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Article

The influence of *Heracleum sosnowskyi* Manden invasion on functional traits of *Corydalis nobilis* (L.) Pers (by the example of the MBG RAS collection of living plants)

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Abstract. In recent years, invasions of aggressive alien species, such as a giant hogweed, have attracted the attention of many botanists. However, the response of individual plants to the presence of invaders has not been studied for most representatives of the cultivated and natural floras. The article presents the results of studying functional traits of the spring ephemeroid *Corydalis nobilis* when *Heracleum sosnowskyi* is introduced into experimental plots. Sharing a common locality with *H. sosnowskyi* causes a decrease in organic reserves of *C. nobilis* phytomass and reduced contribution of its leaves to the total mass of the aboveground parts of plants. We have revealed changes in the pigment complex of *C. nobilis* leaves, manifested as an increased content of the total chlorophyll in the beginning of the growing season. In the studied habitats, *C. nobilis* exhibits a competitive-ruderal life strategy. In general, *H. sosnowskyi* has an extremely adverse effect on *C. nobilis* and vitality of the latter.

Keywords: ephemeroids, invasive species, specific leaf surface, chlorophyll, biomass allocation, ecological-coenotic strategies

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Научная статья**Влияние инвазии *Heracleum sosnowskyi* Manden. на функциональные признаки *Corydalis nobilis* (L.) Pers (на примере коллекции живых растений ГБС РАН)**А.В. Стогова* , О.Е.Воронина , М.А. Зуева 
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Аннотация. Инвазии агрессивных чужеродных видов, таких как гигантские борщевики, в последние годы привлекают внимание многих ботаников. При этом реакция отдельных растений на присутствие инвайдеров для большинства представителей культурной и природной флоры не изучена. В работе приведены результаты исследований функциональных признаков весеннего эфемероида *Corydalis nobilis* при внедрении на опытные участки *Heracleum sosnowskyi*. Произрастание в общем локалитете с *H. sosnowskyi* приводит к снижению запасов органического вещества в фитомассе *C. nobilis* и уменьшению вклада листьев в общую массу надземной части растений. Выявлены изменения в пигментном комплексе листьев *C. nobilis*, проявляющиеся в увеличенном содержании суммы хлорофиллов вначале вегетационного периода. В изученных местообитаниях *C. nobilis* проявляет конкурентно-рудеральную жизненную стратегию. В целом *H. sosnowskyi* оказывает крайне неблагоприятное воздействие на *C. nobilis*, и жизненность особей этого вида сильно снижается.

Ключевые слова: эфемероиды, инвазионные виды, удельная листовая поверхность, хлорофилл, аллокация биомассы, эколого-ценотические стратегии

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Introduction

The introduction of aggressive invasive species significantly affects biodiversity and alters the composition and structure of phytocenoses. In Russia and abroad, the reasons why a particular species becomes invasive are widely discussed in scientific circles. It is extremely difficult to predict and control the expansion of such species. The rapid spread and high degree of adaptation allow invasive species to capture vast territories and cause irreparable economic damage and environmental disasters.

Giant hogweed *Heracleum sosnowskyi* Manden. (Umbelliferae) is one of the most dangerous and aggressive invasive species in the European part of Russia (Ozerova and Krivosheina, 2018; Ozerova et al., 2017; Vinogradova et al., 2010). Its natural range covers the North Caucasus, Azerbaijan, Armenia, Georgia and Turkey (Jahodová et al., 2007; Pimenov and Ostroumova, 2012). In Russia, this species was first introduced into cultivation in the Polar-Alpine Botanical Garden (1947) as a promising silage plant (Tkachenko, 2014). In the 1980s, this culture was recognized as invasive, but the control over its spread was insufficient (Antipina et al., 2017). Because of the downturn of the agro-industrial complex, *H. sosnowskyi* managed to naturalize and significantly broaden its secondary range.

As soon as introduced into plant communities, *H. sosnowskyi* becomes dominant. Similar to the closely related invasive species *Heracleum mantegazzianum* Sommier et Levier, it often forms the monodominant communities in the secondary range (Dalke et al., 2015; Vinogradova et al., 2010). Invasion of *H. sosnowskyi* into phytocenoses poses a serious threat to the native flora and deteriorates biodiversity of vascular plants (Tiunov and Efimik, 2020).

