

# Allelopathic interactions of brown mustard (*Brassica juncea* L.) with other aromatic plants during germination and seedling development

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## Abstract

Organic compounds originating from plant metabolism and reaching the environment may inhibit or stimulate germination and early developmental processes of other plants grown in the vicinity. The aim of this study was to investigate the allelopathic interactions of brown mustard with four other aromatic plants (summer savoury, coriander, caraway and common sage). While health-promoting metabolites of brown mustard are thoroughly investigated and the plant receives an increasing interest from cultivators of aromatic and medicinal plants, its allelopathic interactions with other aromatic plants are poorly documented. The experiments were performed in closed germination vessels, under controlled conditions. The influence of the presence or absence of light, as well as of a sufficient or reduced water supply on the co-germination of brown mustard seeds with each of the other four aromatic plants was also evaluated. The presence of brown mustard reduced the germination velocity of caraway, coriander, sage and savoury. It inhibited stem elongation, but stimulated root growth of savoury. Shoot growth of coriander seedlings was enhanced by the vicinity of brown mustard plantlets. Caraway slowed down the germination of brown mustard seeds, but it stimulated root and stem elongation of the seedlings. The presence of savoury enhanced the fresh biomass production of brown mustard. Common sage inhibited root growth, but stimulated stem elongation of brown mustard plantlets. Most of the allelopathic effects were more pronounced under water shortage than under sufficient water supply. Positive interspecific influences on biomass production were, in most cases, more pronounced in the presence of light. The findings may contribute to optimization of brown mustard cultivation in small parcels, in the vicinity of other aromatic plants, some allelopathic interactions being able to stimulate growth and developmental processes in an environmental-friendly and cost-effective manner.

**Keywords:** aromatic plants; brown mustard; chemical interaction; germination dynamics

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## Introduction

Plant growth and crop yield can be influenced through natural processes, such as the chemical interactions between plants which share the same local habitat. Allelopathic interactions are interspecific relations within a plant community, based on specific secondary metabolites which exert negative or positive

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influence on other plants that come in contact with the active compounds through the root system or via the aboveground organs (Cheng and Cheng, 2015). In most of the cases, plant-derived chemicals that influence physiological processes of other neighbouring plants are phenolic compounds, hydroxamic acids, short-chain fatty acids or essential oil-constituting mono- and sesquiterpenes. They mainly influence germination of seeds and early development of seedlings, in accordance with the fact that these early ontogenetic phases are the most sensitive to external stressors (Li *et al.*, 2010; DeAlbuquerque *et al.*, 2011). Because allelopathic compounds have the main role in the chemically mediated competition of plants for resources, in most cases they inhibit biological processes in other plants. This is why at present there is a special interest in their use as natural herbicides in the weed control. Nevertheless, giving the complexity of chemical interactions between plants, allelopathic compounds may also exert positive effects on certain developmental and metabolic processes of other plants, upon their perception as chemical stimuli or modulators. Scientific information about stimulating influences of plant allelochemicals is insufficient, but more and more research is focusing on the elucidation of action mechanism of these metabolites, to be finally able to apply these natural substances in plant cultivation as environmental-friendly active compounds (Rehman *et al.*, 2019).

Aromatic plants are known to produce a high variety of secondary metabolites, largely used in health-promoting food spices, in the complementary medicine and in the cosmetic industry (Rubio *et al.*, 2013; Dini, 2018). Because there is a growing interest in their use in human nutrition, several aromatic plants are now cultivated under controlled conditions, usually on smaller areas than the conventional crop plants, but in many cases the same producer cultivates several aromatic plant species at the same time and on the same location (Rehman *et al.*, 2019). Because cultivation of aromatic plants has several advantages in comparison with their exploitation from their natural habitats, an even growing number of agencies bring these species into cultivation systems. Thus, a more constant yield can be achieved, and the quality of the product can be controlled. Over-exploitation of wild plant populations may be avoided, and non-native species can be acclimatized. But the costs with plant protection are higher, this is why the better knowledge of chemical interactions between different plant species may be useful in optimizing plant growth and reducing the use of synthetic herbicides (Schippmann *et al.*, 2006).

Among the aromatic plants, brown mustard (*Brassica juncea* L., also known from the literature as oriental mustard, Indian mustard, potherb mustard, wild mustard, vegetable mustard or Chinese leaf mustard) is receiving at present more and more attention. It originates from Central Asia, it is an allotetraploid species which resulted from the natural hybridization of *B. rapa* and *B. nigra*, preserving the genomes of both parent species. It is a valuable source of health-promoting phytochemicals, mainly glucosinolates, isothiocyanates and polyphenols (Sharma *et al.*, 2017; Majdoub *et al.*, 2020). It is also used in the complementary medicine, due to its many beneficial influences on human health (Kumar *et al.*, 2011). Pharmacological studies demonstrated that it has antimutagenic and anticancer effects (e. g. through induction of apoptosis in human colon cancer cells), as well as anti-hyperglycemic, anti-inflammatory, anti-obesity and antioxidant effects. It is also used in the treatment of cataracts, its sinapic acid derivatives exert an antibacterial activity, and its erucic acid has a beneficial influence on cardiac functions (Kumar *et al.*, 2011; Sun *et al.*, 2018). Furthermore, brown mustard can be used for the phytoremediation of soils contaminated with heavy metals and certain pesticides (Alam *et al.*, 2020). It is a good selenium hyperaccumulator (Jaiswal *et al.*, 2012), and the oil extracted from the seeds can be used for biodiesel production (Kumar *et al.*, 2011). Several attempts were made to prime or to harden seeds and seedlings of aromatic plants, to reach a better tolerance to various abiotic stress factors, and in many cases increased stress tolerance could be correlated with an enhanced production of bioactive secondary metabolites (Golubkina *et al.*, 2018; Tsukagoshi and Yamori, 2020; Shah *et al.*, 2022). Drought stress and light stress were among the most important adverse conditions that could modulate the biosynthesis of these bioactive compounds (Sharma *et al.*, 2019; Farooq *et al.*, 2020).

While its application in soil remediation is well documented, and its health-promoting metabolites are thoroughly investigated, the allelopathic interactions of brown mustard with other aromatic plants are poorly

documented. This is why the objective of this study was to investigate the allelopathic interactions between brown mustard and four others, commonly cultivated aromatic plant species, during the earliest and most critical developmental stages, i. e. germination and vegetative growth of seedlings. Another question was if the presence or absence of light, the sufficient or insufficient amount of water, and the combination of different light regimes and water supplies could influence the allelopathic interactions during germination of brown mustard seeds in the vicinity of caraway, coriander, common sage or summer savoury seeds. The results may offer a better insight into the inhibitory or stimulatory allelopathic interactions between aromatic plants, and may be used for optimizing the co-cultivation of the investigated species with a high health-promoting value.

