University of South Bohemia in České Budějovice
Faculty of Biological Sciences

Bachelor´s thesis

Ecological characteristics of nonindigenous congeners varying in their invasive success: Invasive *Galinsoga parviflora* (Cav) and *Galinsoga ciliata* (Raf) vs. *Ageratum houstonianum* (Mill)

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Bernardová A., 2006: Ecological characteristics of nonindigenous congeners varying in their successfulness: Invasive *Galinsoga parviflora* (Cav) and *Galinsoga ciliata* (Raf) vs. *Ageratum houstonianum* (Mill). [Ekologické charakteristiky různě úspěšných nepůvodních kongenerů: Invadující *Galinsoga parviflora* a *G. ciliata* vs. *Ageratum houstonianum*, bakalářská práce] – 35 p., Faculty of Biological Sciences, University of South Bohemia, České Budějovice

Annotation: Seeds of two species *Galinsoga parviflora* and *G. ciliata* were collected from two localities (the north and the south Bohemia) and seeds of *Ageratum houstonianum* were bought in distribution from two different suppliers. A set of germination and growth experiments was performed, the effect of chilling, allelopathy and competition was studied.

I honestly declare to have worked out this thesis on my own, with the use of cited references.

České Budějovice, 27th April 2006

Acknowledgments: I wish to thank to my supervisor Stanislav Mihulka for his constant optimism, moral and technical support. To my family and my friend for patience, to Šuspa who helped me fighting with statistic. To Mao, with which I had spent many a night trying to count chromosomes and to Martin Kovička for all the things he helped me with and many more… especially for enthomological tweezers that became my indispensable helper while planting "weeds".

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1. INTRODUCTION

1.1 Biological invasions

Increasing invasions of exotic species in recent years is associated with increased human transport (Hodkinson & Thompson 1997; Vitousek et al. 1997; Dukes & Mooney 1999) and with producing anthropogenic disturbed areas (Hobbs & Huenneke 1992; McIntyre & Lavorel 1994; Kotanen et al. 1998). Many of successful plant invaders are those species possessing traits that enhance success in such „invasion–prone“ habitats (that means habitat with heterogeneity, frequent and diverse disturbances, and intensive propagule pressure) (Rejmánek 1996, Kowarik 2003, Pyšek et al. 2005).

There are some general and well studied traits shared by successful invasive plants such as high seed production, rapid dispersal, high germinability, rapid growth rate, early maturity, phenotypic flexibility (Pyšek 1995; Mack 1996; Rejmánek 1996, Rejmánek & Richardson 1996, Williamson & Fitter 1996b, Maillet & Lopez-Garcia 2000; Lepš et al., 2002) but any simple formula has not been revealed yet (Edwards et al., 2006). It proves also more and more increasing interest to find the mechanisms that make species invasive. Success or failure depends on interaction of species and community. (D’Antonio 1993, Pyšek & Pyšek 1995, Williamson & Fitter 1996a)

Capability of plant species to adapt and become invasive may be more important that any particular ecological traits currently, because these ecological characteristics are insufficient to explain such invasive success (Ellstrand and Schierenbeck 2000; Sakai et al. 2001, Edwards et al., 2006). That leads to increased interest about this problem (see Leger & Rice, 2003; Bossdorf et al, 2005; Durka et al, 2005; Hierro et al, 2005; Edwards et al, 2006).

Our studied species are the members of *Asteraceae* family, which are the largest angiosperm family and one of the notorious contributors to the naturalized flora of the world (Binggeli, 1996; Pyšek, 1998, Wu & Wang, 2005). Studies focused on closely related alien species differing in their invasive success have the potential to contribute to answer the questions of treats determinig of success in invaded area. Radford & Cousens (2000) in their study of exotic and indigenous

Senecio species suggest that success of *Senecio* species is more contingent on physiological and morphological adaptations to current environment than generalised life history trait performance. Witkowski & Lamont (1997) compared two species – *Banksia goodii* and *B. gardneri* where former is rare and the latter is widespread, but both share similar characteristic. Mihulka & Pyšek (2001) and Burns (2004) studied invasiveness of species within families – *Oenotheraceae* and *Commelinaceae* respectively. Similarly Agrawal & Kotanen (2003) solved problems of leaf herbivory of native and non-native species, or Kolb & Albert, (2003) investegated effects of nitrogen and salinity on exotic plants growth.

.According to Grime (2002), most annuals are R-strategists. Their strategy to survive is early generative reproduction, high number of seeds, high growth rates and spreading many small seeds in space or time. That could be realised by long-distance dispersal or long-living seed bank. Such strategies facilitate invasive plants to occur in habitats unpredictable in space or in time. (van Breemen, 1984). Germination and establishment is a very risky period in plants life and short-living plants often envisage to it (van Breemen, 1984).

Presence of light to germinate is not always necessary (Mikulka & Chodová 1999) and some species prefer darkness (Pons 1992, Jensen 1995, Ku et al. 1996, Jursík et al., 2003). In case of crop weeds, establishing crop canopy and accompanying reduction of red and far-red ratio reduced germination of some weed species (Kruk et al., 2006)

Temperature also influences germination. Values required to break the primary dormancy vary among species and in the dependence of the origin and age of seeds (Jursík et al., 2003). Low temperatures cause the removal of inhibitory compounds in the seed e.g. abscisic acid, derivates of benzoic, jasmon, cinnamon acids, coumarin (Matsuo & Kubota 1993, Procházka et al 1998). This chilling process is termed stratification.

Seed dormancy exists to delay the germination until favourable conditions are present. Fact that seeds do not grow immediately enables the plants to survive. Primary dormancy is generated during the seed development and its length depends on various conditions such as mother plant genotype, degree of seeds maturity, content of chemical compounds, etc. (Martinková and Honěk 1995, 1997; Grime, 2002).

Plants, living or death contain substances, which either directly or indirectly (microbial or fungi transformation in soil) are able to influence growth of neighbour plants. However, some plants contain “secondary” chemicals that could inhibit, for their own benefit, plant growth (Grime, 2002).

Recently many researchers focused their interest on allelopathic effect of aliens. It has been proposed as alternative theory for the success of some invasive plants (Bais et al, 2003, Callaway & Aschehoug, 2000) Some invaders, when introduced into a new area succeed because their chemicals to the communities they invaded are new (Callaway & Aschehoug 2000, Bais et al., 2003, Callaway & Ridenour 2004, Callaway et al., 2004, Callaway et al. 2005). Studies of allelopathic effects of some invasive species to native flora were performed (especially for *Asteraceae* see Ridenour & Callaway, 2001 on *Centaurea maculosa,* Laterra & Bazzalo, 1999 on *Carduus acanthoides*)

Competitive ability is one of the plant traits that enables surviving in plant communities where sources are limited (Grime 2002). Success of introduced species is often explained by evolution of increased competitive ability (EICA) hypothesis (Blossey & Notzeld, 1995). Due to decrease of herbivore pressure, plants could allocate resources to vegetative growth or seed production. EICA hypothesis predicts that there is a selection favourizing genotypes with improved competitive abilities (Blossey & Notzeld, 1995).

2. THE AIMS OF THESIS

In my thesis, I tried to:

1. compare the germination between successful and unsuccessful species and
2. compare relative growth rate (RGR)
3. find, how did the different chilling temperatures affect seed germination and
4. if germination could be affected by watering with leachate from other species (allelopathy)
5. how the competition ability differ among studied species

3. MATERIAL AND METHODS

3.1 Studied species

3.1.1 The origin

Galinsoga ciliata Rafin. (syn. *Galinsoga quadriradiata* Ruiz & Pav., hairy galinsoga or shaggy soldier). The species is native to Central and South America and can be found at elevations of 40-3600m (Warwick & Sweet, 1983), but due to human activity has spread far from its original range to become "a cosmopolitan weed" (Gleason and Cronquist, 1991). It was recorded in the Czech Republic in 1901 for the first time (Pyšek et al., 2002). It has started spreading rapidly after the Second World War (Deyl, 1964).