To combat a giant hogweed, various physical, chemical and biological methods are applied (Vinogradova and Kuklina, 2012). For example, in Latvia, to reduce the number of *H. sosnowskyi* sprouts, seeds of other native species were sown (Ravn et al., 2007). However, the invader suppression lasted for a year, and then its growing continued.

The problem of selecting plants to prevent the expansion of *H. sosnowskyi* remains unsolved. Hence, further search for species of the natural and cultivated floras able to compete with this aggressive invader and stop its spread is urgent. The species composition of phytocenoses dominated by *H. sosnowskyi* is extremely scarce. Moreover, the ecological and biological characteristics of species preserved in the community after *H. sosnowskyi* introduction, or possibly increased in number, remain poorly studied.

The introduction of a new species into a phytocenosis is an important biotic factor, which can have a strong impact on the plant community and its components. The influence of one plant species on another is a complex process, consisting of direct and indirect effects through changes in the environment and consort relationships in biocenosis. *H. sosnowskyi* is a transforming species, which enables to change the environment greatly (Panasenko, 2013; Richardson et al., 2000). *H. sosnowskyi* largely shades shorter species because of its large size and early start of the growing season. In addition, it can alter the edaphic conditions in biocenosis due to its allelopathic effect (Kondratiev et al., 2015; Mishyna et al., 2017) and the ability to quickly absorb environmental resources (Betekhtina et al., 2018; Veselkin et al., 2017). Since it is often difficult to assess the role of the specific mechanisms of influence in situ, we consider invasion of *H. sosnowskyi* as a complex environmental factor.

The response of individual plants to changes in environmental conditions is reflected by functional traits. These are the measurable plant's morphological, physiological and phenological characteristics affecting its adaptability (Cornelissen et al., 2003; Kattge et al., 2011; Violle et al., 2007). The study of functional traits and their intraspecific variability is important when assessing the prospects for interspecific competition, especially in the communities with low diversity (Kraft et al., 2014). However, most publications discuss the dependence of functional traits on the influence of abiotic factors. Note that the study of the relationships between functional traits and invasions have started quite recently.

Changes of life strategy in plants (by the J. Grime classification) caused by invader introductions have not been studied yet. Currently, a method for estimating the share of competitive, ruderal and stress-tolerant strategies based on the set of easily measurable parameters of a specific plant has been developed (Pierce et al., 2017). It allows to study the intraspecific variability of life strategies in plants (Astuti et al., 2019; Popova et al. 2019).

The aim of this work was to evaluate the effect of *H. sosnowskyi* on the functional traits and life strategy in *Corydalis nobilis* (L.) Pers. (Papaveraceae). The tasks included a comparative analysis of the control specimens and those exposed to *H. sosnowskyi* based on the main indicators of plant development: biomass and its allocation to various plant organs, leaf plate area, leaf mass, specific leaf surface, the content of photosynthetic pigments (Chl_(a+b)) in leaves, life strategy in plants according to the J. Grime concept.

Materials and methods

The research was carried out on the territory of the Main Botanical Garden named after N.V. Tsitsin RAS. The object of the study was the noble corydalis *Corydalis nobilis* (Papaveraceae), cultivated in the “Flora of Siberia” exposition of the Laboratory of Natural Flora of the MBG RAS (N 55.841288 E 37.617351) for more than 60 years where the invasive species *H. sosnowskyi* was introduced in 2013.

The competitive advantage of *H. sosnowskyi* is mainly due to its phenology characterized by 7–10 days advance in the seasonal development of native species, primarily large-leaved nitrophilous plants (Panasenko, 2017). Sharing the same habitat, both species *Corydalis nobilis* and *H. sosnowskyi* start to grow in early spring, unfolding their leaves immediately after early April snowmelt. They have similar morphometric parameters at the beginning of the seasonal growing cycle. By June, shoot height reach 60 cm. Later, the growth of *C. nobilis* ceases, whereas shoots of *H. sosnowskyi* continue to lengthen. In early May, the projective cover of *H. sosnowskyi* and *C. nobilis* on the experimental site accounts for 10–25% and 15–20%, respectively (Stogova et al., 2019).