## Materials and Methods

The experiments were performed under controlled laboratory conditions, in a closed system, to minimize the escape of potential volatile organic compounds with a possible allelopathic effect. Relevant parameters of the germination process were selected in order to evaluate allelopathic interactions, parameters which reflect the extent, the speed and the time spread of germination, as well as the growth potential and vigour of young seedlings (Bewley *et al.*, 2013).

### *Biological material*

Five aromatic plant species were used in the experiments: brown mustard (*Brassica juncea* L.), caraway (*Carum carvi* L., also known as meridian fennel or Persian cumin), coriander (*Coriandrum sativum* L., being referred to also as cilantro or Chinese parsley), common sage (*Salvia officinalis* L., also known as medicinal sage) and summer savoury (*Satureja hortensis* L.). Brown mustard belongs to the Brassicaceae family, caraway and coriander are included in the Apiaceae family, while sage and savoury make part of the Lamiaceae family. All of these three families include several species which are considered aromatic or medicinal plants. Seeds of the five species were purchased from the seed bank of Caussade Semences (France).

### *Experimental design*

Before the initiation of germination, seeds were sterilized in 3% sodium hypochlorite for 5 min, then thoroughly washed three times with sterile water. Germination was performed in large Petri dishes (with the diameter of 150 mm), on two layers of filter paper. 40 seeds were put in every dish, in parallel rows, at a similar distance from each other. In the control setups there were 40 seeds of the same species from the ones mentioned in the previous subheading. In the experimental variants where the possible allelopathic interactions were aimed to be observed, 20 brown mustard seeds were alternately placed with 20 seeds of one of the other species taken into study. Every seed had in its closest vicinity seeds of the other species. Normal water supply was represented by 8 mL of distilled water, evenly distributed along the surface of the filter paper. Insufficient water supply was represented by 4 mL distilled water on the same surface, for the same number of 40 seeds. This amount of water was established in previous experiments, as to enable germination and seedling establishment, but to reduce growth of plantlets. Half of the germination vessels received from above a photon flux density of  $330 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  of white light for 16 h per day, while the other half was deprived of light, being covered with aluminium foil. In total, there were 36 experimental variants, each of them being set in five independent repetitions: 1) brown mustard seeds, germinating in light and with sufficient water; 2) caraway seeds, germinating in light and with sufficient water; 3) coriander seeds, germinating in light and with sufficient water; 4) common sage seeds, germinating in light and with sufficient water; 5) summer savoury seeds, germinating in light and with sufficient water; 6) brown mustard seeds, germinating in darkness and with sufficient water; 7) caraway seeds, germinating in darkness and with sufficient water; 8) coriander seeds, germinating in darkness and with sufficient water; 9) common sage seeds, germinating in darkness and with sufficient water; 10) summer savoury seeds, germinating in darkness and with sufficient water; 11) brown

mustard seeds, germinating in light and with insufficient water; 12) caraway seeds, germinating in light and with insufficient water; 13) coriander seeds, germinating in light and with insufficient water; 14) common sage seeds, germinating in light and with insufficient water; 15) summer savoury seeds, germinating in light and with insufficient water; 16) brown mustard seeds, germinating in darkness and with insufficient water; 17) caraway seeds, germinating in darkness and with insufficient water; 18) coriander seeds, germinating in darkness and with insufficient water; 19) common sage seeds, germinating in darkness and with insufficient water; 20) summer savory seeds, germinating in darkness and with insufficient water; 21) brown mustard seeds alternating with caraway seeds, in light and with sufficient water; 22) brown mustard seeds alternating with coriander seeds, in light and with sufficient water; 23) brown mustard seeds alternating with common sage seeds, in light and with sufficient water; 24) brown mustard seeds alternating with summer savoury seeds, in light and with sufficient water; 25) brown mustard seeds alternating with caraway seeds, in darkness and with sufficient water; 26) brown mustard seeds alternating with coriander seeds, in darkness and with sufficient water; 27) brown mustard seeds alternating with common sage seeds, in darkness and with sufficient water; 28) brown mustard seeds alternating with summer savoury seeds, in darkness and with sufficient water; 29) brown mustard seeds alternating with caraway seeds, in light and with insufficient water; 30) brown mustard seeds alternating with coriander seeds, in light and with insufficient water; 31) brown mustard seeds alternating with common sage seeds, in light and with insufficient water; 32) brown mustard seeds alternating with summer savory seeds, in light and with insufficient water; 33) brown mustard seeds alternating with caraway seeds, in darkness and with insufficient water; 34) brown mustard seeds alternating with coriander seeds, in darkness and with insufficient water; 35) brown mustard seeds alternating with common sage seeds, in darkness and with insufficient water; 36) brown mustard seeds alternating with summer savoury seeds, in darkness and with insufficient water.

Germination took place in environmental test chambers, where the temperature was kept constantly at 22 °C, the daily photoperiod was set to 16 h light and 8 h darkness. The relative humidity in the growth chambers was irrelevant for the experiments, because the germination vessels were closed Petri dishes, which allow a very restricted evaporation (Farooq *et al.*, 2020). The experiments lasted 10 days from the time the seeds were placed in the germination vessels.

#### *Protocol for collecting data*

Examination of seed germination was performed on a daily basis, before noon. From the several germination parameters used to characterize percentage, velocity, mean time or spread of germination events, the following seven were selected to be evaluated (Hampton and TeKrony, 1995; Kader, 2005; Aravind *et al.*, 2023):

The final germination percentage of seed populations (FGP):

$$FGP = (N_g - N_t) / 100, \quad (1)$$

where  $N_g$  is the number of germinated seeds, and  $N_t$  represents the total number of seeds in the lot.

The mean germination time (MGT):

$$MGT = \sum f \cdot x / \sum f, \quad (2)$$

where  $f$  represents the number of seeds that germinated on day  $x$ .

The coefficient of velocity of germination (CVG):

$$CVG = N_1 + N_2 + \dots + N_x / 100 (N_1 T_1 + \dots + N_x T_x), \quad (3)$$

where  $N$  is the number of seeds germinated each day, while  $T$  is the number of days from seeding that corresponds to  $N$ .

The germination speed (GS):

$$GS = G_1/1 + G_2/2 + \dots + G_x/x, \quad (4)$$

where  $G_1$  represents the number of seeds that germinated on the first day,  $G_2$  is the number of seeds germinated on day 2,  $G_x$  being the number of seeds that germinated on day  $x$ .

The germination index of the seed lot (GI):

$$GI = (10 \times n_1) + (9 \times n_2) + \dots + (1 \times n_{10}), \quad (5)$$

where  $n_1, n_2, \dots, n_{10}$  represent the number of germinated seeds on the first, second and subsequent days until the last day of germination (in this case the tenth day), while the numbers 10, 9, ..., 1 are weights given to the number of germinated seeds on the first, the second and the following days, respectively.

The germination uncertainty (U):

$$U = - \sum_{i=1}^k f_i \times \log_2 f_i, \quad (6)$$

where  $f_i$  is the relative frequency of germination:  
 $f_i = \frac{N_i}{\sum_{i=1}^k N_i}$  (7)

$N_i$  being the number of germinated seeds in the time interval "i", and "k" representing the number of time intervals.