Galinsoga parviflora Cav. (syn. *Galinsoga quinqueradianta* Ruiz. & Pav., small-flowered galinsoga or gallant soldier) is also native to South and Central America (Chile, Peru, Mexico), in elevations at 150-3270m (Warwick et Sweet, 1983). It was brought to our area with an expedition from Spain and has been planted in Prague botanical garden since 1823. In 1867 was recorded open air for the first time (Pyšek et al., 2002).

Today, both species are considered as invasive neophytes (Pyšek et al., 2003a).

Ageratum houstonianum Mill. (Mexican Ageratum, floss flower) comes from area of southern Mexico and Central America (Keil, 1975). In Europe it has been introduced and planted since seventeenth century as an ornamental flower. It spreads in the warm parts of the Old World (Keil, 1975).

These three species are annual herbs and they have very similar area of origin. Only *Galinsoga* species had spread out of it and invaded, in the early twenties century, North America, Europe and other continents. There, in the second half of twenties century it became a serious issue in a crop management (Warwick et Sweet, 1983). Though *Ageratum houstonianum* is close related to *Galinsoga*, and moreover it is often planted as an ornamental flower in gardens, parks and other public places so that it has a good chance to start a successful invasion, it has never been observed in our conditions spreading.

In two experiments (allelopathy, competition) other three species of family Asteraceae were used as phytometer:

*Conyza canadensis (*L.) Cronquist (= *Erigeron canadensis* L., horseweed) which was chosen as close relative and also invasive plant of the same habitats. It is native to whole North America and Central America, including Alaska, Hawaii and Caribbean Territories. Naturalization of this species in the Old World started in the middle of the seventeenth century, when it was reported from England (in 1640) and from France (in 1653) for the first time (Jäger, 1992; Šída, 2003).

Conyza bonariensis (L.) Cronq. (= *Erigeron bonariense* L., *Erigeron floribundus* Schultz-Bip.) Is native perhaps to South America (Wagner et al*.,* 1999). Presence in Europe has been recorded since eighteenth century (Prieur-Richard et al, 2000). This plant was introduced into the Czech Republic with cotton and occurred in areas of textile factories (Šída, 2003). But only occasional occurrence was observed (Jehlík, 1998, Pyšek et al., 2002).

Senecio vulgaris L. (Groundsel) is an indigenous species in the Czech Republic. It is native to Europe, central Asia, Siberia and North Africa. However, it has spread into the New world. In areas where it is distributed is considered as an important weed of some horticultural crops (Robinson et al., 2003).

3.1.2 Biology

Both *Galinsoga* species occur in disturbed habitats including flower beds, vegetable gardens, cultivated fields, roadsides, waste ground, and railway yards. They prefer damp, rich soil, but they are able to grow on various soil types.

They could flourish under favourable conditions within 2 or 3 weeks. One plant is capable of producing 300 000 achenes (Warwick et Sweet, 1983).

These species are not particularly susceptible to many herbicides used in vegetable crops. *Galinsoga* are not in favour because of harboring various insect pests of crops and transmission of some plant mosaic viruses (Warwick et Sweet, 1983).

Other three species - *Conyza canadensis*, *Conyza bonariensis* and *Senecio vulgaris* share similar ecophysiological traits as foregoing species, such as high fecundity, rapid wind dispersal, continuous germination under a wide range of growing conditions, rapid growth rate, ability to set seed several times per growing season and lack of chemical control options (Thebaud et al., 1996; Prieur-Richard, 2000; Robinson et al., 2003).

3.2 Seed collection

The seeds of *Galinsoga* were collected from two localities in the Czech republic – North Bohemia (Teplice: GPS: Loc: 50° 38' 14.24" N, 13° 49' 33.83" E) and South Bohemia (České Budějovice: GPS Loc: 48° 58' 28.09" N, 14° 28' 27.63" E) during the vegetation season. Seeds were collected from the similar type of habitats (town centre).

Seeds of *Conyza canadensis* and *Senecio vulgaris* were collected in town centre of České Budějovice.

Conyza bonariensis did not occur in Czech Republic, so the seed were collected on Crete - Plakias.

All seeds collections were stored in dark, in paper bags in room temperature.

Because of *Ageratum* does not escape in our conditions come seeds from two different commercially assortments – Seva Flora and Nohel Garden.

For the purposes of experiments seeds not older that one year were used.

3.3 Methods

3.3.1 Germination in different substrates and shading

This experiment was performed as the first to find in what kinds of substrate do the seeds grow best. Germination was tested in an experimental greenhouse of institute of Ecology and landscape in České Budějovice, during July and August 2004, in three soil types: sand, peat and the mixture of peat and sand in proportion 1:1 and in two light treatments – with and without shading. Shading was simulated with a green plastic film fixed at 15cm above the pots. Twenty seeds were sown into each pot (10 x 10 x 7cm) at the soil surface. There were five replicates per treatment.

Numbers of germinated seeds (seeds with visible cotyledons) were counted in regular intervals (5 days); the height of plant was measured at the termination of the experiment.

Repeated measure ANOVA was used to test the differences between germinating of each species in treatments. Two - way ANOVA was used to obtain the general effects of factors. To compare interactions between factors Tukey´s HSD test was used.

3.3.2 Relative growth rate

Relative growth rate was measured (adapted from Hunt et al., 1993); with use of fresh water) in a climate chamber with constant temperature 26°C and photoperiod 14:10 (light : dark).

The seedlings of each species were hardened off and then transplanted into pots (10 x 10 x 7cm) filled with sand - in each pot one seedling and watered sufficiently. There were five replicates per treatment.

After seven days, half of the seedlings were dried and weighted. After another fourteen days, the rest of seedlings was dried and weighted as well. Consequently, the RGR was worked out according to formula:

$RGR = (\ln m_{(21days)} – \ln m_{(7days)}) / 14$,

where m = weight of seedlings after 7 or 21 days.

Data were analysed with nested design ANOVA and with repeated measure ANOVA to obtain how the weight changes in time. To compare interactions between factors Tukey´s HSD test was used.

3.3.3 Germinability after chilling

Three temperatures regimes were tested: -21°C, +5°C and +21°C. Twenty seeds per each species and population were sown in Petri dishes filled with sand and stored at for 9, 6 and 3 weeks. Petri dishes with seeds were placed in a climate chamber and watered sufficiently (adapted from Jursík et al., 2003). There were five replications per treatment.

The dishes were checked every three days; germinated seedlings were counted and removed. The total number of germinated seeds was counted. A seed was considered as germinated when the cotyledons were visible. The experiment was carried out in February in the same climate chamber and conditions as the previous are, and was terminated after three weeks.

Other species used in further experiments (*Conyza bonariensis, Conyza canadensis, Senecio vulgaris*) were tested. To find if second generation of seeds of *Ageratum houstonianum* is able to germinate, seeds were collected in a culture (Teplice) and tested as well. Design of this experiment was identical to the previous one, but the seeds were in current treatment only for three weeks.

Data were analysed using nested design ANOVA. Interactions between factors were evaluated using Tukey´s HSD test.

For this experiment, the seeds of the last generation (collected in October/November 2005) were used.

3.3.4 Effect of allelopathy

In this experiment twenty achenes per Petri dishes were sown in a sand and watered with 5ml of a leachate from other studied species (adapted from Laterra & Bazzalo, 1999), themselves as well and fresh water (–that means ten types of leachate: two populations of *Galinsoga parviflora*, *G. ciliata* and *Ageratum houstonianum*, and one population of *Conyza bonariensis*, *Conyza canadensis*, *Senecio vulgaris* and fresh water). To prepare a leachate handful of seeds was put into a 0,5 l plastic bottle to soak for two days before the experiment started. There were three replications per treatment. The experiment was performed in March 2006 under climate chamber conditions. Dishes were checked after two or three days. The number of germinated seeds was counted and the seedlings (= seed with visible cotyledon) were removed. After a week, all dishes were watered again (with 2.5 ml of a leachate). The experiment terminated after three weeks, when total number of germinated seeds was counted.

