy 153 (2024) 127040

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Potential of different common (*Fagopyrum esculentum* Moench) and Tartary (*Fagopyrum tataricum* (L.) Gaertn.) buckwheat accessions to sustainably manage surrounding weeds

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ARTICLE INFO

Keywords:
Agroecology
Allelopathy
Buckwheat
Polyphenols
Root exudates
Sustainable weed management

ABSTRACT

Twenty-nine accessions of two buckwheat species (*Fagopyrum esculentum* Moench (common buckwheat) and *Fagopyrum tataricum* (L.) Gaertn. (Tartary buckwheat) were evaluated for their allelopathic potential against two resistant weeds, the monocot *Lolium rigidum* Gaud. and the dicot *Portulaca oleracea* L. The bulking use of synthetic herbicides and their consequent contamination of the environment and resulting increment of herbicide-resistant weeds, imminently requires a solution to achieve sustainable weed management without chemical inputs. The results obtained in this study suggest that buckwheat accessions can sustainably manage weeds through plant interference as competition or allelopathy. This research showed that accessions differ in their potential for sustainably managing both weeds with *F. esculentum* accessions being more effective against *L. rigidum* and *F. tataricum* accessions against both, monocot and dicot weeds. The chemical profile of buckwheat accessions was evaluated to know the content of polyphenols in common and Tartary buckwheat accessions and to know more about their ability to manage weeds sustainably. Differences in the chemical profile between the two buckwheat species were clear. While common buckwheat accessions showed more orientin, vitexin and hyperoside, Tartary buckwheat accessions had higher amounts of rutin, quercetin and kaempferol. We propose that the screening and selection of accessions with strong polyphenol content and vigorous growth can be a step towards organic farming due to its relation to the weed management.

1. Introduction

In the current context of growing public concern about the harmful effects of herbicides on the environment and human health, and the increasing number of herbicide-resistant weeds (HRW) (Han et al., 2021; Heap, 2023), the development of environmentally friendly weed control strategies for more sustainable agricultural systems has become an urgent need. The herbicide-resistant-weeds pose a significant threat to global crop production. Unfortunately, during last decades have been emerging HRW cases that affect perennial crops, winter annual crops and summer annual crops, which are estimated to cause more than 34% of economic losses in agroecosystems (Jabran et al., 2015; Montull and Torra, 2023). Herbicides are the most commonly used pesticides in fields, accounting for 47.5% of the total pesticides used (De et al., 2014). Alternative strategies for weed control must be taken immediately, as herbicide-resistant weeds are expected to be continually growing (Montull and Torra, 2023). Even, the adoption of the Sustainable Use of Pesticides Directive (SUD) in 2009, the 2030 Agenda for Sustainable Development of UN in 2015, the Paris Agreement for Climate Change and finally the launch of the EU Green Deal and Farm to Fork Strategy (EU, 2020), find several administrative, economical and agricultural troubles, although all would help to create a favourable environment for the transformation of agricultural systems in order to achieve resilience and sustainability (EU-AGROSTAT; Tataridas et al., 2022).

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https://doi.org/10.1016/j.eja.2023.127040
Received 31 July 2023; Received in revised form 16 November 2023; Accepted 21 November 2023

The contamination and resistance problems associated with the massive use of herbicides call for urgent selection of strong competitive crop accessions, which can manage the growth of adventitious plant species using non-harmful methods (Mwendwa et al., 2021). Different weeds are resistant to different synthetic herbicides. *Lolium rigidum* Gaud. has shown resistance to acetyl-CoA carboxylase (ACCase), acetolactate synthase (ASL), photosystem II (PSII), 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), glutamine synthase, very long-chain fatty acid (VLCFA) synthesis, and protoporphyrinogen oxidase (PPO)-inhibiting herbicides. Moreover, *Portulaca oleracea* L. has been referred to be resistant to Group 5 (Legacy C1 C2) herbicides (PSII inhibitors). Therefore, it is crucial for agroecosystems to find crop accessions that can sustainably control weed development.

Buckwheat is an emergent dicotyledonous pseudocereal crop of the Polygonaceae family known for its high nutritional value and bioactive components (Gabr et al., 2022). Common buckwheat (*Fagopyrum esculentum* Moench) and Tartary buckwheat (*Fagopyrum tataricum* (L.) Gaertn.) are two commonly grown buckwheat species, that have been reported to suppress weeds, likely due to multiple factors such as competition for resources, allelopathy, and soil property alterations (Falquet et al., 2015). Screening and selecting buckwheat accessions that thrive in a sustainable environment and can suppress surrounding weeds in the environment without using or reducing the use of synthetic herbicides, can be a step forward in developing the necessary sustainable agricultural systems (Vieites-Álvarez et al., 2023).

Buckwheat is primarily cultivated to produce food and pharmaceutical products and is increasingly referred to as a promising emerging crop due to its balanced amino acid composition, phenolic compounds, flavonoids, and antioxidant properties (Szwed et al., 2014; Luthar et al., 2020; Vollmannová et al., 2021). It has also recently been suggested as a source of the flavonoid quercetin, which can help diabetics and prevent health problems (Luthar et al., 2020). In agroecosystems, buckwheat is considered a cover crop with the ability to control nearby weeds through plant interference, either by allelopathy or competition (Scavo and Mauromicale, 2021). Moreover, buckwheat is considered a day-neutral plant, as its flowering and growth are not significantly affected by day length. Unlike other plants that have specific day length requirements for flowering, buckwheat can flower and grow regardless of the length of the day making this cultivar a good option for cover cropping (Podolska, 2016).

Currently, plant breeders consider important growth and development traits when breeding locally adapted crop varieties. These traits help broadleaf plants compete and suppress weeds early and fast canopy dominance, along with drought tolerance (Mwendwa et al., 2021). The rapid development of buckwheat can also be an important point for weed suppression as it quickly builds up a dense canopy that limits weed access to light and acts as a good competitor (Bicksler and Masiunas, 2009). Latify et al. (2017) demonstrated that buckwheat has a major impact on weed development, probably due to its rapid emergence (seedlings emerged between 3 and 5 days after sowing), fast growth and upright growth habit (up to 150 cm in height). In addition, the study on the allelopathic potential of buckwheat reported that the main substances in buckwheat tissue, such as flavonoids and phenolic compounds, could also play an important role in weed control. Kalinova et al. (2005) showed that several allelopathic compounds were released into the medium during germination and early development of buckwheat and caused a reduction in root and shoot length of lettuce (*Lactuca sativa* L.), garden cress (*Lepidium sativum* L.), timothygrass (*Phleum pratense* L.) and Italian ryegrass (*Lolium multiflorum* Lam.). In another study, Kalinova et al. (2007) found several phytotoxic molecules in buckwheat water extracts, such as gallic acid, vanillic acid, rutin, epicatechin, vitexin and derivatives, which affected lettuce development. Szwed et al. (2019) also demonstrated that buckwheat effectively restricted the growth and metabolic response of barnyard grass (*Echinochloa crus-galli* (L.) P. Beauv.), wind grass (*Apera spica-venti* L.), cleavers (*Galium aparine* L.) and tiny vetch (*Vicia hirsuta* L.). Gfeller et al. (2018) proposed that compounds present in buckwheat tissues and released to the medium would be responsible for the growth suppression induced by common buckwheat to the weeds: pigweed (*Amaranthus retroflexus* L.), goosefoot (*Chenopodium album* L.) and barnyard grass (*Echinochloa crus-galli* L. Beauv.), with inhibitions of 53%, 42% and 77%, respectively, even without physical contact among roots, as proposed in this study. Moreover, several previous studies also showed the effectiveness of buckwheat to supress a wide range of weeds, as quackgrass (*Elymus repens* L.) (Golisz et al., 2007a; b), amaranth (*Amaranthus powellii* S. Watson), shepherd's-purse (*Capsella bursa-pastoris* L.), or corn chamomile (*Anthemis arvensis* L.) (Kumar et al., 2008; 2009).

Consequently, the screening, selection, development, and evaluation of buckwheat accessions with strong inherent competitiveness against herbicide-resistant weeds is an alternative management strategy of particular interest to agroecological systems. This knowledge is of great benefit to organic farmers, as they can use allelopathic and competitive buckwheat accessions to reduce weed pressure on their crops. In addition, selecting buckwheat accessions that control weeds biologically could increase productivity and efficiency by reducing weed control costs such as labour, equipment, chemicals, and other weed control agents.

This study compares for the first time the ability of twenty-nine different buckwheat accessions belonging to the species common buckwheat and Tartary buckwheat to dominate surrounding environment by plant interference with two weeds of interest, the monocotyledonous annual ryegrass (*Lolium rigidum* Gaud.) and the dicotyledonous common purslane (*Portulaca oleracea* L.). Both weeds are well known due to their acquired resistance to the mode of action of various synthetic herbicides and are among the most aggressive weeds in terms of cereal yields (Busi et al., 2020; Busi and Powles, 2016; Heap, 2023).

The bioherbicidal potential of these accessions was investigated based on the ability of each buckwheat accession to reduce the surrounding space occupied by shoots and roots of the monocotyledonous weed annual ryegrass and the dicotyledonous weed common purslane. Knowing how much space the weeds occupy around crops is important for adjusting the necessary crop inputs as well as the spacing between crops. This research contributes to move forward an agroecological system, as it proposes a solution for weed control that simultaneously protects the environment and improves crop yield and quality.