The germination synchrony (S):

$$S = \frac{\sum_{i=1}^k C N_i, 2}{C \sum N_i, 2}, \quad (8)$$

where  $N_i$  is the number of seeds germinated in the time interval "i",  $C N_i, 2$  represents the partial combination of the  $N_i$  order of two seeds that germinated:

$$C N_i, 2 = N_i \times (N_i - 1) / 2, \quad (9)$$

while  $C \sum N_i, 2$  stands for the partial combination of two germinated seeds in the order of the sum of germinated seeds.

At the end of the ten days period, root length (from the collet to the apex of calyptra), shoot height (from the collet to the top of the apical bud) and fresh weight of plantlets were determined (Hampton and TeKrony, 1995).

### *Statistical analysis*

The sample size was 40 seeds per germination vessel. Controls were represented by 40 seeds of the same species in a germination vessel. There were five repetitions for every experimental variant. For statistical analysis of the experimental data the R software environment was used (version 4.1.0), and calculation of germination parameters was performed with the germinationmetrics package (Aravind *et al.*, 2023). The Shapiro-Wilk test was used for analysis of normality of the distribution of data sets, and Bartlett's test was applied for evaluating the homogeneity of variances. Data sets with normal distribution were evaluated with one-way ANOVA and the Tukey HSD post-hoc test, while for data that were not normally distributed the Kruskal-Wallis test and the Mann-Whitney pairwise test was used to identify significant differences between the means. The thresholds for statistical significance were marked as follows: \* for  $P < 0.05$ , \*\* for  $P < 0.01$  and \*\*\* for  $P < 0.001$ . The standard deviations from means ( $\pm$ SD) were calculated to describe the distribution of the determined values. Data sets were arranged with the help of the dplyr package, and the ggplot2 data visualization package was used in the elaboration of figures (Wickham, 2016).

## **Results**

### *Influence of brown mustard and summer savoury on each other's germination and seedling growth*

Germinating brown mustard seeds did not show any significant influence on final germination percentage, mean germination time, germination uncertainty and synchrony of summer savoury, but caused a delayed germination of savoury seeds and a decreased germination index under the conditions of darkness and sufficient water supply (Table 1). The lack of light reduced the germination percentage and the mean germination time of savoury seeds, with or without the presence of brown mustard (i. e. in the control groups

as well as in the mustard-associated groups). Brown mustard germination was significantly influenced by summer sage only under water insufficiency: the mean germination time and the germination uncertainty were increased, while the coefficient of velocity of germination and the germination synchrony were decreased.

**Table 1.** Influence of brown mustard and summer savory on each other's germination parameters

Species	Conditions	FGP %	MGT (days)	CVG	GS	GI	U	S
savory-c	L + WS	91	3.6	28.00	3.03	5.20	1.75	0.27
savory-a		93	3.6	28.00	3.03	5.20	1.75	0.29
savory-c	L + WI	92	3.6	27.77	2.57	5.50	1.37	0.41
savory-a		91	3.6	27.77	2.57	5.50	1.39	0.41
savory-c	D + WS	86	2.8	36.36	3.58	6.30	1.54	0.35
savory-a		84	2.8	36.36	2.13**	5.10**	1.54	0.35
savory-c	D + WI	81	2.4	40.90	4.10	6.40	0.54	0.75
savory-a		82	2.4	40.90	4.10	6.40	0.54	0.75
mustard-c	L + WS	100	1.2	90.00	9.33	8.80	0.47	0.80
mustard-a		100	1.2	90.90	9.58	8.90	0.47	0.80
mustard-c	L + WI	100	1.4	64.28	7.25	8.20	1.22	0.74
mustard-a		100	1.8*	55.55*	6.66*	8.10	1.48*	0.51*
mustard-c	D + WS	100	1.0	100	10.00	9.00	0.42	1.00
mustard-a		100	1.0	90.90	9.50	8.90	0.41	0.80*
mustard-c	D + WI	100	1.0	100	10.00	9.00	0.40	1.00
mustard-a		100	1.4*	83.33*	8.66*	8.60	0.87*	0.80*

Legend: c – control, a – in association with the other species

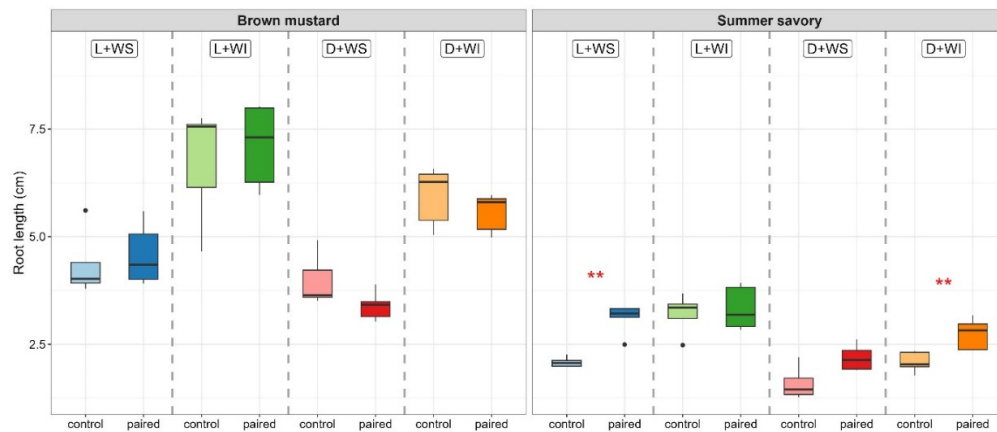
L – light, D – darkness, WS -water sufficiency, WI – water insufficiency

FGP – final germination percentage, MGT – mean germination time, CVG – coefficient of velocity of germination,

GS – germination speed, GI – germination index, U – germination uncertainty, S – germination synchrony.

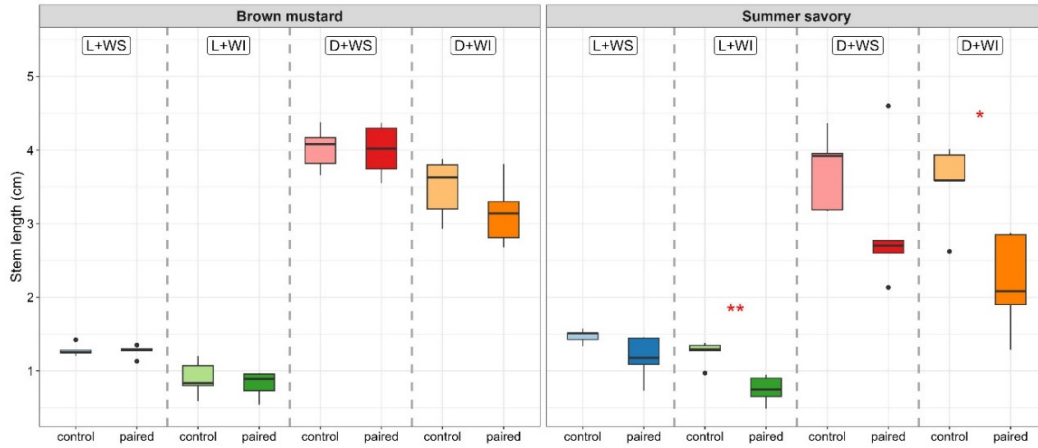
\* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Tukey's HSD test or Mann Whitney test).