Effect of allelopathy was analysed using factorial ANOVA. To compare allopathic effect of each leachate (in comparison with water) Dunnet´s test was used.

3.3.5 Competitive ability

Competition performance was measured as ability of growth suppression of a phytometer. Three species were used as a phytometer: *Conyza bonariensis*, *Conyza canadensis*, and *Senecio vulgaris.* The experimental design required planting one phytometer in the middle of each pot with three individuals (Goldberg 1987, 1990; Keddy et al, 1998). Experiment was carried out for ten weeks. Due to the difficulty in separating phytometer roots from neighbour species roots, only aboveground biomass of phytometers was used. The relative competitive performance of each ‘neighbour species’ was calculated as:

Cpi = [(PA - PT)/PA] * 100,

where PA was aboveground biomass of the phytometer when grown alone, and PT was above ground biomass of the phytometer when grown with neighbour species (Wilson & Keddy 1986a; Keddy 1989). PA and PT (n = 5) were expressed as the mean of the experimental replicates.

To evaluate relative competitive performance factorial ANOVA was used (biomass of phytometers was log-transformed). To compare interactions between factors Tukey´s HSD test was used.

4. RESULTS

4.1 Germination in different substrates and shading

The numbers of successfully germinated seedlings significantly differed among species, substrates and shading. In addition, the performance of individual species differed in time, and time influenced the effects of shading and substrate **(Table 1).**

Table 1 Summary statistics for repeated measure ANOVA analysing the differences in germination between *Ageratum houstonianum*, *G. ciliata* and *G. parviflora*.

effect:	SS	Degr. of Freedom	MS	F	p
Intercept	20060,5	1	20060,5	907,6	***
species	3489,6	2	1744,8	78,9	***
substrate	9762,4	2	4881,2	220,8	***
shadow	1083,9	1	1083,9	49	***
species * substrate	284,7	4	71,2	3,2	*
species * shadow	1008,9	2	504,5	22,8	***
substrate * shadow	599,7	2	299,9	13,6	***
species * substrate * shadow	1172,1	4	293	13,3	***
time	596,6	8	74,6	26,4	***
time * species	832,5	16	52	18,4	***
time * substrate	628,9	16	39,3	13,9	***
time * shadow	100,8	8	12,6	4,5	***
time * species * substrate	421,4	32	13,2	4,6	***
time * species * shadow	77,5	16	4,9	1,7	*
time * substrate * shadow	37,1	16	2,3	0,8	0,66
time * species * substrate * shadow	67,2	32	2,1	0,7	0,84
* p< 0.05, **p< 0.001, *** p< 0.00001					

Ageratum houstonianum germinated better than either *G. parviflora* or *G. ciliata* (Tukey's HSD: P< 0.0001), the germination was best in sand, followed by mixture and peat (Tukey's HSD: P< 0.01). Non-shaded seeds germinated better than shaded ones (Tukey's HSD: P< 0.0001).

The germination of *Ageratum* and *G*. *parviflora* did not differ between shaded and non-shaded treatments. *G*. *ciliata* was considerably more sensitive, it germinated worst of all species in shade (Tukey's HSD: all P= 0.001), but did not differ from G. *parviflora* when non-shaded.

Considering the interactions with time, *Ageratum* germinated faster than the other two species, but the fast outburst was followed by dying of seedlings at about 15-20day, whereas *G. parviflora* and *G. ciliata* germinated more gradually. Temporal effects of shading and soils were as follows.

Unshaded *G. ciliata* germinated better then *G. parviflora*, but almost not at all if shaded **(Figure 1)**. The subsequent mortality of ageratum was evident only in mixture and peat, but not in sand **(Figure 2)**.

Heights of the germinated plants differ between substrates. The highest were plants planted in sand (Tukey's HSD: P= 0.0001).

Figure 1 The differences in numbers of germinated seeds of *Ageratum houstonianum*, *G. ciliata* and *G. parviflora* in time.

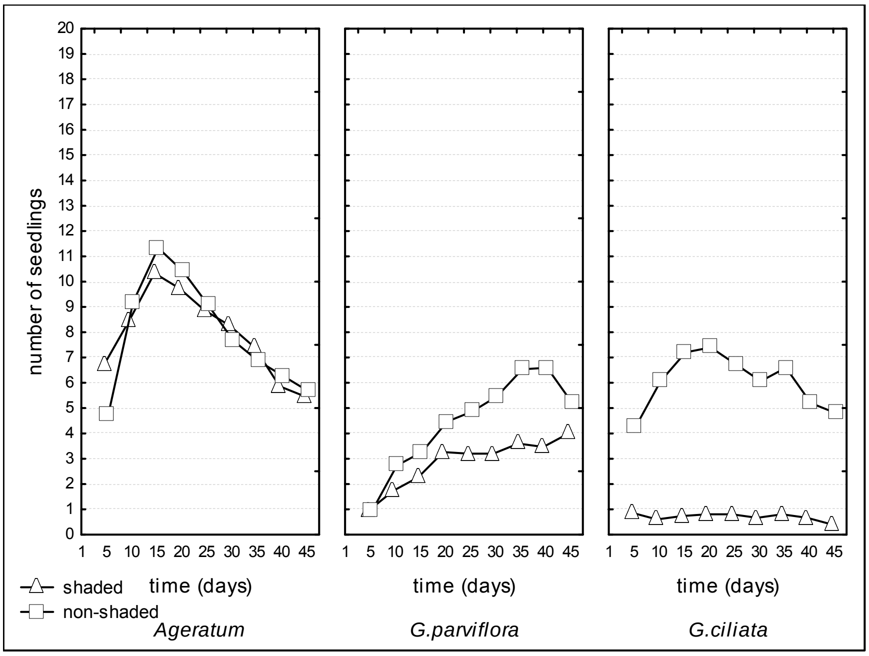
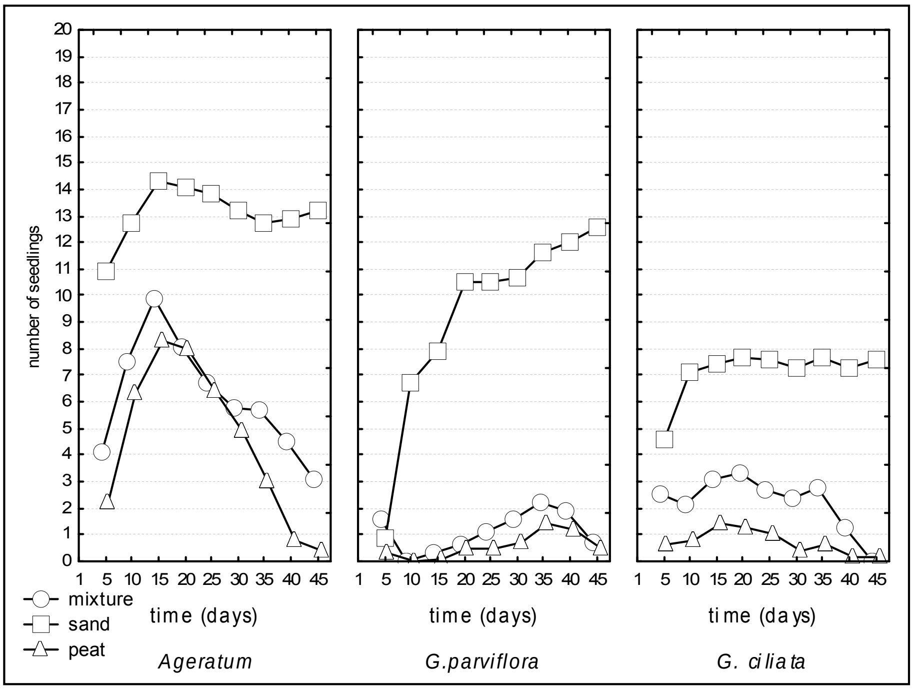


Figure 2 Numbers of germinated seedlings of *Ageratum houstonianum*, *Galinsoga ciliata*



and *G. parviflora* in time in three types of substrate.