2. Material and methods

2.1. Plant material

Twenty-nine buckwheat accessions from two different species common (*Fagopyrum esculentum* Moench) and Tartary buckwheat (*Fagopyrum tataricum* (L.) Gaertn) were previously selected for their potential in organic agriculture in the frame of the ECOBREED project, which received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 771367. All accessions of buckwheat were grown at the Crop research institute in Prague, Czech Republic for three years. The following phenotypic traits such as number of leaves per plant and growth and branch shoot habit were evaluated during the growing seasons according to the international descriptors for buckwheat (International Plant Genetic Resources Institute (IPGRI), 1994) and are given in supplementary Table S1. The 19 accessions of common buckwheat and Východoslovenská krajová (Slovakia), while the 10 accessions of Tartary buckwheat tested are described in Table 1 (name, accession number, taxon, holding institution, acquisition date, and country of origin).

Čebelica, KIS Doris, Osrednje Goričko, Slovenj Gradec, Sveti Miklavž nad Litijo, and Sevnica seed samples were obtained from KIS (Agricultural Institute of Slovenia, Hacquetova ulica 17, SI-1000 Ljubljana, Slovenia). The rest were sourced from the Czech Gene Bank, Crop Research Institute, Drnovská 507/73, Praha 6-Ruzyně, 16106, Czech

Table 1
Genotypes name, accession number of gene bank, taxon, holding Institute, acquisition date, and country of origin of nineteen *Fagopyrum esculentum* accessions (Aelita, Arihira zairai, Ballada, CD7272, Čebelica, Česká krajová, Chernigovskaya 17, Dozhdik, La Harpe, Iwate zairai, Lada, Luba, Monori, Prego, Pulawska II, Skorospelaya, Špačinska 1, Sweden-1 and Vychodoslovenská krajová) and ten *Fagopyrum tataricum* accessions (290, 01Z5100012, Jianzui, KIS Doris, Osrednje Goričko, PI451523, Sarasin a Ployes, Sevnica, Slovenj Gradec and Sveti Miklavž nad Litijo).

Name	Accession Number	Taxon	Holding Institute	Acquisition Date	Country of Origin
Aelita	01Z5000001	*F. esculentum*	CZE122	1992	Former Soviet Union
Arihira Zairai	01Z5000055	*F. esculentum*	CZE122	1992	Japan
Ballada	01Z5000058	*F. esculentum*	CZE122	1993	Former Soviet Union
CD 7272	01Z5000143	*F. esculentum*	CZE122	2003	Czechoslovakia
Čebelica	commercial	*F. esculentum*	commercial	n.a.	Slovenia
Česká krajová	01Z5000131	*F. esculentum*	CZE122	2003	Czechoslovakia
Chernigovskaya 17	01Z5000067	*F. esculentum*	CZE122	1996	Ukraine
Dozhdik	01Z5000071	*F. esculentum*	CZE122	1996	Belarus
Iwate Zairai (MIDOU)	01Z5000046	*F. esculentum*	commercial	n.a.	Japan
La Harpe	commercial	*F. esculentum*	CZE122	1992	France
Lada	01Z5000007	*F. esculentum*	CZE122	1992	Former Soviet Union
Luba	01Z5000129	*F. esculentum*	CZE122	2003	Russian Federation
Monori	01Z5000017	*F. esculentum*	CZE122	1992	unknown
Prego	01Z5000066	*F. esculentum*	CZE122	1994	Germany
Pulawska II	01Z5000137	*F. esculentum*	CZE122	2003	Poland
Skorospelaya	01Z5000061	*F. esculentum*	CZE122	1992	Former Soviet Union
Špačinska 1	01Z5000070	*F. esculentum*	CZE122	1996	Slovakia
Sweden-1	01Z5000141	*F. esculentum*	CZE122	2003	Sweden
Vychodoslovenská krajová	01Z5000069	*F. esculentum*	CZE122	1996	Slovakia
290	01Z5100025	*F. tataricum*	CZE122	2005	Bhutan
Fagopyrum tataricum	01Z5100012	*F. tataricum*	CZE122	1996	Czech Republic
Jianzui	01Z5100041	*F. tataricum*	CZE122	2010	China
KIS Doris	commercial	*F. tataricum*	commercial	n.a.	Slovenia
Osrednje Goričko	2224	*F. tataricum*	SVN018	n.a.	Slovenia
PI 451723	01Z5100013	*F. tataricum*	CZE122	1992	Mexico
Sarasin a Ployes	01Z5100050	*F. tataricum*	CZE122	2009	USA
Sevnica	2337	*F. tataricum*	SVN018	n.a.	Slovenia
Slovenj Gradec	2223	*F. tataricum*	SVN018	n.a.	Slovenia
Sveti Miklavž nad Litijo	2316	*F. tataricum*	SVN018	n.a.	Slovenia

*WIEWS inst. code, n.a. – not available

Republic). All samples were obtained with SMTA. Buckwheat seed samples were pre-selected in the frame of the European project ECO-BREED from a buckwheat diversity panel due to their potential for organic agriculture (i.e., selected traits, level of production, pathogen resistance, etc.). Seeds of annual ryegrass (*Lolium rigidum* Gaud.) and common purslane (*Portulaca oleracea* L.) were obtained commercially from Herbiseed (UK) and 'Semillas Cantueso' (ES), respectively.

2.2. *Preparation of buckwheat samples for UHPLC-ESI-MS/MS analysis*

Samples of grains from all accessions collected each year during field trials conducted in Prague, Czech Republic, were ground, frozen in liquid nitrogen and then ground to a fine powder with a pestle and mortar. Hundred mg of the sample was extracted twice with 1 mL of extraction solvent (comprising 80% methanol with probenecid as an internal standard at a concentration of c=0.1 μg mL^{-1}) in Eppendorf tubes. The extraction was performed using an ultrasonic bath at 45 °C for 60 min. After centrifugation, the resulting supernatants were pooled, filtered and stored at − 18 °C until subjected to UHPLC-ESI-MS /MS analysis.

2.3. *UHPLC-ESI-MS/MS analysis*

Used UHPLC-ESI-MS/MS instrumentation and analysis was described by Janovská et al. (2021). The chromatographic separation employed a gradient elution method with solvent A containing 0.2% formic acid in water, and solvent B containing 0.2% formic acid in methanol. The separation process began with the system running with 99% solvent A and 1% solvent B. Then, at 11 min, a gradient elution was initiated, reaching 40% A and 60% B. Subsequently, the column was eluted with 100% solvent B for 2 min. Equilibration before the next run was accomplished by washing the column with 99% A and 1% B for 2 min. The total analysis time was 15 min. The column was maintained at a temperature of 40 °C with a flow rate of 0.35 mL min^{-1}, and the injection volume was 1 μL. To ensure accuracy and calibration, a reference standard mixture from Thermo Fisher Scientific was used. Data evaluation was performed using the Quan/Qual Browser Xcalibur software, version 4.0.

Following compounds such as catechin, chlorogenic acid, caffeic acid, naringenin, orientin, vitexin, hyperoside, rutin, quercetin and kaempferol were analysed. Data are given as a mean of three replications from three year-analyses and expressed in μg g_{DW}^{-1}.

The determination of phenolic compound concentration in buckwheat samples relied on comparing their retention times to authentic standards and analysing mass spectral data obtained through LC-MS. This data included accurate mass determination, which generated elemental composition and fragmentation patterns of a molecular ion. The comparison was also made with information from previous studies utilizing Orbitrap analysis of phenolic compounds (Li et al., 2019; Jia et al., 2020; Huda et al., 2021).

2.4. *Evaluation of buckwheat potential against weeds*

To evaluate the allelopathic potential of buckwheat against weeds, the protocol of Wu et al. (2000) was used with slight modifications. Buckwheat seeds were surface sterilized by soaking in 70% ethanol for 5 min, then rinsed in distilled water, and immersed in 4% sodium hypochlorite for 30 min in agitation. Finally, seeds were washed for 3 times with distilled water. After sterilization, buckwheat seeds were left to germinate in a growth chamber with 20 ºC of day and night temperature and 12/12 h light/dark photoperiod for 7 days. Then, 10-pregerminated buckwheat seeds (0.5 cm radicle) were placed in one half of a plastic tray (3220×6 cm) filled with 5 cm deep layer of perlite (500 g/tray) and watered with distilled water (pH 6.0). A sterilized plastic piece was inserted across the centre and down the middle of the plastic tray. The piece of plastic was placed up to 3 cm below the surface of the perlite leaving 1 cm between the piece of plastic and the bottom of the plastic tray. The tray was divided into two equal compartments to minimize competition for space and light between buckwheat accessions and weed seedlings. The arrangement was such that any allelochemical produced and released by the buckwheat seedlings could diffuse throughout the entire medium reaching also weed seeds and seedlings, but roots and shoots of buckwheat and weeds were never in direct contact. Buckwheat seedlings were grown for 10 days in a growth chamber with the same conditions as those used for germination. After buckwheat was growing alone for ten days, ten seeds of annual ryegrass or common purslane were placed in the other half of the plastic tray and left in a controlled growth chamber for one week. After one week of co-cultivation, the germination and growth of buckwheat and weeds were measured. At this point, in the BBCH scale, ranged from 0 to 9, 20-day old buckwheat plants are in the stage n2 (between the emerge of the third leaf and before flowering). The growth parameters of the weeds were compared with the control (weeds growing alone). A randomised block design with three replicates was used for each accession. The five treatments were: (1) buckwheat seedlings growing alone for 17 days; (2) buckwheat seedlings (10 days after germination) + annual ryegrass (10 seeds); (3) buckwheat seedlings (10 days after germination) + common purslane (10 seeds); (4) annual ryegrass seedlings alone; (5) common purslane seedlings alone.