After germination, the presence of brown mustard resulted in an enhanced root elongation of savoury seedlings (Figure 1), while stem elongation of savoury was inhibited by mustard when the water supply was insufficient (Figure 2). On the other hand, summer savoury plantlets exerted a positive influence on fresh biomass accumulation of mustard seedlings in light (Figure 3).

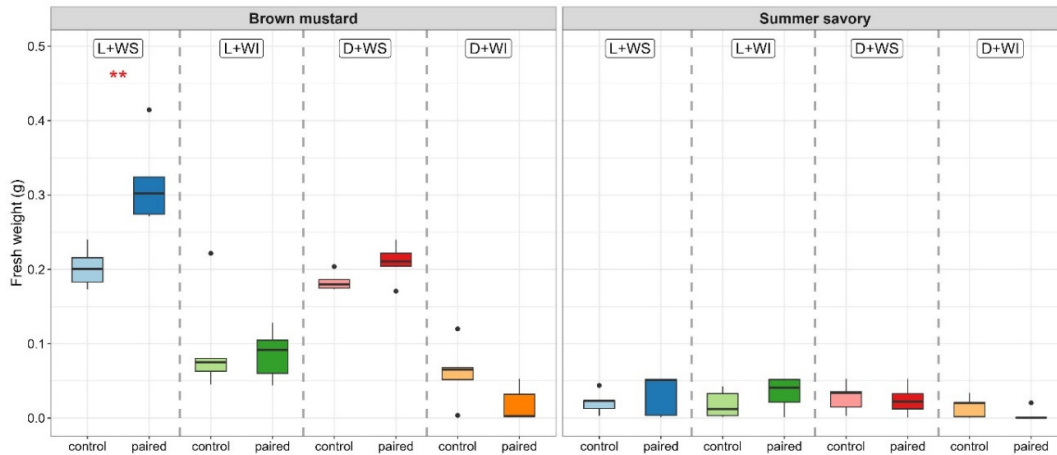


**Figure 1.** Influence of brown mustard and summer savoury seedlings on each other's root growth under different conditions (light and darkness, sufficient or insufficient water)

Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)



**Figure 2.** Influence of brown mustard and summer savory seedlings on each other's shoot growth under different conditions (light and darkness, sufficient or insufficient water)  
Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)



**Figure 3.** Influence of brown mustard and summer savory seedlings on each other's fresh weight under different conditions (light and darkness, sufficient or insufficient water)  
Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)

*Influence of brown mustard and caraway on each other's germination and seedling growth*

The presence of brown mustard stimulated germination of caraway seeds under conditions of darkness and water deficiency, mainly by increasing germination speed and germination index (Table 2). On the contrary, germination of brown mustard seeds was disturbed by the vicinity of caraway: the mean germination time of mustard was increased (in a higher extent under water deficiency), the coefficient of velocity of germination was reduced (in accordance with a lower germination speed), the germination index was significantly reduced in darkness, the germination uncertainty became higher, and the germination synchrony registered significantly lower values. Caraway seeds showed a much lower final germination percentage than brown mustard seeds, but under conditions of co-germination none of these two species significantly modified the other's germination percentage.

**Table 2.** Influence of brown mustard and caraway on each other's germination parameters

Species	Conditions	FGP %	MGT (days)	CVG	GS	GI	U	S
caraway-c	L + WS	42	6.0	16.66	0.31	0.40	1.00	0.15
caraway-a		44	6.0	16.66	0.31	0.40	1.00	0.15
caraway-c	L + WI	36	3.6	25.00	0.33	0.60	0.30	0.15
caraway-a		35	3.6	25.00	0.33	0.60	0.30	0.15
caraway-c	D + WS	34	4.0	18.75	0.25	0.50	0.20	0.15
caraway-a		32	4.0	18.75	0.25	0.50	0.20	0.15
caraway-c	D + WI	30	5.0	20.00	0.20	0.40	0.20	0.10
caraway-a		31	5.0	20.00	0.38**	0.64*	0.20	0.10
mustard-c	L + WS	100	1.2	90.00	8.75	9.50	0.50	0.77
mustard-a		100	1.6*	60.00**	6.66**	8.90	1.44**	0.33**
mustard-c	L + WI	92	1.4	69.23	7.33	8.80	1.22	0.74
mustard-a		92	2.4*	41.66**	5.04**	8.30	1.85*	0.32**
mustard-c	D + WS	100	1.0	100	9.00	9.60	0.55	1.00
mustard-a		96	1.6*	61.53**	7.16*	8.20*	1.30**	0.49**
mustard-c	D + WI	95	1.2	90.00	9.00	9.20	0.46	0.80
mustard-a		98	2.6**	38.46**	4.25**	8.30*	1.91**	0.39**

Legend: c – control, a – in association with the other species

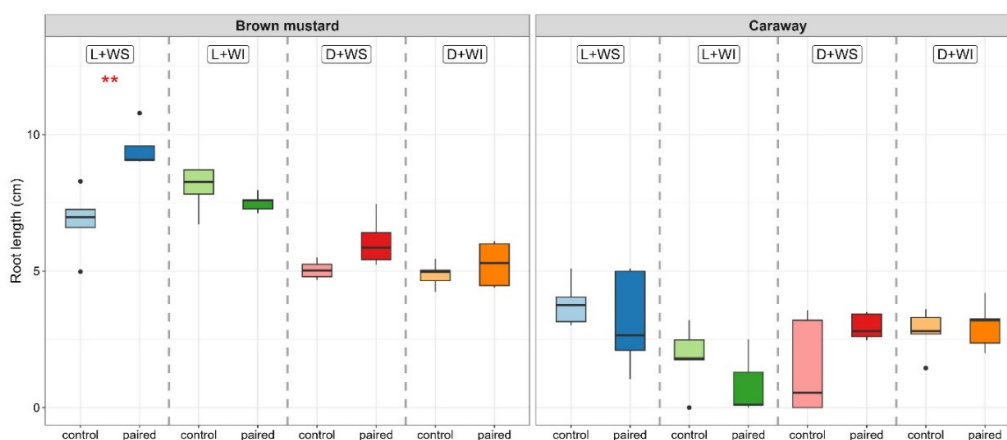
L – light, D – darkness, WS – water sufficiency, WI – water insufficiency

FGP – final germination percentage, MGT – mean germination time, CVG – coefficient of velocity of germination,

GS – germination speed, GI – germination index, U – germination uncertainty, S – germination synchrony.