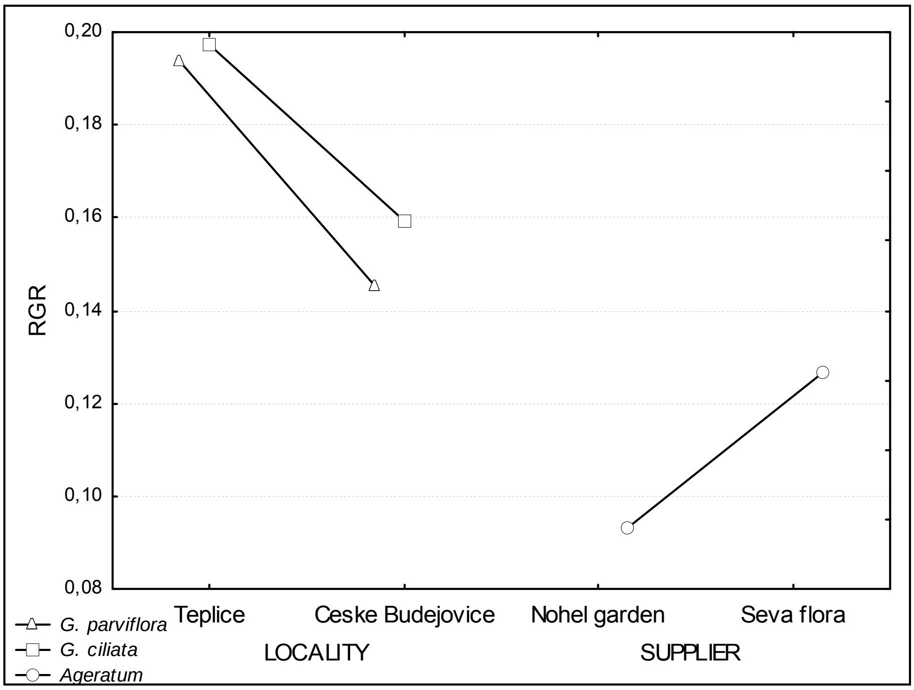
4.2 Relative growth rate

Relative growth rate differed between species and localities (**Table 2**). The two Galinsoga had higher RGR than Ageratum (Tukey's HSD: P< 0.0001), and both Galinsoga from North Bohemia (Teplice) had higher relative growth rate than species from the South Bohemia (České Budějovice) (Tukey's HSD: P< 0.001) (**Figure 3**).

Table 2: Summary statistics for nested design ANOVA (locality is nested within "species") analysing differences between RGR of *Ageratum houstonianum*, *G. ciliata* and *G. parviflora.*

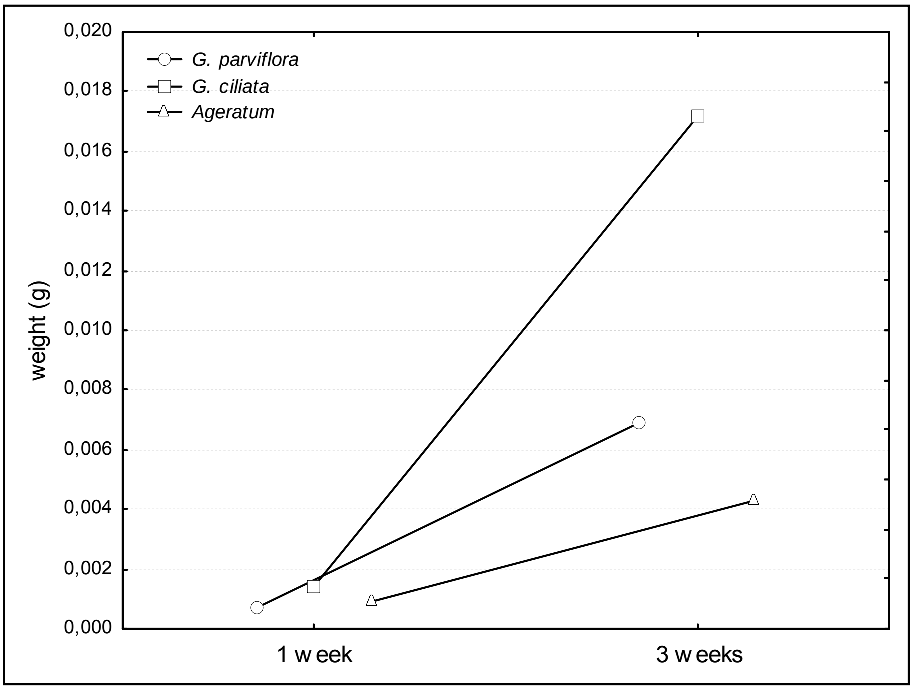
	SS	Degr. of Freedom	MS	F	p
Intercept	0,7	1	0,7	5940,7	***
species	0,0	2	0,0	117,1	***
locality(species)	0,0	3	0,0	34,8	***
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 3 Differences in RGR between two localities of *Galinsoga parviflora* and *ciliata* and two seed collections of Ageratum *houstonianum*.



Repeated measures ANOVA were used to test how does the plant weights differ during the three weeks of growth (**Figure 4**). It is obvious, that *Galinsoga* *ciliata* starts growth more rapidly that remaining *G. parviflora* and *Ageratum houstonianum*.

Figure 4 The comparison of weights of three species – *G. parviflora, G. ciliata and Ageratum* in two temporal periods. (F= 94,650, p= 0, 00000)



4.3 Germinability after chilling

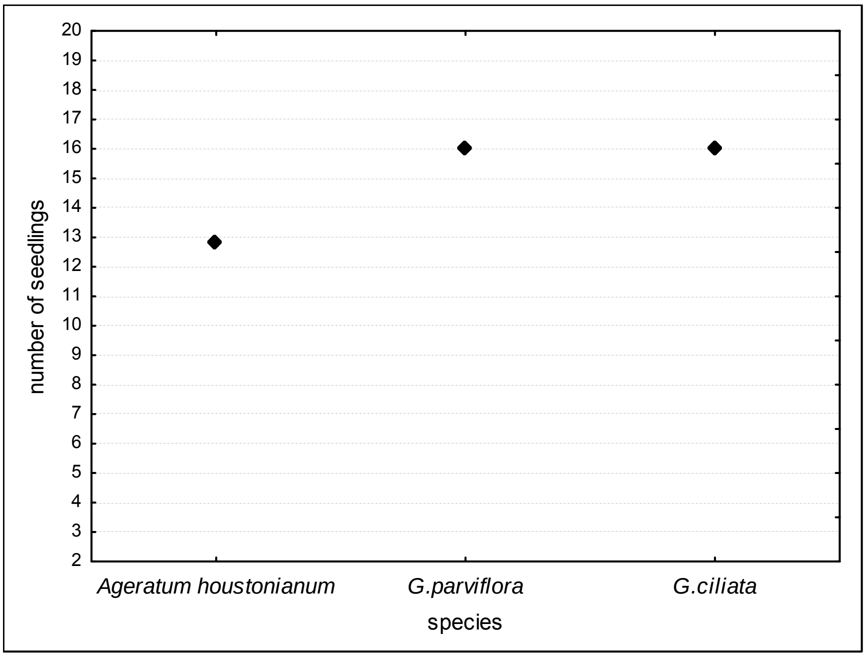
The numbers of successfully germinated seeds differ among species and the temperature when stored. Storage period did not have a significant effect (**Table 3**).

Ageratum germinated worse that both *Galinsoga ciliata* and *Galinsoga parviflora*, which did not differ (Tukey´s HSD: P= 0.00002) (**Figure 5**).