The parameters measured on buckwheat plants were shoot and root length, shoot and root weight of each buckwheat accession at the end of the experiment. The parameters measured in both weed plants (*L. rigidum* and *P. oleracea*) were Shoot and Root Invasive Capacity (SIC and RIC), Seedling Vigour Index (SVI) and Specific Plant Length (SPL).

Shoot invasive capacity (SIC) and root invasive capacity (RIC) have been determined for the first time to provide information about the invasiveness of crops and weeds. SIC and RIC put light on of the ability of weed species to colonize and occupy space considering both germination and developmental ability. The equations used for the calculation of these two indexes were:

RIC = Σ root length of all treated-seeds/total number of treated seeds (root length of ungerminated seeds after 7 days treatment was assumed as zero and included in the calculation).

SIC = Σ shoot length of all treated-seeds/total number of treated seeds (shoot length of ungerminated seeds after 7 days treatment was assumed as zero and included in the calculation).

The third parameter measured, SVI, which represents the extent of damage that accumulates a weed as viability declines, and the damage accumulated in seeds until the seeds are unable to germinate and eventually die (Zhao et al., 2016), was calculated according to Abdul-Baki and Anderson (1973) with the following equation:

SVI = % germination x (Mean shoot length + mean root length) (cm).

Finally, specific plant length (SPL), which gives information about the capacity of the plant to respond in front of environmental stress, was calculated according to Abideen et al. (2018) with the following equation:

$$\mathrm{SPL} = \text{plant length (cm) x dry weight } (\mathrm{mg}^{-1})$$

Data were given as percentage of the control for all the parameters.

2.5. Statistical analysis

The experiments were carried out using a completely randomized design with three replications (each replication was a tray consisting of 10 buckwheat and 10 weed plants). IBM SPSS software (SPSS Inc., Chicago, Illinois, version 25.0) was used to analyse the data. An exploratory data analysis was performed to detect outliers. The Kolmogorov-Smirnov test was used to check for deviation from normality, and the Levene test was used to check for homogeneity. Depending on the homoscedasticity of the samples, one-way ANOVA or Kruskal Wallis tests were performed to establish the significant effect ($p \leq 0.05$) of the treatments (different accessions). Results were presented in the tables as percentage of the control (i.e., control = 100%).

To determine correlations between SVI and SPL variables with the most important metabolites of each buckwheat species, the Pearson correlation coefficient (PCC) was evaluated (PPC = 1: perfect positive correlation; $1 > \mathrm{PPC} > 0$ = positive correlation; $0 > \mathrm{PPC} > -1$ = negative correlation PPC = −1: perfect negative correlation). In Pearson correlation test, the perfect correlation is assumed when the value is ± 1. The correlation will be positive when both variables increase and will be negative when one variable increases while the other decreases.

3. Results

Our results showed that different buckwheat accessions behave differently depending on the surrounding weed.

After analysis of the data, we found accessions that mainly affected the development of annual ryegrass, accessions that mainly affected the development of common purslane, and accessions that strongly affected the development of both weed species. Surprisingly, most of the accessions induced inhibition on at least one of the two weeds tested, and just one (Ballada) out of the 29 accessions tested in this study did not show neither inhibitory nor stimulatory activity on any of the weeds.

In general, the accessions of common buckwheat affected the growth of annual ryegrass more than the growth of common purslane, as ten of the 19 buckwheat accessions tested (Arihira zairai, Chernigovskaya 17, La Harpe, Iwate zairai, Čebelica, Luba, Monori, Pulawska II, Skorospelaya and Východoslovenská krajová) promoted the growth of annual ryegrass (Table 2), while only two accessions (Ballada and Česká krajová) did not cause significant inhibition in this species. Moreover, seven accessions (Arihira zairai, CD7272, Chernigovskaya 17, Dozhdik, Iwate zairai, Luba and Prego) also caused a reduction in the four parameters measured in common purslane, while nine accessions did not affect a single parameter of this weed. No stimulation was observed after co-planting both weeds with any of the common buckwheat accessions.

Common buckwheat accessions mainly affected SIC and SVI of *L. rigidum*, as 15 out of the 19 common buckwheat accessions tested induced a reduction on these parameters. The accessions that more affected the development of *L. rigidum* shoots, when compared to the control, were La Harpe (34% of the control) followed by Čebelica (28% of the control), Luba (24% of the control), Monori (22% of the control), and Iwate zairai (10% of the control) SVI was also more inhibited after co-cultivation with these same accessions, Čebelica (35%) followed by La Harpe (32%), Luba (28%), Monori (25%), and Iwate zairai (12%). However, only 10 out of the 19 common buckwheat accessions (Arihira zairai, Čebelica, Chernigovskaya 17, La Harpe, Iwate zairai, Luba, Monori, Pulawska II, Skorospelaya, and Východoslovenská krajová) were able to control root development of *L. rigidum* inducing a significant reduction in RIC. The most inhibitory accession was also Čebelica (37%) followed by Luba (31%), La Harpe (30%), Monori (24%), and Iwate zairai (18%). Finally, SPL, i.e., the ability of *L. rigidum* plants to respond in front of environmental stress, the results showed a significant reduction of this parameter after co-cultivation of *L. rigidum* with 14 out of the 19 buckwheat accessions tested, being once more La Harpe (22%), but also Pulawska II (22%), Luba (19%), Monori (12%), and Iwate zairai (7%) the accessions with the greatest ability to reduce SPL.

Regarding the dicot weed *P. oleracea*, the impact of the different common buckwheat accessions on its development was in general stronger than for *L. rigidum*, although the number of accessions that affected the different parameters was lower (Table 2). This is especially true for RIC, SVI and SPL, which showed values as low as 4% of the control for CD7272, Chernigovskaya 17 and Luba. As shown in Table 2, ten accessions (Arihira zairai, CD7272, Chernigovskaya 17, Dozhdik, Luba, Monori, Prego and Špačinska 1) induced a significant reduction in the SIC of this dicot weed, being more pronounced after co-cultivation with Dozhdik (23%), Luba (19%), Arihira zairai (16%), CD7272 (15%), and Chernigovskaya 17 (10%). Similarly, the RIC was lower than

Table 2

Shoot Invasive Capacity (SIC), Root Invasive Capacity (RIC), Seedling Vigour Index (SVI) and Specific Plant Length (SPL) of *Lolium rigidum* and *Portulaca oleracea* after co-culture with different common buckwheat accessions (Aelita, Arihira zairai, Ballada, CD7272, Čebelica, Česká krajová, Chernigovskaya 17, Dozhdik, La Harpe, Iwate zairai, Lada, Luba, Monori, Prego, Pulawska II, Skorospelaya, Špačinska 1, Sweden-1 and Vychodoslovenská krajová). Values are presented as % of the control (i.e., weed species grown alone, being the control the 100%). Significance of differences according to Kruskal Wallis test * , $p < 0.05$. Shaded cells indicate significant inhibition while bold numbers indicate significant stimulation for each of the indexes calculated in the weeds (i.e., SIC, RIC, SVI, SPL), when compared to those indexes in weed seedlings (*L. rigidum* or *P. oleracea*) growing alone. Three replicates with ten buckwheat and ten weed seedlings per replication were used for each accession.

Lolium rigidum

Accession	SIC	RIC	SVI	SPL
Aelita	70 ± 17	65 ± 20	67 ± 15	81 ± 12
Arihira zairai	47 ± 16	43 ± 7	45 ± 10	53 ± 30
Ballada	105 ± 28	85 ± 17	93 ± 22	92 ± 14
CD7272	59 ± 31	69 ± 30	64 ± 19	58 ± 24
Čebelica	28 ± 18	37 ± 7	35 ± 13	34 ± 21
Česká krajová	99 ± 23	89 ± 22	97 ± 19	110 ± 47
Chernigovskaya 17	64 ± 8	72 ± 9	68 ± 19	76 ± 20
Dozhdik	64 ± 12	69 ± 23	66 ± 11	68 ± 27
La Harpe	34 ± 44	30 ± 37	32 ± 41	22 ± 28
Iwate zairai	10 ± 6	18 ± 5	12 ± 0.2	7 ± 3
Lada	62 ± 19	94 ± 22	80 ± 20	70 ± 6
Luba	24 ± 17	31 ± 22	28 ± 19	19 ± 17
Monori	22 ± 20	24 ± 22	25 ± 23	12 ± 14
Prego	57 ± 19	77 ± 16	72 ± 14	87 ± 32
Pulawska II	36 ± 11	42 ± 5	38 ± 7	22 ± 6
Skorospelaya	68 ± 17	57 ± 15	66 ± 14	67 ± 9
Špačinska 1	92 ± 5	83 ± 10	87 ± 4	92 ± 29
Sweden-1	70 ± 13	72 ± 18	71 ± 15	65 ± 24
Vychodoslovenská krajová	61 ± 23	47 ± 16	56 ± 26	30 ± 9