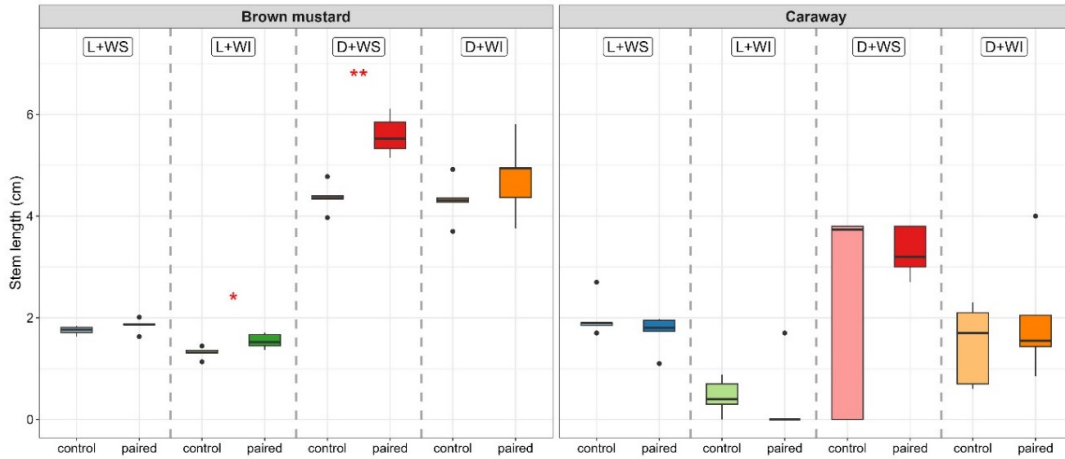
\* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Tukey's HDS test or Mann Whitney test).

While the presence of brown mustard seedlings did not significantly influence root elongation of caraway seedlings, root growth of brown mustard was inhibited by caraway when these two plants were co-germinated in the presence of light and with a sufficient water supply (Figure 4). Main roots of mustard plantlets were generally longer in the presence of light than in darkness. Stem elongation of caraway was also not influence by brown mustard seedlings in a statistically significant degree, while stem growth of brown mustard was inhibited in light and insufficient water supply, and mainly in darkness and sufficient water supply (Figure 5). The stem of the brown mustard seedlings was longer in darkness than in light, which is a normal response of plantlets to the lack of light. The fresh weight of seedlings (ten days after the seeds were set to germinate) was not significantly modified by the presence of the other species (data not shown).



**Figure 4.** Influence of brown mustard and caraway seedlings on each other's root growth under different conditions (light and darkness, sufficient or insufficient water)

Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)



**Figure 5.** Influence of brown mustard and caraway seedlings on each other's shoot growth under different conditions (light and darkness, sufficient or insufficient water)

Vertical lines represent  $\pm$ SD from means (n = 5), \* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Mann Whitney test)

*Influence of brown mustard and coriander on each other's germination and seedling growth*

The presence of brown mustard exerted a statistically significant influence on germination of coriander seeds only when absence of light was combined with water shortage. Under these circumstances, brown mustard caused an increased mean germination time, a lower germination speed and a decreased germination index for coriander seeds (Table 3). Coriander modified several germination parameters of brown mustard under water shortage, irrespective of the presence or absence of light: it reduced the final germination percentage, germination speed, germination index, as well as germination uncertainty of brown mustard seeds, while the germination synchrony was increased.

**Table 3.** Influence of brown mustard and coriander on each other's germination parameters

Species	Conditions	FGP %	MGT (days)	CVG	GS	GI	U	S
coriander-c	L + WS	93	6.8	9.17	0.73	2.30	2.12	0.14
coriander-a		93	6.8	9.17	0.73	2.30	2.12	0.14
coriander-c	L + WI	100	5.4	18.51	1.93	7.80	2.12	0.17
coriander-a		100	5.4	18.51	1.93	7.80	2.12	0.17
coriander-c	D + WS	91	6.6	9.43	0.43	1.50	1.15	0.12
coriander-a		93	6.6	9.43	0.43	1.50	1.15	0.12
coriander-c	D + WI	100	5.4	18.59	1.95	3.10	1.68	0.28
coriander-a		100	7.2*	13.81*	0.97**	2.30*	1.68	0.28
mustard-c	L + WS	100	1.2	50.00	3.83	8.50	1.06	0.76
mustard-a		97	1.2	50.00	3.50	8.40	0.59*	0.87*
mustard-c	L + WI	98	1.8	44.44	4.50	10.80	0.88	0.74
mustard-a		77*	1.8	50.00	3.33*	8.40*	0.61*	0.88*
mustard-c	D + WS	100	2.0	50.00	5.00	9.20	0.82	0.71
mustard-a		95	1.8	56.25	4.80	8.60	0.86	0.67
mustard-c	D + WI	96	1.8	55.55	4.83	10.80	0.86	0.68
mustard-a		71*	2.0	50.00	4.00*	8.50*	0.59*	0.84*

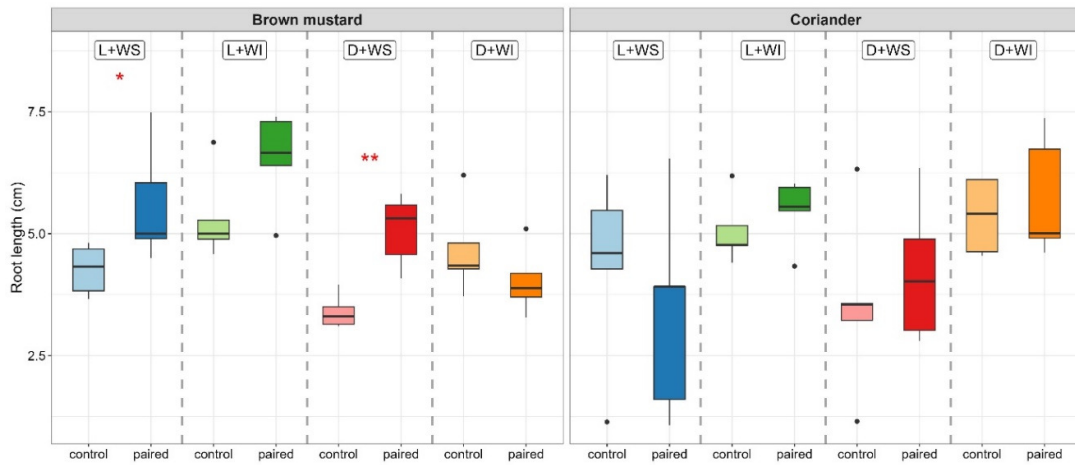
Legend: c – control, a – in association with the other species