Table 3: Summary of all effects for factorial ANOVA, without the treatment „locality“ analyzing the effects of temperature when stored (= treatment) and storage period on germination of *Ageratum houstonianum, G. parviflora* and *G. ciliata.*

	SS	Degr. of Freedom	MS	F	p
Intercept	60121,6	1	60121,6	6671,3	***
species	614,5	2	307,2	34,1	***
treatment (= storage temperature)	70,8	2	35,4	3,9	*
time	7,2	2	3,6	0,4	0,67
species * treatment	53,8	4	13,5	1,5	0,21
species * time	58,3	4	14,6	1,6	0,17
treatment * time	19,6	4	4,9	0,5	0,7
species *treatment * time	111,2	8	13,9	1,5	0,14
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 5 Differences between germination of three species *Ageratum houstonianum, G. parviflora* and *G. ciliata.*



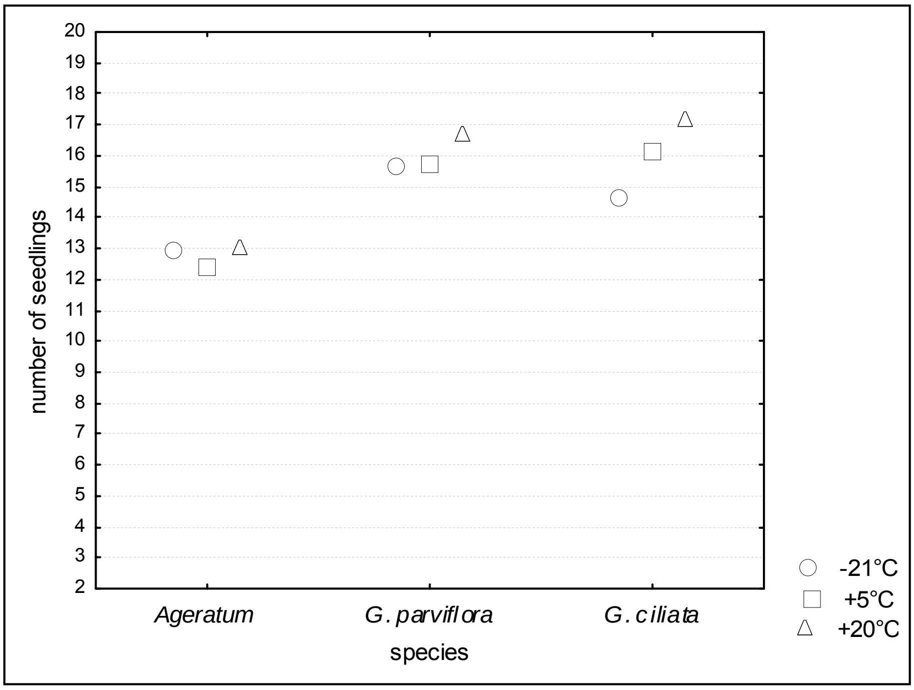
Seeds that were stored in normal room temperature (21°C) germinated best Tukey´s HSD: P= 0.02). Cold and freezing treatment did not significantly differ from each other (**Figure 6**)

Considering „locality“ as a random factor nested within “species” germination of *Galinsoga* species from České Budějovice and Teplice and also two assortments of *Ageratum* did not significantly differ between themselves (**Table 4**).

Table 4 Summary statistics for nested design ANOVA, with reference to locality analyzing the differences in germination of three species: *Ageratum houstonianum*, *G. parviflora* and *G. ciliata*

	Effect (F/R)	SS	Degr. of Freedom	MS	F	p
Intercept	Fixed	60121,6	1	60121,6	3183,53	***
species	Fixed	614,5	2	307,2	16,27	*
locality(species)	Random	56,7	3	18,9	2,07	0,11
treatment	Fixed	70,8	2	35,4	3,88	*
time	Fixed	7,2	2	3,6	0,40	0,67
* p< 0.05, **p< 0.001, *** p< 0.00001						

Figure 6 Difference between the number of germinated seedlings of *Ageratum houstonianum, G. parviflora* and *G. ciliata* in three storage temperatures (-21°C, +5°C, +21°C), (F=1,4931, p=0,20487)

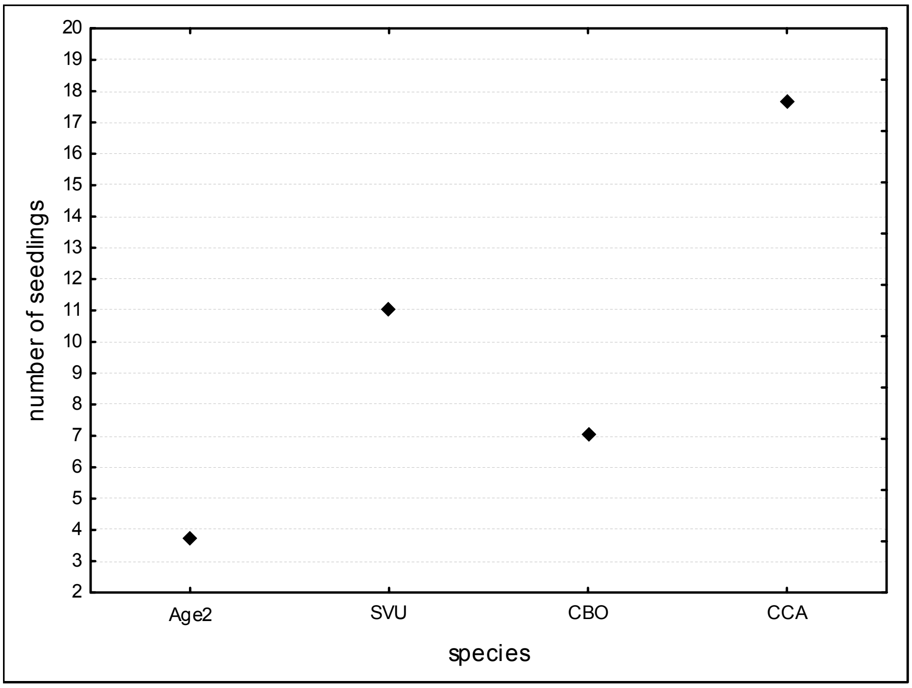


Additional test of germination of other four species (*Ageratum houstonianum, Senecio vulgaris, Conyza bonariensis and C. canadensis)* revealed differences between all species and treatments (**Table 5**). The differences, in descending order, were as follows: *Conyza canadensis* > *Senecio vulgaris* > *Conyza bonariensis* < *Ageratum houstonianum* respectively (Tukey's HSD: P< 0.012) (**Figure 7**).

Table 5 Factorial ANOVA test comparing differences in germination of species Ageratum houstonianum, Senecio vulgaris, Conyza bonariensis and C. canadensis.

	SS	Degr. of Freedom	MS	F	p
Intercept	5841,1	1	5841,067	740,1563	***
species	1613,7	3	537,911	68,1619	***
treatment	80	2	40,017	5,0707	*
species*treatment	138,4	6	23,061	2,9222	*
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 7 Differences between numbers of germinated seedlings of four species: *Ageratum houstonianum, Senecio vulgaris, Conyza bonariensis* and *Conyza canadensis.* (Symbols: Age2 = *Ageratum houstonianum* [second generation of seeds], SVU = *Senecio vulgaris*, CBO = *Conyza bonariensis*, CCA = *Conyza canaden*sis)



A comparison between successful and unsuccessful invaders in Czech Republic (after three weeks of experiment) shows that species significantly differ and chilling temperature did not have significant effect (**Table 6**, **Figure 8**).