Portulaca oleracea

Accession	SIC	RIC	SVI	SPL
Aelita	87 ± 9	83 ± 19	82 ± 12	83 ±19
Arihira zairai	16 ± 10	12 ± 1.5	13 ± 4	12 ± 1
Ballada	93 ± 59	123 ± 94	99 ± 67	153 ± 134
CD7272	15 ± 7	4 ± 3	8 ± 0.7	6 ± 5
Čebelica	83 ± 8	96 ± 15	88 ± 13	81 ± 20
Česká krajová	81 ± 9	47 ± 16	58 ± 15	48 ± 15
Chernigovskaya 17	10 ± 3	17 ± 14	14 ± 10	22 ± 17
Dozhdik	23 ± 10	35 ± 21	34 ± 16	49 ± 26
La Harpe	113 ± 29	94 ± 35	96 ± 28	107 ± 30
Iwate zairai	57 ± 13	40 ± 7	44 ± 7	42 ± 8
Lada	82 ± 26	116 ± 40	103 ± 20	124 ± 36
Luba	19 ± 12	5 ± 6	12 ± 5	4 ± 4
Monori	61 ± 6	77 ± 15	67 ± 19	73 ± 13
Prego	34 ± 9	28 ± 13	30 ± 11	22 ± 21
Pulawska II	69 ± 29	73 ± 36	68 ± 30	52 ± 30
Skorospelaya	73 ± 25	82 ± 48	75 ± 37	102 ± 46
Špačinska 1	52 ± 24	96 ± 18	77 ± 7	98 ± 52
Sweden-1	105 ± 16	86 ± 11	88 ± 3	98 ± 14
Vychodoslovenská krajová	76 ± 46	66 ± 56	67 ± 48	65 ± 48

the control after growing with almost the same accessions (Arihira zairai, CD7272, Česká krajová, Chernigovskaya 17, Dozhdik, Luba, Monori and Prego). The most effective accessions against root development of *P. oleracea* were Prego (28%), Chernigovskaya 17 (17%), Arihira zairai (12%), Luba (5%), and CD7272 (4%). In this way, the accessions that mainly affected the shoot and root development of *P. oleracea* also induced the reduction of the SVI of this weed, being Arihira zairai (13%), Luba (12%), CD7272 (8%), and Chernigovskaya 17 (4%) the most competitive accessions. Finally, the SPL of *P. oleracea* was significantly inhibited by the same accessions mentioned before, being the more remarkable Chernigovskaya 17 (22%) and Pulawska II (22%), Arihira zairai (12%), CD7272 (6%), and Luba (4%).

Summarising, the common buckwheat accessions Arihira zairai, Iwate zairai, CD7272 Luba and Luba were the accessions with the stronger impact on both weeds.

Regarding Tartary buckwheat accessions (Table 3), the general reduction observed on weeds' development was generally weaker than that induced by common buckwheat accessions, and even two Tartary accessions (KIS Doris and Sarasin a Ployes) statistically stimulated some of the parameters recorded for *P. oleracea*.

As shown in Table 3, six Tartary accessions (Jianzui, PI451723, 290, Osrednje Goričko, Sevnica and Sveti Miklavž nad Litijo) induced the inhibition of SIC and RIC of *L. rigidum*, being the most effective Sveti Miklavž nad Litijo (only 19% of the control for both SIC and RIC), followed by PI451723 (47% and 33%, respectively) and Sevnica (46% and 55%, respectively). The same pattern of reductions was observed for SVI and SPL, as the same accessions induced a significant reduction in these parameters, inducing again Sveti Miklavž nad Litijo the most remarkable reduction of SVI (21% of the control) and SPL (11% of the control).

Regarding the effects found on *P. oleracea*, KIS Doris induced a significant increment (140%, 150%, 139% and 196%) on the four parameters (SIC, RIC, SVI and SPL, respectively) measured on this dicot weed. Similarly, Sarasin a Ployes also induced an increase on SPL (170%) of *P. oleracea.* However, some accessions of Tartary buckwheat had the ability to inhibit the growth of this dicotyledonous weed. After coculture with 01Z5100012, PI451723, Slovenj Gradec and Sveti Miklavž nad Litijo, the SIC, RIC, SVI and SPL of *P. oleracea* were significantly reduced. The most remarkable accession was 01Z5100012, as the SIC of *P. oleracea* was only 40% of the control after growing with this accession, while RIC, SVI and SPL were 30%, 38% and 39% of the control, respectively. Finally, only two Tartary buckwheat accessions, PI451723 and Sveti Miklavž nad Litijo, affected the four parameters of both weeds, in contrast with the 10 common buckwheat accessions able to inhibit those four parameters in *L. rigidum* and *P. oleracea*.

On the other hand, as shown in Tables 4 and 5, root and shoot development of buckwheat was generally higher for common (Table 4) than for Tartary (Table 5) buckwheat, as most of the common buckwheat accessions exceeded 9 cm shoot length and 15 cm root length, while only a few Tartary buckwheat accessions reached those values.

As far as root length is concerned, 74% of common buckwheat accessions growing alone, 89% of common buckwheat accessions growing with *L. rigidum* and 100% of the common buckwheat accessions growing with *P. oleracea* exceeded 15 cm in length, while only 50% of Tartary buckwheat accessions growing alone, 30% of Tartary buckwheat accessions growing with *L. rigidum* and 20% of the Tartary buckwheat accessions growing with *P. oleracea* exceeded 15 cm in length. This difference in growth between the common and Tartary accessions was also observed in the shoots of both species, as 37% of the common buckwheat accessions growing alone, 68% of the common buckwheat accessions growing with *L. rigidum* and 53% of the common accessions growing with *P. oleracea* had shoots longer than 9 cm, while only 10% of the buckwheat accessions growing alone, 10% of Tartary buckwheat accessions growing with *L. rigidum* and none of the Tartary buckwheat accessions growing with *P. oleracea* had shoots exceeding this value of 9 cm.

As shown in Table 4, significant differences were found when

Table 3

Shoot invasive capacity (SIC), root invasive capacity (RIC), seedling vigour index (SVI) and specific plant length (SPL) of *Lolium rigidum* and *Portulaca oleracea* after coculture with different Tartary buckwheat accessions (01Z5100012, Jianzui, KIS Doris, PI451523, Sarasin a Ployes, 290, Osrednje Goričko, Slovenj Gradec, Sveti Miklavž nad Litijo, and Sevnica). Values are presented as % of the control (i.e., weed species grown alone, being the control the 100%). Significance of differences according to Kruskal Wallis test * , $p < 0.05$. Shaded cells indicate significant inhibition while bold numbers indicate significant stimulation for each of the indexes calculated in the weeds (i.e., SIC, RIC, SVI, SPL), when compared to those indexes in weed seedlings (*L. rigidum* or *P. oleracea*) growing alone. Three replicates with ten buckwheat and ten weed seedlings per replication were used for each accession.

Lolium rigidum

Accession	SIC	RIC	SVI	SPL
290	76 ± 16	66 ± 5	49 ± 10	44 ± 13
01Z5100012	94 ± 1	90 ± 14	93 ± 19	97 ± 19
Jianzui	67 ± 18	60 ± 14	63 ± 14	70 ± 24
KIS Doris	113 ± 68	130 ± 67	123 ± 66	154 ± 103
Osrednje Goričko	58 ± 40	42 ± 19	50 ± 30	47 ± 37
PI451723	47 ± 7	33 ± 2	41 ± 6	28 ± 7
Sarasin a Ployes	85 ± 22	74 ± 27	81 ± 24	69 ± 31
Sevnica	46 ± 15	55 ± 12	50 ± 12	37 ± 18
Slovenj Gradec	93 ± 25	58 ± 22	80 ± 35	81 ± 32
Sveti Miklavž nad Litijo	19 ± 8	19 ± 9	21 ± 8	11 ± 7

Portulaca oleracea

Accession	SIC	RIC	SVI	SPL
290	60 ± 18	57 ± 13	55 ± 13	67 ± 23
01Z5100012	40 ± 5	30 ± 22	38 ± 16	39 ± 1
Jianzui	36 ± 22	56 ± 13	50 ± 10	73 ± 22
KIS Doris	**140 ± 18**	**150 ± 35**	**139 ± 16**	**196 ± 81**
Osrednje Goričko	92 ± 21	69 ± 10	73 ± 13	60 ± 37
PI451723	52 ± 19	36 ± 11	42 ± 11	53 ± 6
Sarasin a Ployes	95 ± 14	115 ± 8	106 ± 10	**170 ± 48**
Sevnica	62 ± 38	61 ± 43	60 ± 40	58 ± 42
Slovenj Gradec	64 ± 1	48 ± 8	52 ± 5	53 ± 11
Sveti Miklavž nad Litijo	60 ± 25	43 ± 18	46 ± 19	49 ± 13

Table 4
Growth data of *F. esculentum* accessions (Aelita, Arihira zairai, Ballada, CD7272, Čebelica, Česká krajová, Chernigovskaya 17, Dozhdik, La Harpe, Iwate zairai, Lada, Luba, Monori, Prego, Pulawska II, Skorospelaya, Špačinska1, Sweden-1 and Východoslovenská krajová) growing alone or in association with the monocot weed *Lolium rigidum* or the dicot weed *Portulaca oleracea.* SL: shoot length; RL: root length. Present data are the mean of 30 plants for each accession (N = 30) and the standard deviation. Bold numbers indicate a significant increase while grey cells indicate a significant decrease of shoot length or root length of buckwheat seedlings, after co-growing with *L. rigidum* (LR) or *P. oleracea* (PO), when compared to buckwheat seedlings growing alone for 17 days.