L – light, D – darkness, WS -water sufficiency, WI – water insufficiency

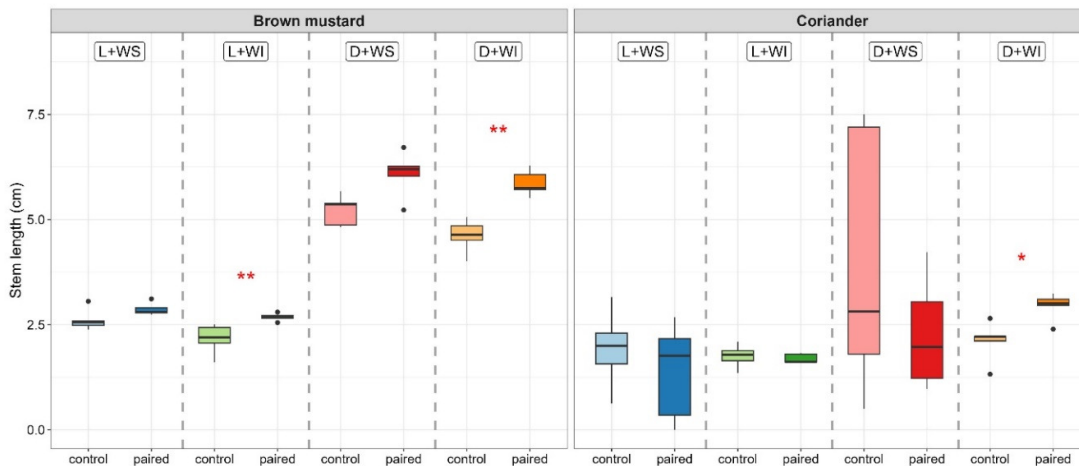
FGP – final germination percentage, MGT – mean germination time, CVG – coefficient of velocity of germination, GS – germination speed, GI – germination index, U – germination uncertainty, S – germination synchrony.

\* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Tukey's HDS test or Mann Whitney test).

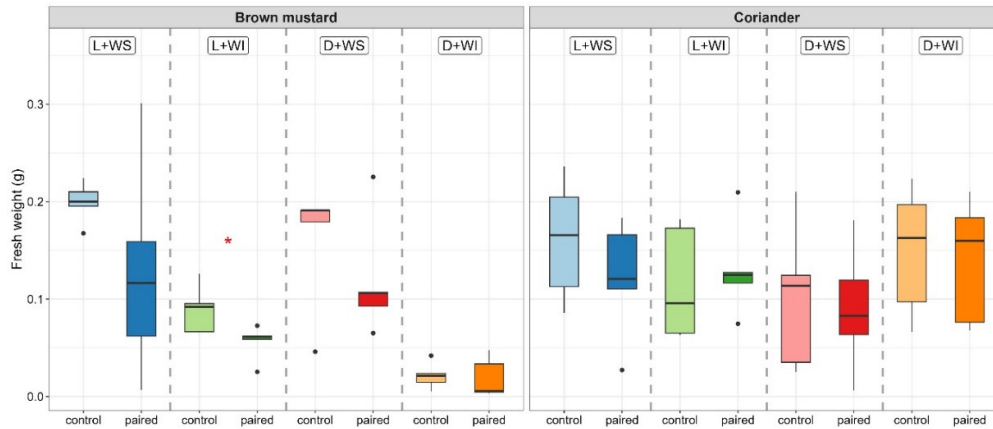
After germination, brown mustard did not exert any significant influence on root growth of coriander, while the vicinity of coriander inhibited root elongation of brown mustard seedlings in the well-watered variants, both in light and in darkness (Figure 6). Brown mustard stimulated stem elongation of coriander seedlings under conditions of darkness and water insufficiency, while coriander inhibited shoot growth of brown mustard under water deficiency, both in light and in darkness (Figure 7). While the presence of brown mustard did not have any significant influence on fresh biomass of coriander seedlings, coriander exerted a stimulating effect on fresh weight gain of brown mustard under two growth conditions: in light and water shortage, and in darkness and sufficient water supply, respectively (Figure 8). It can also be observed that the biomass of mustard seedlings was the lowest under darkness and water shortage, both in the control groups and in the lots which germinated in the presence of coriander. On the other hand, fresh biomass of coriander was not significantly affected by the applied water shortage.



**Figure 6.** Influence of brown mustard and coriander seedlings on each other’s root growth under different conditions (light and darkness, sufficient or insufficient water)  
 Vertical lines represent  $\pm$ SD from means (n = 5), \* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Mann Whitney test)



**Figure 7.** Influence of brown mustard and coriander seedlings on each other’s shoot growth under different conditions (light and darkness, sufficient or insufficient water)  
 Vertical lines represent  $\pm$ SD from means (n = 5), \* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Mann Whitney test)



**Figure 8.** Influence of brown mustard and caraway seedlings on each other's fresh weight under different conditions (light and darkness, sufficient or insufficient water) Vertical lines represent  $\pm$ SD from means (n = 5), \* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Mann Whitney test)

*Influence of brown mustard and common sage on each other's germination and seedling growth*

In the case of common sage, the presence of brown mustard significantly reduced the germination percentage and the mean germination time. The speed of germination was also decreased, while under conditions of light and water shortage the germination uncertainty and germination synchrony of sage seeds were both increased by the vicinity of brown mustard (Table 4). Common sage exerted a significant influence on brown mustard only when co-germination took place in darkness and water insufficiency. In this case speed, uncertainty and synchrony of germination of brown mustard seeds were reduced by germinating sage seeds. It was also found that sage seeds had a lower germination percentage even in the control lots, especially when the process was under the influence of water shortage or lack of light. The combination of darkness and water insufficiency also resulted in a moderate decrement of germination percentage of brown mustard seeds, irrespective of the presence of sage seeds.

**Table 4.** Influence of brown mustard and common sage on each other's germination parameters

Species	Conditions	FGP %	MGT (days)	CVG	GS	GI	U	S
sage-c	L + WS	63	6.2	15.78	0.83	2.70	1.20	0.18
sage-a		64	6.6	14.28	0.75	2.60	1.48	0.15
sage-c	L + WI	55	6.0	16.66	2.25	3.10	1.00	0.09
sage-a		51	6.8	14.81	1.27*	3.10	1.55*	0.17*
sage-c	D + WS	46	7.4	12.50	0.40	1.20	0.45	0.20
sage-a		45	7.8	12.00	0.21*	1.20	0.45	0.20
sage-c	D + WI	34	7.6	11.43	1.50	1.80	1.00	0.10
sage-a		22*	6.4*	5.85*	0.94*	1.66	0.86	0.10
mustard-c	L + WS	100	1.2	92.85	7.22	9.60	0.92	0.80
mustard-a		100	1.2	92.85	7.22	9.60	0.92	0.80
mustard-c	L + WI	100	2.2	75.71	9.71	9.20	0.74	0.75
mustard-a		100	2.2	75.71	9.71	9.20	0.74	0.75
mustard-c	D + WS	100	1.2	83.33	8.41	10.80	0.57	0.80
mustard-a		100	1.2	83.33	8.41	10.80	0.57	0.86
mustard-c	D + WI	96	1.8	87.36	9.70	8.90	0.97	0.68
mustard-a		93	1.8	87.36	8.14*	9.20	0.81*	0.44*