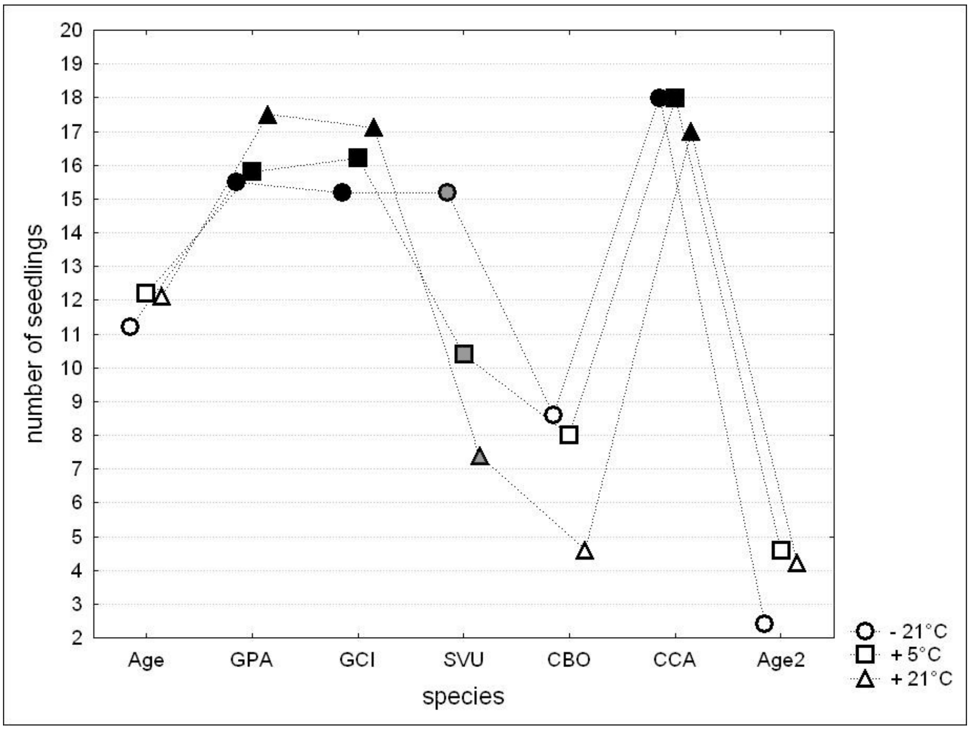
Germination of *Galinsoga* species and *Conyza canade*nsis did not differ one from another and significantly differ from the rest of the species (Tukey's HSD: P= 0.00003). Germination of *Senecio vulgaris* differ in various treatments, best germinated after storage in -21°C, worst in treatment without lower temperatures (Tukey´s HSD: P= 0.003).

Table 6 Summary of all effects for germination of species *Ageratum houstonianum* (commercially assortments and second generation), *Galinsoga parviflora*, *G. ciliata, Senecio vulgaris*, *Conyza bonariensis*, C*. canadensis* in three storage temperatures (-21°C, +5°C, +21°C).

	SS	Degr. of Freedom	MS	F	p
Intercept	19121,7	1	19121,7	2533,6	***
species	2858,6	6	476,4	63,1	***
treatment	20,4	2	10,2	1,4	0,26
species*treatment	263,8	12	22,0	2,9	**
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 8 Number of germinated seeds of six species in three storage temperatures. Spreading species are marked black, native grey, non-spreading white.

(Symbols: Age = *Ageratum houstonianum* (commercially assortments, Age2 = second generation), CPA = *Galinsoga parviflora*, GCI = *G. ciliata*, SVU = *Senecio vulgaris*, CBO = *Conyza bonariensis*, CCA = *C. canadensis*)

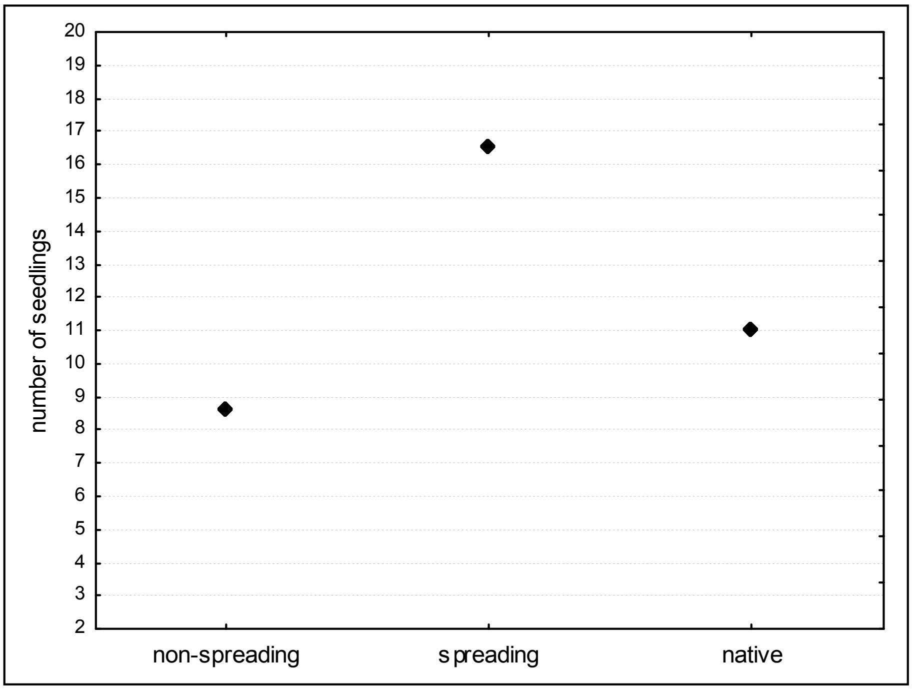


When dividing species according to their invasiveness into groups, “spreading species” (*Galinsoga ciliata, G. parviflora* and *Conyza canadensis*) germinated best (Tukey´s HSD: P= 0.0002), then “native” *Senecio vulgaris* and worst “non-spreading” *Conyza bonariensis* and *Ageratum houstonianum* (**Table 7, Figure 9**) but there is no significant effect between “native” and “non-spreading” group.

Table 7 One-way ANOVA analyzing differences between germination groups of species according to their invasiveness.

	SS	Degr. of Freedom	MS	F	p
Intercept	13499	1	13498,9	1007,8	***
species	2129	2	1064,5	79,5	***
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 9 Number of germinated seeds in groups varying in their invasive success ("spreading species" = *Galinsoga ciliata, G. parviflora* and *Conyza canadensis*), "non-spreading" = *Conyza bonariensis* and *Ageratum houstonianum,* "native" = *Senecio vulgaris*)



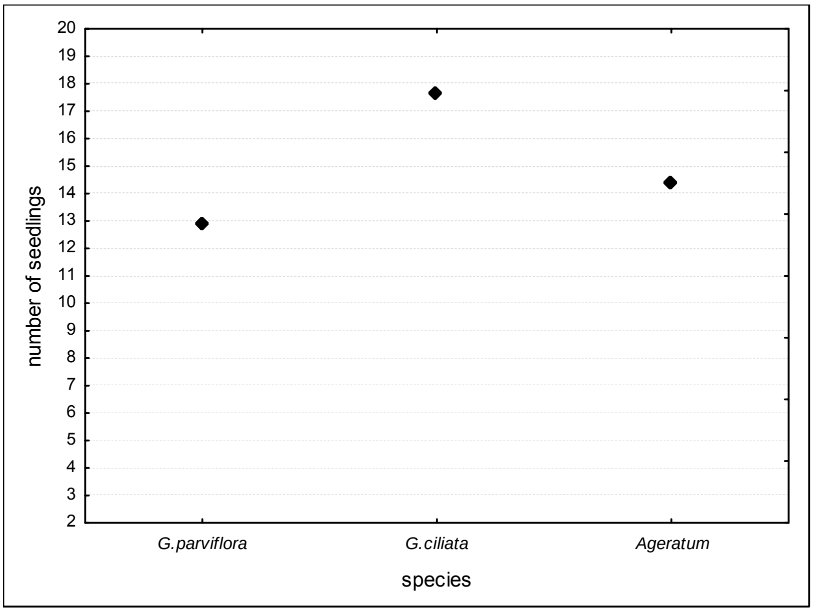
4.4 Effect of allelopathy

As shows, the numbers of successfully germinated seeds differed among species, but not between localities (**Table 8)**. Worst of all germinated *Galinsoga parviflora*, then *Ageratum* and on *G. ciliata* took watering with various leachates any effect (Tukey´s HSD: P< 0.01) (**Figure 10**).

Table 8 Summary statistics for nested design ANOVA analyzing the differences in germination in treatments with different leachates.