	SL (cm)			**RL (cm)**		
	Alone	*LR*	*PO*	Alone	*LR*	*PO*
Aelita	8.34 ± 1.25	11.7 ± 2.26	10.2 ± 1.44	23.1 ± 3.54	18.6 ± 2.32	15.2 ± 1.35
Arihira zairai	8.43 ± 1.16	8.42 ± 1.42	8.28 ± 0.58	17.3 ± 2.94	**24.2 ± 3.23**	23.7 ± 2.93
Ballada	11.2 ± 1.56	10.7 ±1.67	**16.6 ± 2.40**	18.9 ± 0.29	18.8 ± 2.20	22.1 ± 2.59
CD7272	8.51 ± 0.32	11.8 ± 2.36	9.01 ± 1.66	14.3 ± 0.42	**25.8 ± 1.94**	**17.1 ± 2.12**
Čebelica	11.7 ± 2.58	9.61 ± 0.70	9.79 ± 0.77	23.4 ± 1.84	**26.6 ± 2.54**	21.2 ± 3.58
Česká krajová	7.19 ± 0.85	**10.5 ± 1.15**	9.82 ± 0.76	22.1 ± 0.16	22.4 ± 2.76	21.6 ± 3.38
Chernigovskaya 17	7.96 ± 0.93	9.50 ± 1.38	9.63 ± 1.21	20.3 ± 1.52	26.2 ± 1.06	**25.5 ± 2.02**
Dozhdik	7.43 ± 1.26	9.88 ± 1.27	8.68 ± 0.98	7.96 ± 1.71	**23.5 ± 0.30**	**18.1 ± 1.43**
Iwate zairai	6.69 ± 1.38	**10.7 ± 1.62**	**10.2 ± 1.57**	10.2 ± 3.99	**23.5 ± 4.44**	**20.2 ± 5.62**
La Harpe	13.1 ± 2.70	10.1 ± 2.11	8.76 ± 0.62	25.4 ± 2.19	24.4 ± 1.39	23.7 ± 2.80
Lada	9.69 ± 0.19	6.10 ± 0.44	10.0 ± 1.36	23.5 ± 1.70	14.2 ± 2.44	20.8 ± 0.72
Luba	7.75 ± 2.70	9.83 ± 0.62	8.69±0.92	23.9 ± 0.95	21.4 ± 1.00	20.0 ± 1.01
Monori	7.61 ± 1.64	6.49 ± 0.64	7.49±0.14	16.6 ± 3.21	15.4 ± 3.45	20.8 ± 3.20
Prego	11.5 ± 1.52	12.8 ± 1.84	11.1±0.37	17.5 ± 1.32	20.6 ± 4.76	20.8 ± 5.02
Pulawska II	3.96 ± 0.33	**7.37 ± 2.29**	**7.01±0.79**	10.7 ± 0.50	11.1 ± 3.01	**17.7 ± 1.89**
Skorospelaya	10.2 ± 1.91	7.76 ± 0.89	8.84±1.42	18.3 ± 2.95	19.6 ± 2.52	19.4 ± 1.34
Špačinska1	10.9 ± 1.16	11.6 ± 1.28	7.67±0.16	22.3 ± 3.86	21.8 ± 4.80	15.3 ± 0.60
Sweden-1	8.04 ± 1.45	9.67 ± 1.24	10.5±1.08	24.9 ± 2.66	16.8 ± 1.15	23.1 ± 4.11
Východoslovenská krajová	7.94 ± 0.60	8.11 ± 1.16	8.81±1.31	13.6 ± 1.96	**21.8 ± 0.52**	**17.4 ± 1.94**

Table 5
Growth data of *F. tataricum* cultivars (01Z5100012, Jianzui, KIS Doris, PI451523, Sarasin a Ployes, 290, Osrednje Goričko, Slovenj Gradec, Sveti Miklavž nad Litijo and Sevnica) growing alone or in association with the monocot weed *Lolium rigidum* or the dicot weed *Portulaca oleracea.* SL: shoot length; RL: root length. Present data are given as a mean of 30 plants of each cultivar (N = 30) and standard deviation. Bold numbers indicate a significant increase while grey cells indicate a significant decrease of shoot length or root length of buckwheat seedlings, after co-growing with *L. rigidum* (LR) or *P. oleracea* (PO), when compared to buckwheat seedlings growing alone for 17 days.

	SL (cm)			**RL (cm)**		
	Alone	*LR*	*PO*	Alone	*LR*	*PO*
290	3.67 ± 0.23	3.73 ± 0.97	4.05 ± 0.57	11.6 ± 1.23	8.89 ± 3.14	14.8 ± 3.55
01Z5100012	5.1 ± 0.86	5.83 ± 0.48	5.39 ± 0.48	16.6 ± 1.64	13.3 ± 1.33	13.2 ± 3.30
Jianzui	8.35 ± 1.66	9.12 ± 1.66	8.00 ± 1.13	17.3 ± 3.70	19.6 ± 3.41	12.4 ± 3.67
KIS Doris	4.75 ± 0.63	**7.10 ± 0.86**	5.74 ± 0.71	12.3 ± 1.52	15.7 ± 3.84	11.7 ± 1.56
Osrednje Goričko	5.43 ± 0.65	8.23 ± 2.04	6.95 ± 1.93	10.6 ± 3.99	10.5 ± 2.95	8.24 ± 2.92
PI451523	3.23 ± 1.01	3.02 ± 1.91	3.95 ± 1.21	3.42 ± 1.70	3.48 ± 1.32	3.37 ± 0.14
Sarasin a Ployes	10.0 ± 0.90	7.74 ± 0.39	8.20 ± 0.52	20.0 ± 0.79	21.1 ± 1.18	21.8 ± 4.64
Sevnica	6.75 ± 1.53	7.71 ± 1.78	5.71 ± 0.50	15.6 ± 2.6	12.6 ± 2.86	11.2 ± 0.52
Slovenj Gradec	6.02 ± 0.27	6.92 ± 0.58	7.12 ± 0.59	14.3 ± 2.39	14.9 ± 2.52	12.2 ± 2.30
Sveti Miklavž nad Litijo	5.31 ± 0.53	4.28 ± 0.27	4.40 ± 0.52	16.7 ± 1.71	13.2 ± 1.21	15.9 ± 2.74

comparing the growth of common buckwheat accessions growing alone with common buckwheat growing in co-culture with *L. rigidum* or *P. oleracea*. After 10 days of co-cultivation with *L. rigidum*, the following 6 common accessions were found to have longer roots than the control: Dozhdik (295% of the control), Iwate zairai (230%), CD7272 (180%), Východoslovenská krajová (160%), Arihira zairai (141%), and Chernigovskaya 17 (129%). As well, after growing in combination with *P. oleracea*, also the following 6 common accessions had longer roots than the control: Dozhdik (227%), Iwate zairai (198%), Pulawska II (165%), Východoslovenská krajová (128%), Chernigovskaya 17 (126%), and CD7272 (119%). For shoot length, the differences between the control accessions and those cultivated with *L. rigidum* and *P. oleracea* were not as strong as for root length, as only the common buckwheat accessions Pulawska II (186%), Iwate zairai (160%) and Česká krajová (146%) were longer than the control when growing with *L. rigidum*, and the accessions Pulawska II (177%) and Iwate zairai (152%) were longer when grown together with *P. oleracea*, highlighting the induced root stimulation for common buckwheat in the presence of weeds. In contrast, only the roots of two common buckwheat accessions grew less than the control with *L. rigidum* (Lada and Sweden-1) and with *P. oleracea* (Aelita and Špačinska 1). Also, with *L. rigidum* (Lada and Skorospelaya) and with *P. oleracea* (La Harpe and Špačinska 1) only the shoots of two common accessions were shorter than those of the control. In summary, up to 5 common accessions (CD7272, Chernigovskaya 17, Dozhdik, Iwate zairai and Východoslovenská krajová) showed stimulated root growth in the presence of both weeds, *L. rigidum* and *P. oleracea*, while only Iwate zairai showed stimulated shoot growth in the presence of both weeds.

As shown in Table 5, root and shoot stimulation of Tartary buckwheat accessions after co-growing with both weeds (*L. rigidum* and *P. oleracea*) was much lower than that of common buckwheat accessions, as just the shoot length of one Tartary buckwheat accession, KIS Doris, was stimulated with *L. rigidum*, while no accessions were stimulated with *P. oleracea*, neither shoot nor root length. However, after co-cultivation with *L. rigidum*, a significant decrease in root length of 01Z5100012 and Sveti Miklavž nad Litijo, and in shoot length of Sarasin a Ployes was found. As well, when Tartary buckwheat accessions were grown with *P. oleracea,* shoot length of Sarasin a Ployes and root length of 01Z5100012 and Sevnica were also significantly reduced.

The chemical analysis of the different buckwheat accessions also showed differences between species. Fig. 1 shows the chemical profile of three accessions of *F. esculentum* (Pulawska II, CD7272 and Luba) and three accessions of *F. tataricum* (Osrednje Goričko, Slovenj Gradec and Sveti Miklavž nad Litijo) with ability to inhibit all four measured parameters of *L. rigidum* (Osrednje Goričko and Pulawska II), *P. oleracea* (Slovenj Gradec and CD7272) or both weeds (Sveti Miklavž nad Litijo and Luba). The chemical profile analysis of the remaining accessions (17 in total) is shown in supplementary Table S2. As shown in Fig. 1, clear differences in polyphenol accumulation were observed among accessions, but these differences were especially strong among species.