Legend: c – control, a – in association with the other species

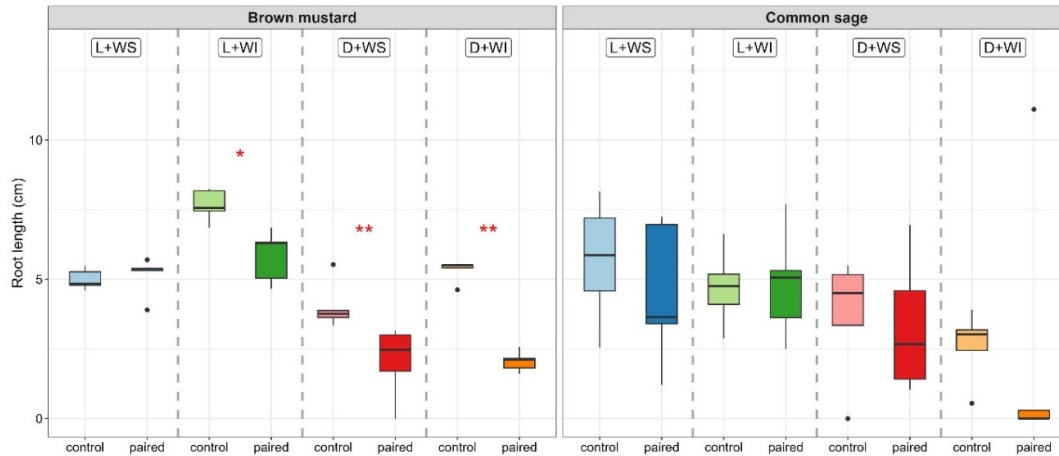
L – light, D – darkness, WS -water sufficiency, WI – water insufficiency

FGP – final germination percentage, MGT – mean germination time, CVG – coefficient of velocity of germination,

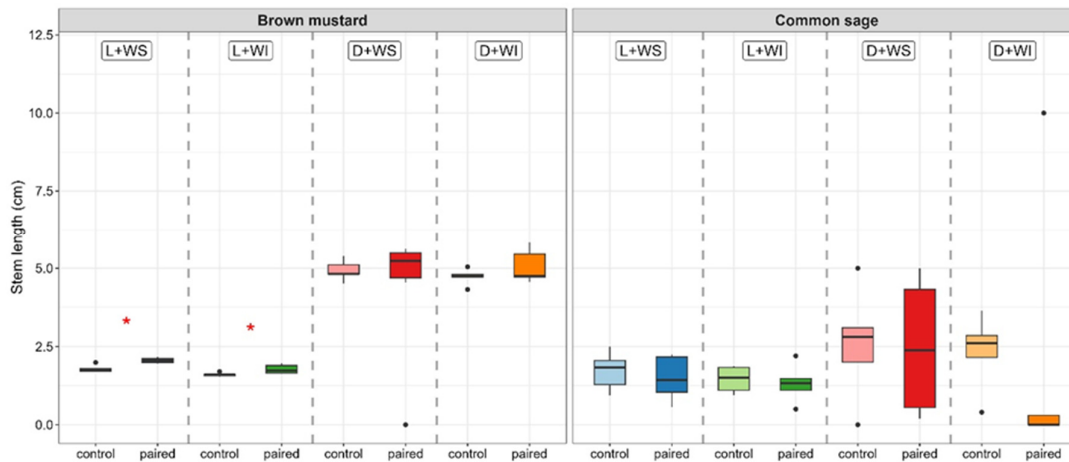
GS – germination speed, GI – germination index, U – germination uncertainty, S – germination synchrony.

\* denotes significant difference from its control at p < 0.05, and \*\* represents significant difference from its control at p < 0.01 (Tukey's HDS test or Mann Whitney test).

Root growth of sage seedlings was stimulated by brown mustard when germination took place in darkness and water shortage. In the presence of sage, mustard seedlings developed a shorter tap root than their control groups both in darkness and under water deficiency (Figure 9). As in the case of roots, stem elongation of common sage was also stimulated by brown mustard, but only in conditions of darkness and water shortage. Mustard shoot growth was moderately, but in a statistically significant degree enhanced by the presence of brown mustard seedlings when light was present. In darkness, brown mustard stem elongation was more pronounced than in light but could not be enhanced by sage seedlings (Figure 10). Fresh weight of brown mustard and common sage seedlings could not be modified significantly by the presence of individuals of the other species.



**Figure 9.** Influence of brown mustard and common sage seedlings on each other's root growth under different conditions (light and darkness, sufficient or insufficient water)  
 Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)



**Figure 10.** Influence of brown mustard and common sage seedlings on each other's shoot growth under different conditions (light and darkness, sufficient or insufficient water)  
 Vertical lines represent  $\pm$ SD from means ( $n = 5$ ), \* denotes significant difference from its control at  $p < 0.05$ , and \*\* represents significant difference from its control at  $p < 0.01$  (Mann Whitney test)

## Discussion

Several interactions could be revealed between germinating brown mustard seeds and the four other aromatic plants taken into study: caraway, coriander, common sage and summer savoury, interactions that were monitored during germination and early seedling growth. Some interspecific effects were specifically manifested under certain conditions: in light or in darkness, under sufficient or insufficient water supply. In most cases the presence of one species inhibited growth and adversely affected certain germination parameters of the other species, but in some cases stimulatory effects were also observed, which have not been reported previously in the literature. This is why it would be necessary to study not only the pharmacological effects of these aromatic plants, but also their allelopathic capacity, which might be applied in environmental-friendly horticultural methods and plant protection (DeAlbuquerque *et al.*, 2011).

Brown mustard influenced only two of the investigated germination parameters for summer savoury and for caraway, and only in the absence of light. But the influence was different on these parameters for the two aromatic plant species: while germination speed and germination index were lowered by brown mustard in the case of summer savoury, the same parameters were increased for caraway. The decrement of germination speed is an inhibitory effect, because a higher vigour of the embryo is reflected by a higher speed of germination (Hampton and TeKrony, 1995). Germination index emphasizes on both the percentage of germination and its velocity, so its higher value denotes a higher degree and a higher rate of seed germination (Kader, 2005). Because brown mustard increased the germination index of caraway in darkness and under water shortage, it can be assumed that the allelopathic influence could compensate for the adverse environmental conditions during germination of caraway seeds, as it was also observed in the case of some other plant species (Bewley *et al.*, 2013; Xie *et al.*, 2019).