C. nobilis – the spring ephemeroïd, large-leaved nitrophile growing in nature and distributed in the forest belt of Altai and in the mountains of China. With age, this rhizomatous perennial forms a rosette with numerous leaves of 50–60 cm high with powerful generative shoots. The beginning of the growing season of *C. nobilis* in the MBG territory occurs at the end of March – beginning of April. Flowering begins at the end of April – beginning of May, and seed dispersal – in the first decade of May. The period of autumn extinction starts in the first ten days of June. By mid June, the growing season ends.

Outside its natural range, *C. nobilis* develops mainly in cultivation. In Europe, this species is widely used in landscaping. In some places, it has been naturalized (Brandes, 2013; Mayorov et al., 2013). Among wilding plants of the Moscow botanical gardens, *C. nobilis* is considered as a potentially invasive species (Mayorov et al., 2013). In the State Botanical Garden RAS, it appeared in 1957 due to seeds obtained from the Altai Botanical Garden (Ridder, Kazakhstan). Nowadays, *C. nobilis* represents a stable population that produces abundant self-seeding and actively spreads to the “Flora of Siberia” open-ground plant exhibitions.

To study the effect of *H. sosnowskyi* on *C. nobilis* growth and development, the specimens of the latter located at a distance 1–1.5 m were selected. As the control, we used plants collected at a distance of 30–40 m from the sinusium of *H. sosnowskyi*. A total of 10 experimental and control specimens were collected. Our investigations were conducted during the growing seasons of 2019–2021.

To study the biomass allocation, five phytomass components were identified (Poorter and Nagel, 2000). The plants were dug up in the first decade of May 2020. Each specimen was divided by components: underground organs, basal leaves, stem leaves, stems and inflorescences. First, the specimens were dried in air, then immediately before weighing they were placed in an oven at a temperature of 90 °C for 24 hours. Weight was estimated to an accuracy of 0.01 g using the OHAUS Adventurer balance.

Leaf samples were collected in the first decade of June 2019, 2021. A leaf area of *C. nobilis* was measured at full turgor based on traditional methods using photography (Perez-Harguindeguy et al., 2016). Photographs were analyzed by means of EasyLeafArea (Easlon and Bloom, 2014). Specimens for measuring the chlorophyll content were taken five times in five repetitions during an active vegetation of the growing season (2020). The total chlorophyll was estimated by the spectrophotometric method using a SPEKOL 11 spectrophotometer (Carl Zeiss Jena, Germany DR). The optical density of the alcohol plant extract was measured at wavelengths of 617.8, 648.6 and 664.2 nm (Lichtenthaler, 1987).

Life strategies and complex indicators (specific leaf surface area, water content in leaves) were determined with the use of the StrateFy method developed by S. Pierce et al. (2017).

For statistical data processing, we applied PAST 4.03 and Microsoft Excel 2016 programs, as well as the statistical environment R. The normality of the data distribution was defined based on the Shapiro–Wilk test and the significance of differences between the averages of the measured parameters – by the Student’s t-test. Calculations were made at a given significance level of $p < 0.01$ for $\text{Chl}_{(a+b)}$, in other cases at $p \leq 0.05$ (Lakin, 1990). Tables and figures present the arithmetic means and their standard errors.

Results

Mass of a single plant of *C. nobilis* influenced by *H. sosnowskyi* showed three times drop, as compared to the control ($p < 0.01$) (Fig. 1). Mass of each phytomass component also decreased significantly (Table 1). The greatest reduction in biomass (compared to control) was noted in the aboveground parts of plants (3.3 times).

With a decline in the total plant mass, the change in the ratio between the above- and underground parts was negligible. No significant differences were detected between the specimens from sites with and free from *H. sosnowskyi* ($p > 0.05$) (Fig. 2A). In the aboveground biomass of *C. nobilis*, influenced by *H. sosnowskyi*, the proportion of assimilating organs (mainly basal leaves) increased ($p < 0.05$) (Fig. 2B).

Wet weight and leaf area of the experimental plants were lower than in the control ones, whereas dry weight - higher (Fig. 3, Table 2). Because of the *H. sosnowskyi* impact, the specific leaf surface area (SLSA) decreased and dry weight of a plant increased. The difference between the options was not statistically confirmed ($p > 0.05$). We did not establish any correlation between the leaf area and SLA.