Actually, as can be seen in Fig. 2, the Unsupervised Principal Component Analysis (PCA) that was performed by comparing common

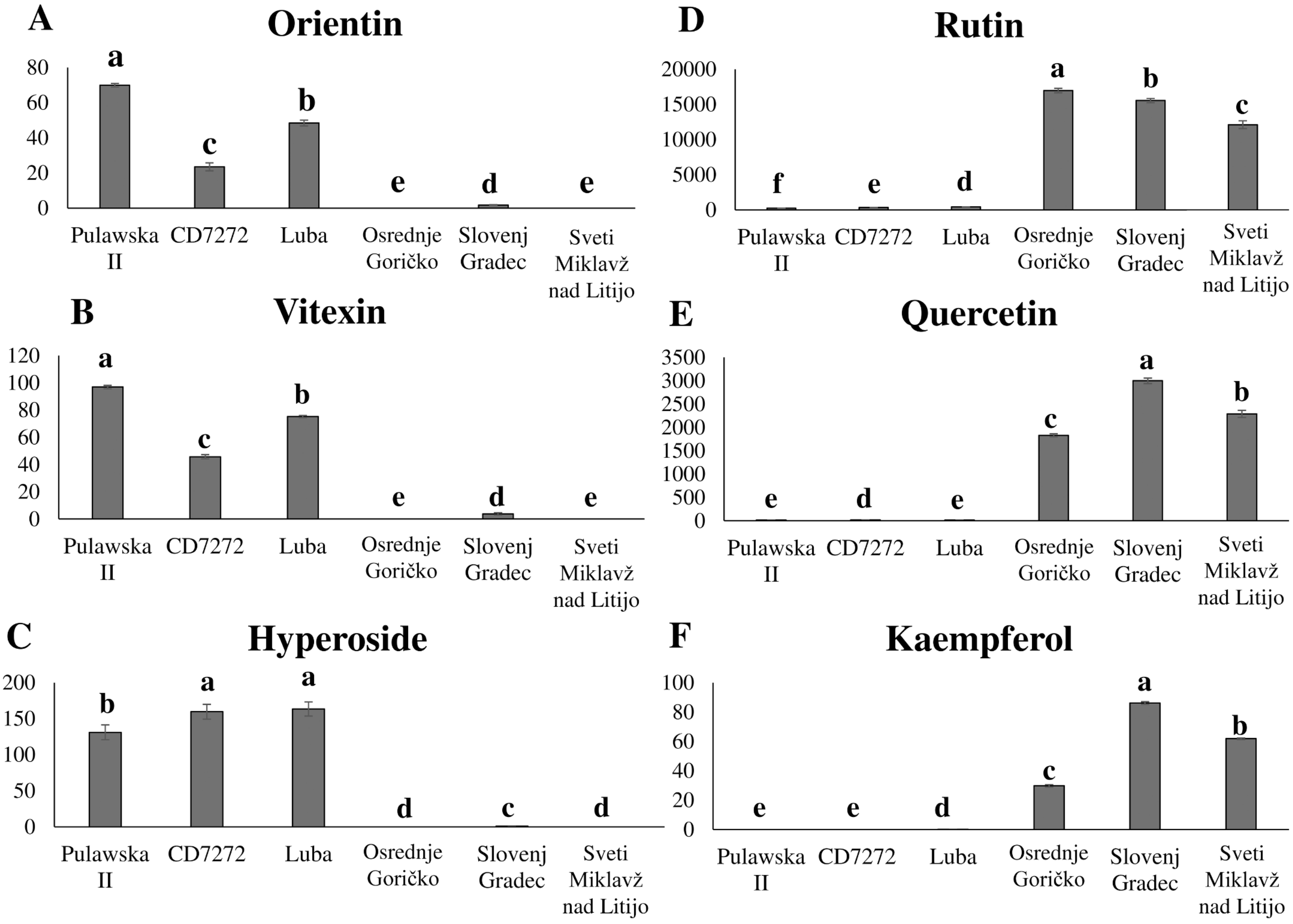

Fig. 1. Chemical profile of three common buckwheat accessions (Pulawska II, CD7272 and Luba) and three Tartary buckwheat accessions (Osrednje Goričko, Slovenj Gradec and Sveti Miklavž nad Litijo) comparing the phenolic compounds (A) orientin, (B) vitexin, (C) hyperoside, (D) rutin, (E) quercetin and (F) kaempferol.

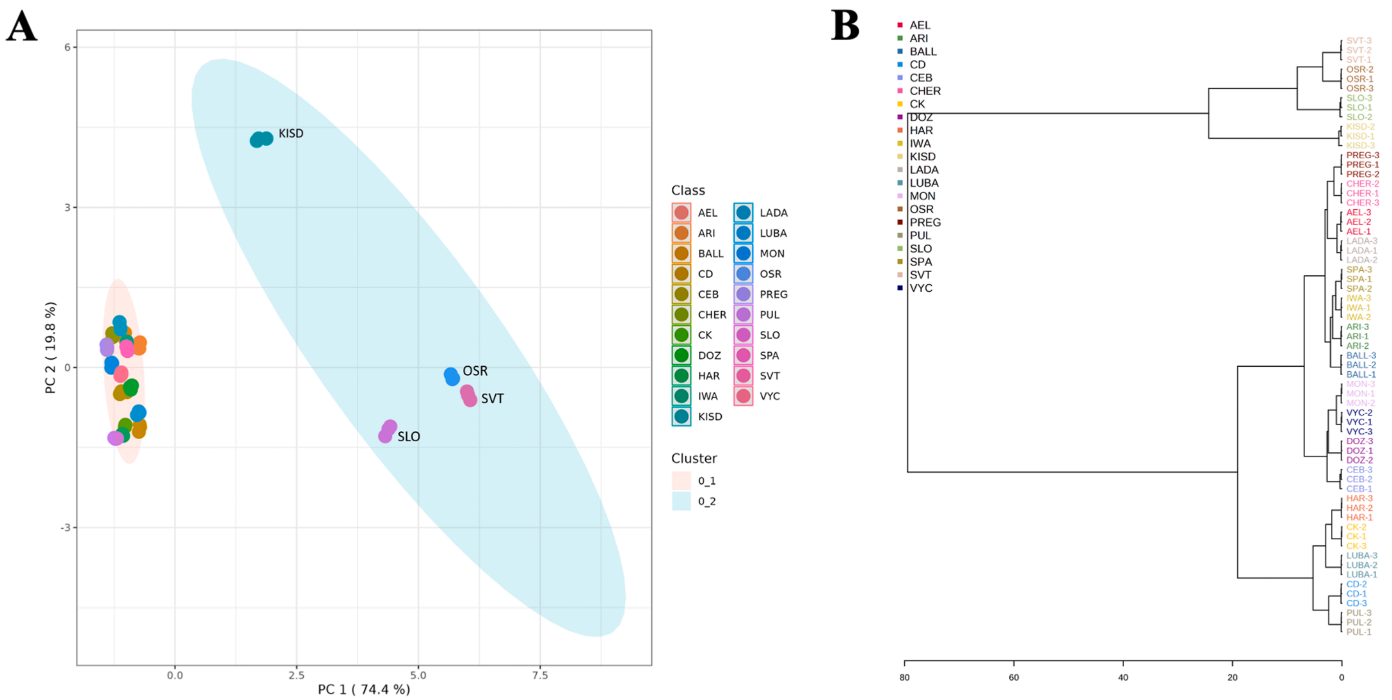

Fig. 2. Discrimination through Principal Component Analysis (PCA) of the chemical profile measured on common and Tartary buckwheat accessions. A) PCA scores plot between the selected PCs; B) Clustering result shown as a dendrogram (distance measure using euclidean, and clustering algorithm using ward). Separation between groups is represented through colors. Common buckwheat accessions: AEL: Aelita; ARI: Arihira zairai; BALL: Ballada; CEB: Čebelica; CD: CD7272; CHER: Chernigovskaya 17; CK: Česká krajová; DOZ: Dozhdik; HAR: La Harpe; IWA: Iwate zairai; LADA: Lada, LUBA: Luba; MON: Monori; PREG: Prego; PUL: Pulawska II; SPA: Špačinska1; and VYC: Východoslovenská krajová. Tartary buckwheat accessions: KISD: KIS Doris; OSR Osrednje Goričko; SLO: Slovenj Gradec; and SVT: Sveti Miklavž nad Litijo.

and Tartary buckwheat plants, showed two clearly well-differentiated groups (Fig. 2A), with common buckwheat accessions (Aelita, Arihira zairai, Ballada, Čebelica, CD7272, Chernigovskaya 17, Česká krajová, Dozhdik, La Harpe, Iwate zairai, Lada, Luba, Monori, Prego, Pulawska II, SPA: Špačinska1, and Východoslovenská krajová) grouped independently from Tartary buckwheat accessions (KIS Doris, Osrednje Goričko, Slovenj Gradec, and Sveti Miklavž nad Litijo), which were grouped together, although PCA revealed also a higher similarity among common buckwheat accessions than among Tartary buckwheat accessions. The generated score plot of the PCA built on the first (PC1) and second component (PC2), explained a total variance of 94.2% and revealed a clear separation between sample groups (Fig. 2). PC1 explained 74.4%, whereas PC2 explained 19.8% of the total variance. This grouping was also clearly observed in the clustering results shown as a dendrogram in Fig. 2B, where branches of *F. esculentum* and *F. tataricum* species were completely independent.