Brown mustard and summer savoury influenced each other's development even after germination: mustard stimulated root growth and inhibited stem elongation of savoury seedlings under water shortage, while in the presence of savoury, mustard seedlings had a higher fresh biomass. While no reference could be found about the allelopathic relations of brown mustard with the other four aromatic plants used in the experiments, some of the allelopathic relations of these other species are known from previous studies. For example, summer savoury inhibited the germination of the weed species *Setaria glauca* and *Echinochloa crus-galli* (Dikic, 2005). The essential oil extracted from savoury leaves also had an inhibitory influence on the germination of several other plant species (Taban *et al.*, 2013). These results agree with the findings of the present study, where savoury exerted a negative influence on brown mustard, by decreasing the coefficient of velocity of germination, by increasing the germination uncertainty, and by causing an elevated uncertainty of germination. The coefficient of velocity of germination is an indicator of the rapidity of germination, and its value is higher when the number of germinated seeds is increased and the time required for germination is shorter (Kader, 2005). A better seed population usually has a lower value of the germination uncertainty and a higher synchrony of germination. All of these reflect that summer savoury had an inhibitory effect on germination of brown mustard, but this influence was observed only under water shortage. In other experiments, drought stress was shown to enhance the biosynthesis of secondary metabolites which confer a higher success in the competition for resources (Li *et al.*, 2010; Tsukagoshi and Yamori, 2020).

Caraway exerted a much more extended negative influence on germination of brown mustard, because its presence resulted in higher mean germination time, higher germination uncertainty and lower synchrony of germination, irrespective of the presence or absence of light and of a sufficient quantity of water. In the case of mean germination time, a lower value is better because it signifies that the seed population has germinated faster. The results are in agreement with other studies which revealed a strong inhibitory effect of caraway extracts on germination and growth of several other plant species (Dikic, 2005; Azirak and Karaman, 2008). On the other hand, the positive effects of caraway on the root growth in the presence of light and on the stem elongation of brown mustard seedlings in darkness and water deficiency were not reported previously. These influences may be explained by the fact that the given conditions (light for the root, darkness and water shortage

for the shoot) are unfavourable for a normal development of the young vegetative organs, and the interaction with caraway plantlets or with their released metabolites compensated for the inadequate environmental conditions. Similar compensatory reactions were also reported for other plant species exposed to abiotic stressors during their early development (Farooq *et al.*, 2020).

When one compares the effects of brown mustard on germination of caraway and coriander seeds, it can be noticed that in both cases the presence of brown mustard had an influence only under conditions of darkness combined with water shortage. This influence was exerted mainly on germination speed and germination index. But, while these parameters were increased in the case of caraway (stimulatory effect), a significant reduction of germination speed and of germination index could be registered for coriander. Germination index is considered a good marker of this very sensitive developmental process, because it characterizes the relationship between the percentage and the speed of germination, its lower value denoting a generally weakened germination capacity of the seed population (Kader, 2005; Nonogaki *et al.*, 2010). Also, in darkness and water insufficiency, brown mustard seedlings exerted a positive influence on stem elongation of coriander plantlets. This is somehow contradictory with the results which reported an inhibitory influence of some Brassica species on other plants grown in their close vicinity (Rehman *et al.*, 2019), but could be explained, as in the case of caraway, by the fact that bioactive compounds released by mustard seedlings could reduce the negative influence of darkness and water shortage (Tian and Deng, 2020; Tsukagoshi and Yamori, 2020). The fact that coriander decreased the final germination percentage of brown mustard under water shortage is in agreement with other studies which reported an inhibitory influence of coriander or of its extracts on germination of several other plant species, especially weeds (Dikic, 2005; Azirak and Karaman, 2008). But, while other studies also documented the negative allelopathic influence of coriander on growth parameters of different plants, in the present study it was found that for brown mustard seedlings stem elongation under water shortage and root growth under sufficient water supply were stimulated by the presence of coriander plantlets. This could be related to a lower concentration of the bioactive compounds released by coriander under the given conditions, because it was demonstrated that their inhibitory effect on other plants is highly dependent on their concentration (Li *et al.*, 2010; Rubio *et al.*, 2013).

The founding that under water insufficiency brown mustard and common sage seeds exerted a reciprocal inhibitory effect during germination is also in agreement with previous results which demonstrated a negative allelopathic influence of sage on other plant species, as well as of different Brassica species on the germination process of several seeds (Azirak and Karaman, 2008; Rehman *et al.*, 2019). No reference could be found in relation with the finding that the presence of sage seedlings stimulated stem growth of brown mustard in the presence of light. One study reported inhibitory effects of sage on seeds and seedlings of hoary cress (Ravlic *et al.*, 2013), in agreement with the present results concerning inhibition of root growth of brown mustard in the presence of sage, under conditions of darkness and water shortage. The main allelopathic metabolites of sage species were identified as monoterpenes (e. g. camphor) from the composition of essential oils which are released in the atmosphere (Cheng and Cheng, 2015).

To be able to explain the physiological background of the stimulatory or inhibitory interactions between different aromatic plants grown close to each other, a better knowledge of their bioactive metabolites and of their action mechanism in other plants would be required. Thus, a more efficient and sustainable co-cultivation of aromatic and medicinal plants could be achieved, even on smaller areas or in continuous greenhouse growth systems.

## Conclusions

Brown mustard reduced germination speed of summer savoury in darkness, stimulated root growth and inhibited stem elongation of savoury under water shortage. Germination of caraway was facilitated by brown mustard in darkness and under water deficiency. Brown mustard influenced coriander mainly in darkness and under water deficiency, by increasing main germination time, reducing the coefficient of velocity of germination and stimulating stem growth. In the case of common sage, brown mustard decreased germination speed in light and water shortage, caused a lower final germination percentage in darkness and water deficiency, but it stimulated root and stem elongation in darkness and water shortage. On the other hand, germination and growth of brown mustard was modulated by the presence of the other four aromatic plants taken into study. Summer savoury enhanced fresh weight accumulation of brown mustard seedlings, stimulated root growth in the presence of light and stem elongation in darkness and water shortage. An increment of the mean germination time and a lower coefficient of velocity of germination, as well as a decreased germination synchrony of brown mustard seeds were observed in the presence of caraway. Coriander inhibited germination of brown mustard seeds in light and water shortage, but it stimulated stem growth under water deficiency and root growth under sufficient water supply. Fresh biomass of brown mustard seedlings was lowered by coriander. Common sage did not exert any significant influence on germination parameters of brown mustard, but it stimulated stem elongation in light and inhibited root growth in darkness and water shortage. It may be stated that the presence or absence of light, as well as the degree of water supply may influence the result of allelopathic interactions during germination and seedling growth.

Because allelopathic interrelations of brown mustard are largely unknown, but it is more and more frequently cultivated, together with other aromatic plants, the present research provides new information about both inhibitory and stimulatory influences of four other aromatic plant species on germination characteristics and plantlet growth parameters of brown mustard, as well as on the effects of its germination on the seeds and seedlings of these other aromatic plants, when grown close to each other. These findings may contribute to an optimized cultivation of brown mustard as a source of health-promoting compounds in the human diet and in pharmacology, using an environmental-friendly and cost-effective approach.

## Authors' Contributions

Conceptualization LF; Data analysis PK; Data curation LF; Investigation PK and LF; Measurements PK and LF; Methodology LF and PK; Resources LF; Supervision LF; Writing - original draft PK; Writing - review and editing LF. All authors read and approved the final manuscript.

## Ethical approval (for researches involving animals or humans)

Not applicable.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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