Analysis of the content and accumulation dynamics of the amount of chlorophyll *a* and *b* during the growing season revealed significant differences between the control specimens and *C. nobilis* sharing the same habitat with *H. sosnowskyi* ($p < 0.01$) (Fig. 4). The maximum content of $\text{Chl}_{(a+b)}$ in the control specimens was recorded in April 30 – May 10; for those growing in unfavorable conditions (poor illumination under the canopy of *H. sosnowskyi*), this period started 6 days later (May 6–16). It should be noted that at the beginning of the growing season, the content of photosynthetic pigments in control plants was lower; a peak accumulation corresponded to phenological phases of flowering and fruiting.

The data obtained suggest that *C. nobilis* has the pronounced characteristics of a competitor, i.e. storing underground organs, large size and rapid growth (Fig. 5). The ruderal component is characteristic of all spring ephemerals. This is because unfolding of tree leaves results in severe shading of plants that affects their growth and development. Statistical processing of the obtained data demonstrates a low reliability of the results ($p > 0.05$).

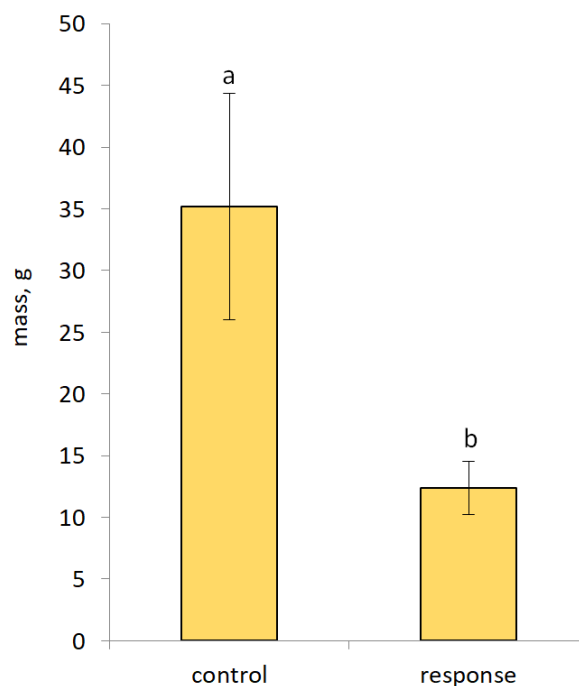


Fig. 1. Mass of a plant *C. nobilis*. Here and further, significant difference is indicated by different letters.

Table 1. Mass of individual organs of *C. nobilis*, g.

Variant	Phytomass component				
	Belowground	Rosette leaves	Cauline leaves	Stems	Inflorescences
Control	12.4 ± 2.3	8.5 ± 2.1	4.2 ± 1.5	7.3 ± 2.6	2.8 ± 0.9
Response	5.4 ± 1	3.7 ± 0.6	0.9 ± 0.3	1.7 ± 0.4	0.6 ± 0.1
<i>p</i> -value	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05

Table 2. Functional traits of *C. nobilis* leaf.

Variant	Leaf fresh weight, mg	Leaf dry weight, mg	Specific Leaf Area, mm ² /mg
Control	1455 ± 247	136 ± 29	281 ± 23
Response	1395 ± 111	146 ± 13	236 ± 15
<i>p</i> -value	0.49	0.17	0.16

Discussion

A decrease in plant phytomass is the most obvious consequence of suppression of the native flora by invasive species. Other researchers report about this trend as well. For instance, a change in biomass and its allocation in the local species *Vaccinium vitis-idaea* L. and *V. myrtillus* L. occurs with introduction of alien *Quercus rubra* L. (Woziwoda et al., 2019, 2021).