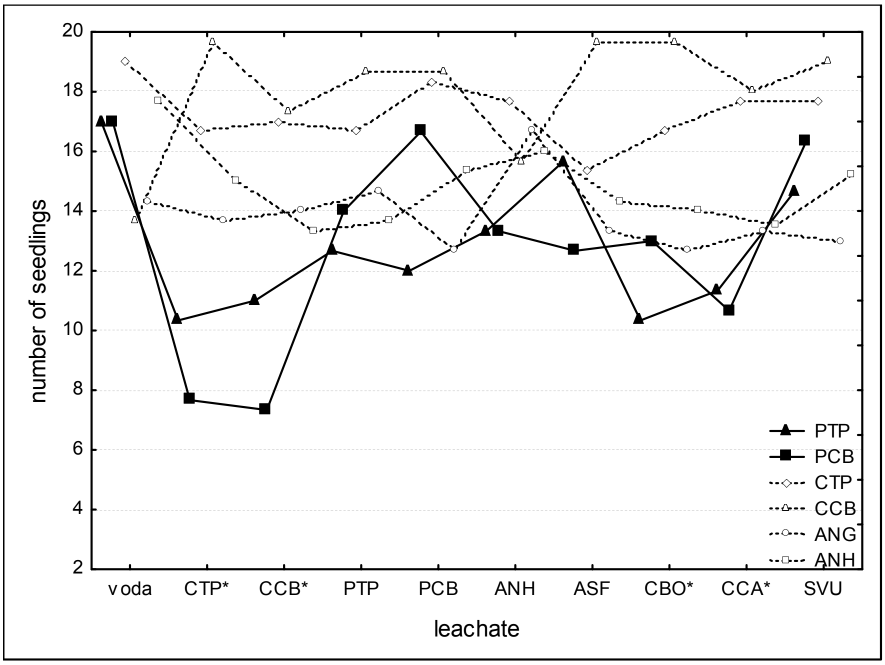
	Effect (F/R)	SS	Degr. of Freedom	MS	F	p
Intercept	Fixed	40120.5	1	40120.5	5415.7	***
species	Fixed	720.4	2	360.2	48.6	*
locality(species)	Random	22.2	3	7.4	1.0	0.43
leachate	Fixed	159.7	9	17.6	2.2	*
* p< 0.05, **p< 0.001, *** p< 0.00001						

Figure 10 Differences between the number of germinated seeds of *G. parviflora, G. ciliata* and *Ageratum* (F=51.673, p=0.0000)



Considering the allelopathic effect of a leachate none of all species was not influenced but *G. parviflora*. In comparison with water (as a control group) the influence of leachate from *G. ciliata* (both populations), *Conyza canadensis* and *Conyza bonariensis* was evident (Dunnett´s test P < 0.02). (**Figure 11**)

Figure 11 Comparison of amounts successfully germinated seeds of all species considering populations. Leachates marked with an asterisk had significantly influence on germination of both populations of *G. parviflora* (full markers) F = 1.7740, p = 0.00737) (Symbols: PTP = *Galinsoga parviflora*, Teplice; PCB = *G. parviflora*, České Budějovice; CTP = *G. ciliata*, Teplice; CCB = *G. ciliata*, České Budějovice, ANG = *Ageratum houstonianum*, supplier Nohel Garden; ASF = *Ageratum houstonianum*, supplier Seva Flora, CBO = *Conyza bonariensis*, CCA = *Conyza canadensis*, SVU = *Senecio vulgaris*)



4.5 Competitive ability

Studied species differ in ability to suppress growth of phytometers. Phytometers also differ among themselves (**Table 9**). The strongest competitor is *G. ciliata* (Tukey´s HSD: P= 0.002) that significantly differ from *G. parviflora* and *Ageratum houstonianum.* (**Figure 12**).

Lowest biomass of all phytometers had *Conyza bonariensis* (Tukey's HSD: P= 0.0001) Biomass of native phytometer (*Senecio vulgaris*) did not significantly differ from non-native successful phytometer (*Conyza canadensis*).

Table 9 Summary of all effects for biomass of phytometers (Senecio vulgaris, Conyza canadensis and Conyza bonariensis) planted with various competitors (Galinsoga parviflora, G. ciliata and Ageratum houstonianum)

	SS	Degr. of Freedom	MS	F	p
Intercept	558.1	1	558.1	5361.2	***
phytometer	6.9	2	4.0	32.9	***
competitor	3.0	6	0.6	5.6	***
phytometer*competitor	1.0	12	0.1	0.8	0.62
* p< 0.05, **p< 0.001, *** p< 0.00001					

Figure 12 Total biomass of phytometers planted with three species *Galinsoga parviflora, G. ciliata* and *Ageratum houstonianum.*

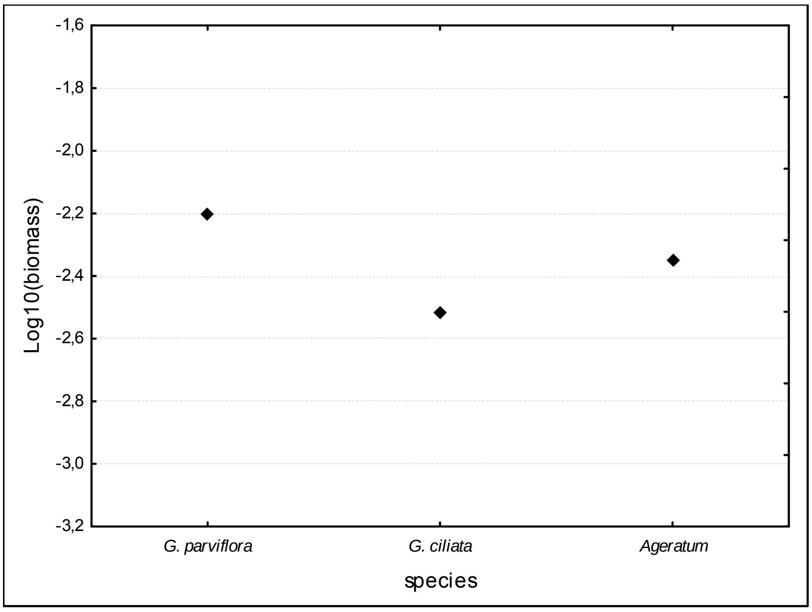
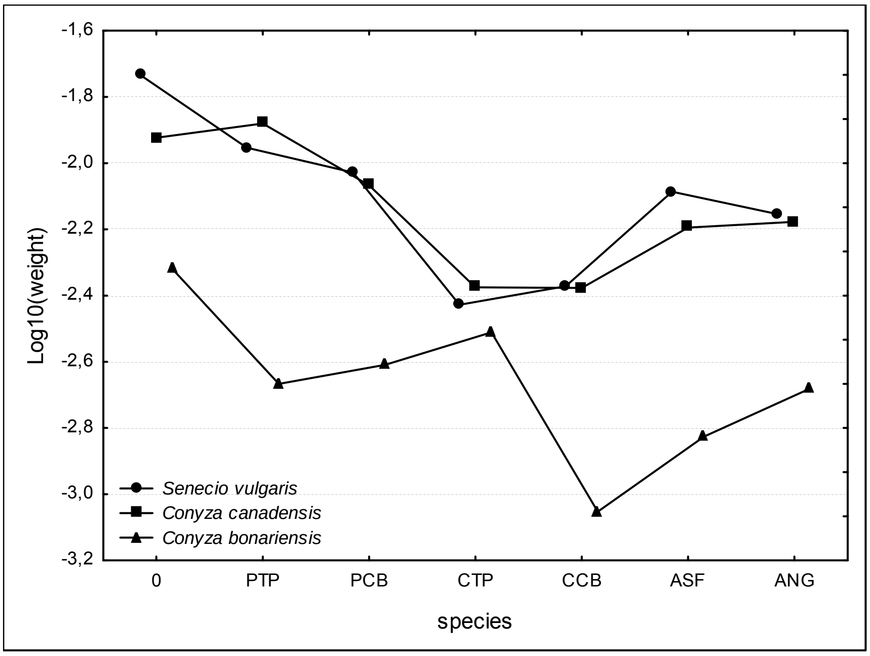


Table 10 The comparison of Relative competitive ability indexes (RCP) of studied species. Values were computed as means of single RCP for each phytometer.

species:	**RCP**
Galinsoga ciliata, České Budějovice	14,61774
Galinsoga ciliata, Teplice	8,873015
Ageratum, Seva Flora	5,28232
Ageratum, Nohel Garden	3,645892
Galinsoga parviflora, České Budějovice	2,047894
Galinsoga parviflora, Teplice	-0,44825

Figure 13 takes into account the influence of competitors from studied populations on biomass of three types of phytometer. *Conyza bonariensis* significantly differ (Tukey's HSD: P= 0.0001) from other phytometers.