As shown in can be seen from Fig. 1, while *F. esculentum* accessions showed a strong accumulation of vitexin (between 45.77 and 96.94 $\mu g/g_{DW}$), orientin (between 23.45 and 69.94 $\mu g/g_{DW}$) or hyperoside (between 130.89 and 163.32 $\mu g/g_{DW}$), while these compounds were found in *F. tataricum* accessions in very small amounts, i.e., 3.84 $\mu g/g_{DW}$ for vitexin, 1.79 for orientin and 0.89 in Slovenj Gradec and none of any of these compounds in Osrednje Goričko and Sveti Miklavž nad Litijo. Contrary, Tartary buckwheat accessions showed a much stronger accumulation of other polyphenols such as rutin (between 12121.68 and 16988.52 $\mu g/g_{DW}$), quercetin (between 1830.61 and 2998.26 $\mu g/g_{DW}$) and kaempferol (between 29.72 and 86.14 $\mu g/g_{DW}$). Although these compounds were also found in common buckwheat accessions, the amount was extremely low compared to the Tartary buckwheat accessions (i.e., between 247.7 and 426.67 $\mu g/g_{DW}$ for rutin, between 13.66 and 21.81 for quercetin and between 0 and 0.1 for kaempferol). Surprisingly, as shown in Supplementary Table S2, none of the common buckwheat accessions could accumulate as many specialised metabolites as the Tartary buckwheat accessions. In fact, the sum of all specialised metabolites analysed in any of the common buckwheat accessions reached the levels of rutin or quercetin found in the Tartary buckwheat accessions.

The quantity of specialised metabolites also varied between accessions of the same species. Among the common buckwheat accessions, orientin showed values that for orientin ranged from 8.19 $\mu g/g_{DW}$ in Iwate zairai to 96.6 $\mu g/g_{DW}$ in La Harpe (Table S2), for vitexin showed values that ranged from 20.08 $\mu g/g_{DW}$ in Skorospelaya to 107.78 $\mu g/g_{DW}$ in La Harpe, and for hyperoside showed values that ranged from 30.92 $\mu g/g_{DW}$ in Ballada to 181.73 $\mu g/g_{DW}$ in Sweden-1 (Table S2). As well, also accession-dependent differences were found in Tartary buckwheat accessions for rutin, quercetin and kaempferol, which were highly accumulated compounds in *F. tataricum* accessions. In this way, accession-dependent differences were also observed. Thus, rutin showed values that ranging from 1768.74 $\mu g/g_{DW}$ in KIS Doris to 16988.52 $\mu g/g_{DW}$ in Osrednje Goričko, while quercetin showed values that ranging from 555.79 $\mu g/g_{DW}$ in KIS Doris to 2998.26 $\mu g/g_{DW}$ in Slovenj Gradec, and kaempferol showed values that ranging from 0.1 $\mu g/g_{DW}$ in KIS Doris to 86.14 $\mu g/g_{DW}$ in Slovenj Gradec (Fig. 2). Contrary, as shown in Supplementary Table S2, no such pronounced differences were found among the other specialized metabolites analysed in these accessions such as catechin, caffeic acid, chlorogenic acid or naringenin. Catechin was found to be around 31.49 (± 20.72) $\mu g/g_{DW}$ in *F. esculentum* accessions and 30.0 (± 19.56) $\mu g/g_{DW}$ in *F. tataricum* accessions, while caffeic acid was found in amounts of 0.26 (± 0.13) and 0.61 (± 0.39) $\mu g/g_{DW}$ in common and Tartary buckwheat accessions, respectively, and naringenin was around 0.49 ± 0.38 $\mu g/g_{DW}$ in common buckwheat accessions and around 0.89 ± 0.66 $\mu g/g_{DW}$ in Tartary buckwheat accessions. Finally, the content of chlorogenic acid in the tissues of *F. esculentum* was 0.77 ± 0.51 $\mu g/g_{DW}$ and 18.29 ± 27.83 $\mu g/g_{DW}$ in the accessions of *F. tataricum*, this difference being mainly due to the high content of chlorogenic acid in Sveti Miklavž nad Litijo (59.75

± 4.71 μg/g_{DW}).

The five common buckwheat accessions that accumulated more specialised metabolites were CD7272, Česká krajová, La Harpe, Luba and Sweden-1, while the Tartary buckwheat accessions that had more content of specialised metabolites were Osrednje Goričko and Sveti Miklavž nad Litijo.

After correlation analysis between the different compounds and the effects on weeds (on SVI and SPL), a significant correlation ($p < 0.05$) was found between the amount of kaempferol accumulated in the plants of *F. esculentum* and the effect on *L. rigidum* (Table 6). The higher the amount of kaempferol in the plant, the lower the reduction of SVI and SPL of *L. rigidum*.

However, an almost perfect negative correlation was observed between the amount of quercetin in *F. tataricum* accessions and the reduction of SVI of *P. oleracea* (Table 7).

Table 6

Correlation between the amount of kaempferol present in *F. esculentum* accessions and seedling vigour index (SVI) and specific plant length (SPL) of *L. rigidum*.

		SVI	SPL
Kaempferol	Pearson correlation	0.518*	0.553
	Sig. (bilateral)	0.023	0.014
	N	19	19

* . Significant correlation when $p < 0.05$

Table 7

Correlation between the amount of quercetin present in *F. tataricum* accessions and SVI (Seedling Vigour Index) of *P. oleracea*.

		SVI
Quercetin	Pearson correlation	-0.957*
	Sig. (bilateral)	0.043
	N	19

* . Significant correlation when $p < 0.05$

4. Discussion

In the present study, we have demonstrated for the first time the ability of twenty-nine accessions of two buckwheat species (*F. tataricum* and *F. esculentum*) to sustainably control two herbicide-resistant weeds (*L. rigidum* and *P. oleracea*). Our results show that different buckwheat accessions differ in their ability to sustainably control weeds in the environment, but also that the same accession can behave differently depending on the weed it is confronted with. For this reason, studies such as those conducted in this paper, which evaluate different accessions of buckwheat that can control the presence of weeds in their environment as a crop (living plants), are extremely important for organic farming.

The studied common buckwheat accessions were generally more effective against monocot and dicot weeds than the Tartary buckwheat accessions. Four of the five accessions that strongly affected *L. rigidum* (Monori, Čebelica, Iwate zairai and La Harpe) and the five accessions that strongly affected the development of *P. oleracea* (Arihira zairai, Chernigovskaya 17, Dozhdik, CD7272, and Prego) were *F. esculentum*. Growth data of these accessions revealed that roots and shoots of buckwheat plants were significantly longer in the presence of *L. rigidum* and *P. oleracea* than when growing alone for 17 days. This suggests that selecting accessions with fast growth and establishment in the environment could be a useful strategy to cope with weeds. According to Kunstler et al. (2016) and Khalaf (2019) crop:weed competition may be due to root or shoot growth, and accessions with higher initial growth and faster canopy development can establish quickly in a crop-weed ecosystem and being less affected by weed competition. Actually, in the present study, the only accession (KIS Doris) with which the four parameters measured in *P. oleracea* were significantly stimulated, showed also the lower number of leaves (1–3 leaves) when compared to the other evaluated accessions, corroborating the previously mentioned studies.

However, the reduction of weed development it's not only due to this competition, but the bioactive compounds present in buckwheat tissues and extracts play an important role in weed growth inhibition. This phenomenon is named allelopathy (Kalinova et al., 2007; Kumar et al., 2008; Worthington and Reberg-Horton, 2013). Plants can synthetize compounds that could be used for defence or protection when accumulated, or as allelochemicals when released or exuded to the medium (Hussain et al., 2022). Flavonoids, ubiquitously occurring polyphenolic compounds, are the main allelochemicals present in buckwheat, and their content and profile is different depending on the species, the accession, and the organ of the plant (Matsui and Walker, 2020).

The chemical analysis corroborated that common buckwheat accessions accumulate different amounts and types of polyphenols than Tartary buckwheat accessions. Common buckwheat accessions showed strong accumulation of orientin, vitexin, and hyperoside (compounds almost not found in Tartary buckwheat), while Tartary buckwheat accessions showed strong contents of rutin, quercetin, and kaempferol (compounds found in low quantities in common buckwheat). Genetic factors and gene expression may influence flavonoid accumulation in different plant species. The flavonoid biosynthesis pathway differs between buckwheat species. Starting from the flavonoid naringenin (found in similar quantities in both species), *F. esculentum* accessions followed the C-glucosyltransferase pathway ending in the formation of flavones as vitexin or orientin and *F. tataricum* accessions followed the flavanone-3-hydroxylase pathway in which kaempferol is first formed and then, via flavonol synthase, leads to the formation of flavonols (quercetin and rutin) (Matsui and Walker, 2020).

The chemical profile and polyphenol content of Tartary buckwheat and common buckwheat accessions may influence their development and growth patterns observed between species. Brown et al. (2001) demonstrated that an increase in flavonoids can inhibit auxin transport, leading to reduced growth in *Arabidopsis* plants. Tartary buckwheat accessions accumulated more polyphenols in their shoots and leaves than common buckwheat, which could be affecting their growth patterns.

These flavonoids can be relocated and released to the medium affecting the development of surrounding weeds. Therefore, the inhibitory effects observed in this study could be also attributed to the allelopathic potential of each plant species' root exudates.