We have not revealed any reliable alterations in the ratio of under- and aboveground biomass. The increase in the mass fraction of basal leaves in the aboveground biomass may be related with *C. nobilis* shading induced by the *H. sosnowskyi* canopy. A similar response to insufficient light was observed for *Impatiens parviflora* DC. In a shaded spruce forest, 77.8% of its dry biomass is concentrated in leaves; a larger proportion of phytomass falls on stems and roots under more illuminated and drier conditions (Markov et al., 1997). It is worth noting that our results are not consistent with the data of other researchers who inform about augmentation of the mass fraction of stems under strengthening competition through reaching the increased plant density (Poorter et al., 2012; Postma et al., 2021) or the introduction of alien species (Woziwoda et al., 2019, 2021). Perhaps, the reason is that *C. nobilis* has a semi-rosette form, and its stem does not play a significant role in competition for light, but rather serves as a peduncle. Stem leaves are relatively small, and under the influence of *H. sosnowskyi* their share in the mass of assimilating organs declines. On the other hand, an increase in the mass fraction of basal leaves may be associated with resource distribution between vegetative growth and seed reproduction since under unfavorable conditions the generative sphere suffers first. Similar results are shown for *Impatiens noli-tangere* L. For instance, when shaded, the reproductive efforts are reduced, seed reproduction is suppressed, and a plant can enter a vegetative state (Markov et al., 1997). In this aspect, the role of interspecific competition has not been properly studied, but it is obvious that with the increase in density of single-species plantings, the mass fraction of reproductive organs decreases (Postma et al., 2021).

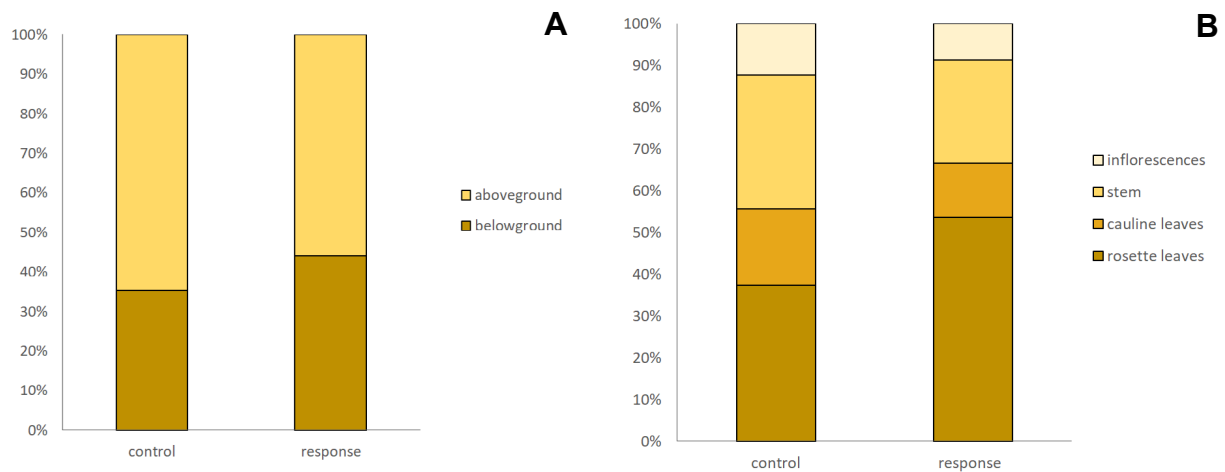


Fig. 2. Allocation of *C. nobilis* biomass. **A** – ratio of the mass of under- and aboveground organs; **B** – distribution of biomass of aboveground organs.

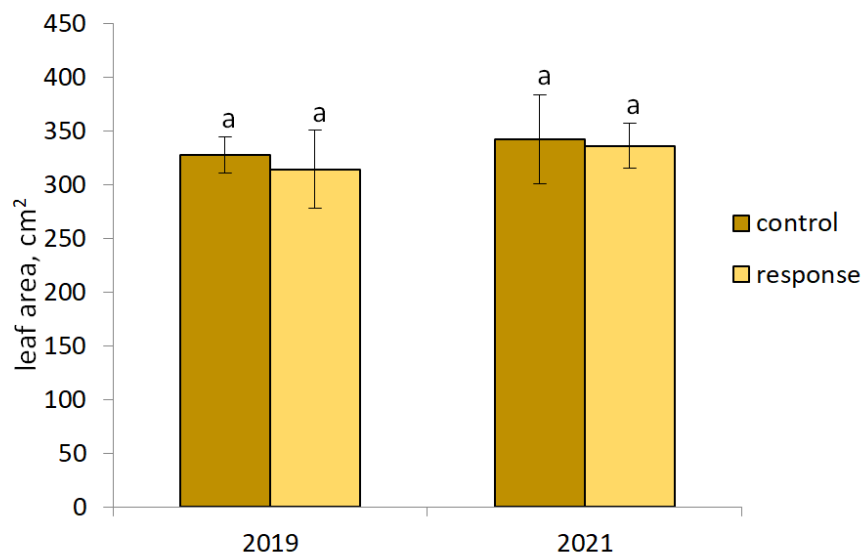


Fig. 3. Leaf area of *C. nobilis*.