Figure 13 The comparison of biomass of three phytometers in competition with *Galinsoga parviflora, G. ciliata* and *Ageratum houstonianum*.



5. DISCUSSION

5.1 Germination in different substrates and shading

The best substrate for germination was sand. In peat and even in a mixture, the seeds did not germinate at all. Only Ageratum was able to germinate in those treatments. The species did not differ in a number of germinated seeds, but in their "survival". In case of *Ageratum houstonianum* quickly germinated lot of seeds which died during next days. Only in sand was this decrease not so dramatical. The more gradual germination of *Galinsoga parviflora* and *G. ciliata* suggest that *Galinsoga* species cannot germinate in unfavourable conditions and "create "seed bank.

Need for light to germinate was evident in *G. ciliata*. It does not germinate at all when shaded. Jursík et al (2003) also observed low germination of *G. ciliata* in dark. On the other hand Havlová (2005) found the opposite using mixture of peat and sand. Simulated shading with green plastic film did not cause any differences in number of germinated seeds in other species studied. Kruk et al (2006) found, when comparing germination of various weeds in dependence of changing ratio of red : far red light, that germination of *G. parviflora* was inhibited at more lower values that other species.

Demand of light of *G. ciliata* to germinate could be why did not often grow together *G. parviflora* on similar microhabitats

Some authors reported unequal germinability of various types of *Galinsoga* achenes within species of family *Asteraceae* (Joley et al, 1997 for *Centaurea solstitialis*; Espinosa-García et al. 2003 for *Galinsoga parviflora*; Brandel 2004 for *Bidens odorata*). In this work, mixture of achenes was used, so the statistical analyses should not be influenced by such a dimorphism.

5.2 Relative growth rate

RGR of invasive *Galinsoga* species was much higher than in non-invasive *Ageratum*. Similary Burns (2004) found that invasive Commelinaceae congeners have generally higher RGR than non-invasive ones. Other studies focused on RGR of invasive and non-invasive congeners (Maillet & Lopez-Garcia, 2000; Grotkopp et al., 2002) denote higher RGR of invasive species. Differences between studied localities could be interpreted as differences in genotype of these populations. They could also reflect complex effect of local conditions such as climatic effects, altitude or precipitation. The sampling localities differ in altitude (Teplice 228m a.s.l, České Budějovice 381m a.s.l.) Average year temperatures are lower in Teplice (6.5°C) despite of its altitude. This town lies in the rain shadow of Ore Mountains and from across, there are Czech central mountains. Average year temperature in České Budějovice is higher, 8.2°C.

Almost three times higher weight of *Galinsoga ciliata* in three weeks could be indicative of successfulness of this species in non-shaded habitats contrasting the slower growth of *G. parviflora. G. parviflora* could profit in shaded habitats where *G. ciliata* does not germinate at all.

5.3 Germinability after chilling

All studied species are generally native to area of tropics, where the plants do not produce dormant seeds (Holm et al. 1977; Joshi et al. 1992; Sahoo 1998). To survive low winter temperatures of the temperate zone long primary dormancy was selected for (Jursík et al., 2003).

The number of successfully germinated seeds is greater in case of spreading species than in non-invasive. Considering all studied species, indigenous *Senecio vulgaris* and non-indigenous both *Galinsoga* and *Conyza canadensis* were able to resist cold and frost and germinated well, while *Ageratum* and *Conyza bonariensis* do not. That also may explain why *Conyza bonariensis* and also *Ageratum* are not spreading in mild zone.

Higher germination of *Galinsoga* after storage in low temperatures may be due the fact that they, in their native range, occur also in high altitudes (Warwick & Sweet, 1983) and Ageratum only in warmer areas (Keil, 1975). However, that do not rule in general – for example, *Amaranthus hybridus* native to tropical North, Central and South America is successfully spreading in temperate conditions. (Pyšek et al., 2002)

5.4 Effect of allelopathy

Because of fact, that studied species are all annual plants whose seeds remains buried in soil and created seed bank, we investigated allelopathic effects using seed extract. *Ageratum houstonianum* is known to cause toxic dermatitis or, in a worse case, haemorrhages in the large muscle tissues such as liver, kidney and heart and subsequent death in zebu cattle. (That do not match together with German name for *Ageratum* “Leberbalsam“.)(Noa et al., 2004) Until now, studies of biological effects of Galinsoga did not exist. Chemical compounds of remaining species considered here, or close relative species are well studied e.g. *Conyza canadensis* (Mukhtar et al, 2002; Lis et al, 2003), *C. albida* (Economou et al, 2002), *C. bonariensis* (Chaudhry et al, 2001; Kong et al., 2001), *Ageratum conyzoides* (Singh et al, 2003).

Galinsoga parviflora was most markedly inhibited by species occurring in its original habitat. This contradicts the theory of Calaway et al (2005), that allelopathic interactions should be more intense between native and non-native species. Allelopathic effect of *Conyza canadensis* and *C. bonariensis* is maybe due contained phytotoxins (Kong et al, 2001; Mukhtar et al., 2002; Lis et al 2003)

Economou et al, 2002 in their study of phytotoxicity on *Conyza albida* and Singh et al, 2003 in a study on *Ageratum conyzoides* concluded, leaves and inflorescence showed the highest phototoxic effect. On the other hand, Laterra & Bazzalo (1999) observed that seed leachate from *Carduus acanthoides* could inhibit germination of *Lotus corniculatus*.

5.5 Competitive performance

We have used seedlings competition, because phase of establishment is the most critical especially in case of annuals (van Breemen, 1984). Mature-plant competition could give different results.

Galinsoga ciliata behaves as an efficient competitor. Competition power of *G. parviflora* was the weakest. *Ageratum* performed intermedially and it is possible that could success in competition with other plants better that *G. parviflora*. But first the plant has to germinate, and in this respect *Ageratum houstonianum* (especially its second generation) in our experiments mostly failed. Responding phytometers on competition agree with their success in our conditions. Introduced *Conyza canadensis* and native *Senecio vulgaris* were not so inhibited as *Conyza bonariensis*. That correspond to EICA hypothesis (Blossey & Notzold, 1995) –

individuals of *G. ciliata* allocated resources in growth (Grime, 2002). In case of *Ageratum,* it could be due the cultivation.

6. CONCLUSION

Germination of alien species is influenced by soil type and light conditions. Studied taxons differ among each other in germination when shaded, *G. ciliata* did not germinate at all.

Number of germinated seeds is higher in non-spreading Ageratum, but it is followed by high mortality. Ageratum, though it is cultivated as ornamental plant, is able to produce seeds. That seeds could germinate, however, their germination is low.

Significant success-factor is probably higher relative growth rate in spreading species, than in *Ageratum*.

Species response to chilling was negatively affected. Nevertheless, *G. parviflora* and *G. ciliata* germinated still better than *Ageratum houstonianum*. Low temperatures did not prosper to *Galinsoga* species, but they could fairly survive it.

Response to low temperatures of other species was not evidential. Nevertheless, in comparison of total number of germinated seeds between spreading (*Galinsoga ciliata, G. parviflora* and *Conyza canadensis*), non-spreading (*Conyza bonariensis* and *Ageratum houstonianum*) and native species (*Senecio vulgaris*), top-level reach the spreading one.

Lower viability due the allelochemicals was observed only in *Galinsoga parviflora*. It is interesting, that its germination and growth was inhibited i.a. just with an extract from seeds of *Galinsoga ciliata.* That could advert to low co-occurrence of that species together.

Success of *G. ciliata* is supported with his competitive ability. *Conyza canadensis* and *Senecio vulgaris* respond similarly when in competition, that could point at long co-occurrence.

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