Some studies showed that the main molecules found in *F. esculentum* (orientin, vitexin and hyperoside) have allelopathic potential against weeds when exuded to the surrounding environment or used as extract. Ghimire et al. (2020) found that orientin was the dominant allelochemical in *Miscanthus sacchariflorus* (Maxim.) Franch. extracts inducing inhibitory effects on the germination and growth of weeds such us *Bidens frondose* L., *Echinochloa crus-galli* (L.) P. Beauv., and *Erigeron canadensis* L. Another study examined the allelopathic potential of *Cyperus esculentus* L. (tiger nut) and found that orientin, among other compounds, induced a significant inhibitory effect on the growth of lettuce seedlings (Zhang et al., 2022). As well, the flavonoid vitexin was identified as one of the compounds present in *Lantana camara* L. responsible for the observed growth inhibition of target species as *Rumex acetosa* L., *Phalaris minor* Retz., *Avena fatua* L. and *Chenopodium album* L. (Kato-Noguchi and Kurniadie, 2021). Moreover, Dhaou et al. (2022) showed vitexin as a potent compound against *E. crus-galli* germination. In our study, the common buckwheat accessions La Harpe and Pulawska II showed the higher concentrations of orientin and vitexin among all accessions, coinciding with of inhibition observed of all parameters of *L. rigidum.* As after the co-culture with these accessions no effects were seen in *P. oleracea*, our results suggest that *L. rigidum* is more sensitive to these compounds. However, hyperoside was found in higher concentrations in all accessions, those affecting only *L. rigidum*, those affecting only *P. oleracea* and those affecting both weeds which could suggest a role of hyperoside in the inhibitory potential of these accessions. The observed effects are in agreement with those found in the study of Puig et al. (2018), where aqueous extracts of *Eucalyptus globulus* Labill., with high hyperoside content, affected significantly the germination and development of *Lactuca sativa* L. in a concentration-dependent way, as our results also showed that one of the accessions with the stronger concentration of hyperoside (CD7272) induced also the maximum reduction found in the root invasive capacity of *P. oleracea*.

The main compounds found in *F. tataricum* are also known for its allelopathic activity when they are in the medium. Golisz et al. (2007) demonstrated that rutin can inhibit root and hypocotyl growth of lettuce seedling while Fonseca et al. (2017) also showed that rutin together with chlorogenic acid, both present in the leaves of *Smilax brasiliensis* Spreng., were responsible for the inhibition of growth of *Allium cepa* L. seedlings. These results could explain why Sveti Miklavž nad Litijo, despite of being the Tartary buckwheat accession with the lowest levels of rutin, was the most effective accessions in our study controlling the development of both weeds, as the amount of chlorogenic acid was more than 8-times higher than in other Tartary buckwheat accessions (and 50-times higher than common buckwheat accessions), which could be inducing synergistically inhibitory effects together with rutin.

Quercetin has been found to reduce germination, weight and length of alfalfa seeds and seedlings respectively (Ghimire et al., 2019), as well as primary roots in leguminous plants such as *Senna obtusifolia* (L.) Irwin & Barneby (Coelho et al., 2017) and were found that can affect *Microcystis aeruginosa* Kutzing's photosynthesis, respiration, cell membrane, and enzymatic system causing oxidative damage in concentration-dependent mode (Chen et al., 2019; Zhao et al., 2023). Our results showed that the Tartary buckwheat accession with the largest amount of quercetin was Slovenj Gradec, the same with higher amounts of kaempferol, and the one that induced the reduction of all parameters measured in *P. oleracea*, suggesting that these compounds could play a role in the development of this dicot weed. Furthermore, these results are supported by the negative correlation obtained between the amount of quercetin found in these accessions of *F. tataricum* and the inhibition to SVI of *P. oleracea* as quercetin levels increase, the viability of common purslane plants decreases. (Macias et al., 2020) showed also that high concentrations of rutin and quercetin could inhibit plant seed germination by affecting respiration and ATP levels in embryogenic cells via substrate oxidation or phosphate uptake inhibition, which could explain the inhibitory potential of Osrednje Goričko, as was the Tartary buckwheat accession with the highest total sum of quercetin and rutin and was also able to inhibit all of the parameters measured in *L. rigidum* and RIC and SPL of *P. oleracea*.

On the other hand, although all these flavonoids have been previously related to the allelopathic phenomenon, they are also well known for their antioxidant activity when accumulated in the different plant tissues (Agati et al., 2020). These flavonoids help plants defend against abiotic (drought, cold, heat, salt, nutrient deficiency, etc.) and biotic stress (pathogen infection, herbivores attack, etc.), preventing crop losses (Baskar et al., 2018) The strong antioxidant activity of flavonoids is due to their ability to scavenge free radicals and prevent oxidative stress (Raman et al., 2016). Recently, Jan et al. (2022) demonstrated that transgenic rice plants with higher accumulation of kaempferol and quercetin were able to enhance tolerance to drought and ultraviolet radiation stress by mitigating the accumulation of ROS. This could be associated with the correlation observed among high kaempferol levels in *F. esculentum* plants and lower reduction of SVI and SPL in *L. rigidum*. As *L. rigidum* plants had similar SVI and SPL to the control, *F. esculentum* plants could accumulate this antioxidant flavonoid as method of defence. Ismail et al. (2015) reported that exogenous application of the flavonoid rutin to glycophyte bean leaves improved tissue tolerance and reduced effects of salinity on leaf photochemistry suggesting that rutin accumulation in the cytosol scavenges hydroxyl radical formed in response to salinity treatment. This protective role could be key in this study, as some of the accessions that accumulated more polyphenols, such as La Harpe, Luba, Česká krajová, Sweden-1, Osrednje Goričko, Slovenj Gradec or Sveti Miklavž nad Litijo, were also the accessions that did not experience any kind of stimulation in their growth in the presence of *L. rigidum* or *P. oleracea*. This could indicate that buckwheat plants put their energy into synthesising protective metabolites rather than competing for growth. This could be another strategy of defence or protection against the surrounding weeds.

Furthermore, a number of health advantages have been connected to the antioxidant properties of flavonoids. According to previous studies (Pandey et al., 2009; Rudrapal et al., 2022) flavonoids may help to reduce the risk of chronic diseases like cardiovascular disease, certain types of cancer, and neurodegenerative disorders. According to Boots et al. (2008), flavonoids may also have anti-inflammatory properties that could help to avoid inflammation and enhance general health. Therefore, choosing accessions with high flavonoid concentrations may be advantageous for both the ecosystem and human health.

In short, we found that each accession can show different strategies for sustainable weed management. On the one hand, there are accessions as Iwate zairai, Arihira zairai and Chernigovskaya 17 that inhibited all parameters of both weeds and that compete with weeds for space by increasing leaf or root growth despite not having a large accumulation of phenolic compounds, while other accessions as Luba or Sveti Miklavž nad Litijo manage the surrounding weeds by synthesising and accumulating higher amounts of phenolic compounds, despite not increasing significantly in size.

5. Conclusion

To select a good accession for organic farming, it is necessary to consider three points (i) the accession must be able to control weeds without the use of synthetic herbicides, (ii) the accession has to have good growth as it has an impact on crop productivity and (iii) the accession has to have a high flavonoid (antioxidant) content as it is beneficial for both plant and human health and the flavonoid content is closely correlated to the allelopathic activity and development of cultivars. In this context, we propose different buckwheat accessions for sustainable weed control. In the case of predominance of monocotyledonous weeds, La Harpe and Pulawska II were chosen because of their high potential to control this type of weeds as well as the good growth of the plants, and the high accumulation of antioxidants, when growing in the presence of weeds. When dicotyledonous weeds predominate, the *F. esculentum* accessions CD7272 and Prego and *F. tataricum* accession Slovenj Gradec had the highest potential to control these weeds while having a good growth. Finally, *F. esculentum* accessions Chernigovskaya 17 and Luba and the *F. tataricum* accession Sveti Miklavž nad Litijo could manage both *L. rigidum* and *P. oleracea* development, while having good growth and quantity of phenolic compounds in plant tissues being suitable for organic farming. The selection of accessions was done based on their allelopathic potential, the unaffected root and/or shoot development when growing in the presence of weeds, and the content of flavonoids in the buckwheat plants. In the future, it would be necessary testing under natural conditions the weed management potential of the most promising accessions selected in this study.

Funding

This project was funded by the European Union's Horizon 2020 Research and Innovation Program under Grant Agreement No. 771367, ECOBREED (Increasing the Efficiency and Competitiveness of Organic Crop Breeding). Funding for open access charge: Universidade de Vigo/CISUG.

CRediT authorship contribution statement

Conceptualization: AMSM, MJR, VM; Data curation: YVA, AK, PHC; Formal analysis: YVA, DJ, AK; Funding acquisition: MJR, VM; Investigation: YVA, AK, PHC; Project administration: AMSM, DJ, VM; Supervision: AMSM, DJ; Visualization: YVA, AMSM, DJ, AK, PHC; Writing - review & editing: YVA, AMSM, DJ, MIH, MZ, PHC.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Adela M Sanchez-Moreiras reports financial support was provided by European Union's Horizon 2020 research and innovation program under grant agreement No. 771367.

Data Availability

Data will be made available on request.

Acknowledgements

We would like to thank Dr Michal Jagr for the analysis of phenolic compounds. Further, we would like to thank the Agricultural Institute of Slovenia and the Czech Gene Bank, Crop Research Institute, Czech Republic for providing us with seed samples of buckwheat.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2023.127040.

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