Compared to the control specimens, plants growing together with *H. sosnowskyi* had an increased content of the total chlorophyll at the beginning of the growing season and a decreased one during the flowering period. It is known that under short-term shading the amount of chlorophyll rises, while at a long lasting one it drops (Bell and Danneberger, 1999). Other experiments show that chlorophyll concentrations increase in response to low levels of stress and decrease at high stress (Agathokleous et al., 2020). It can be concluded that at the beginning of the growing season, *H. sosnowskyi* does not have a very strong effect on *C. nobilis*. Perhaps a little shading leads to chlorophyll increase. As *H. sosnowskyi* grows, its impact intensifies, and the level of chlorophyll in plants of the same locality becomes lower than in the control ones. The only peak in $\text{Chl}_{(a+b)}$ accumulation at the end of the growing season is, apparently, associated with the formation of viable seed progeny and plant preparation for the next growing season. Thus, our findings are indicative of the depressed state of plants growing in the close proximity to *H. sosnowskyi*.

It is hardly possible to make valid conclusions about ecological-centotic strategies in *C. nobilis* because of insufficiency of the obtained results. Meanwhile, we can assume that deterioration of edaphic

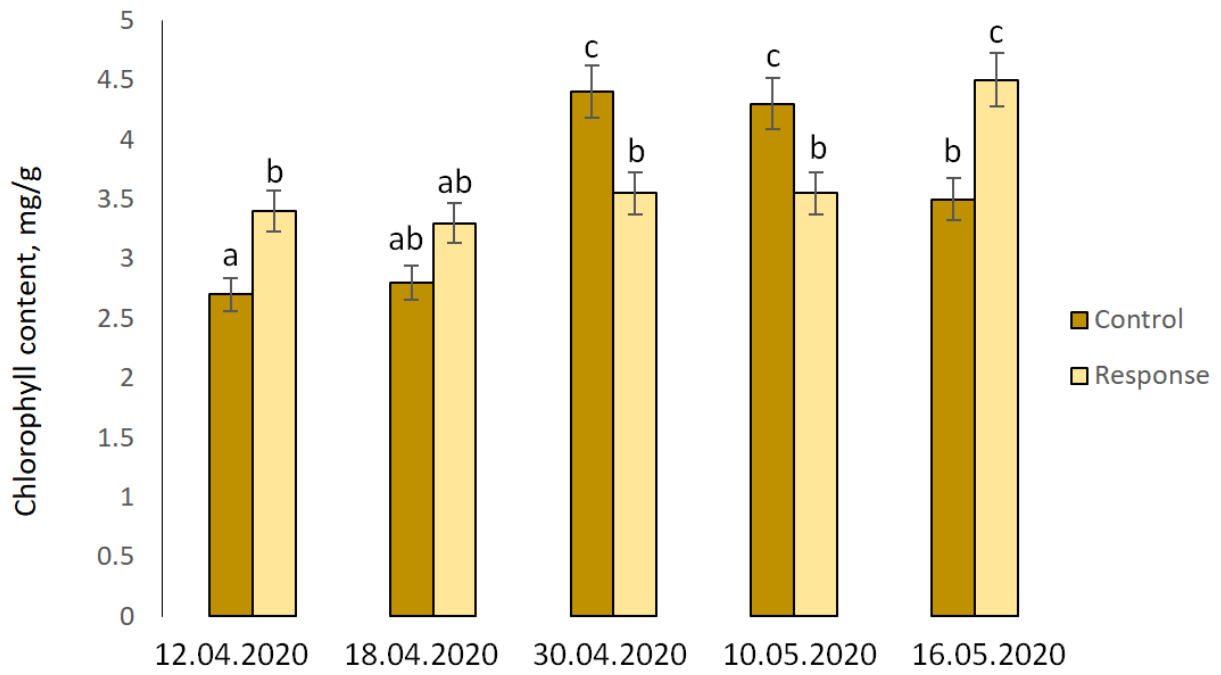


Fig. 4. $Chl_{(a+b)}$ content in leaves of *C. nobilis* collected during the active growth period.

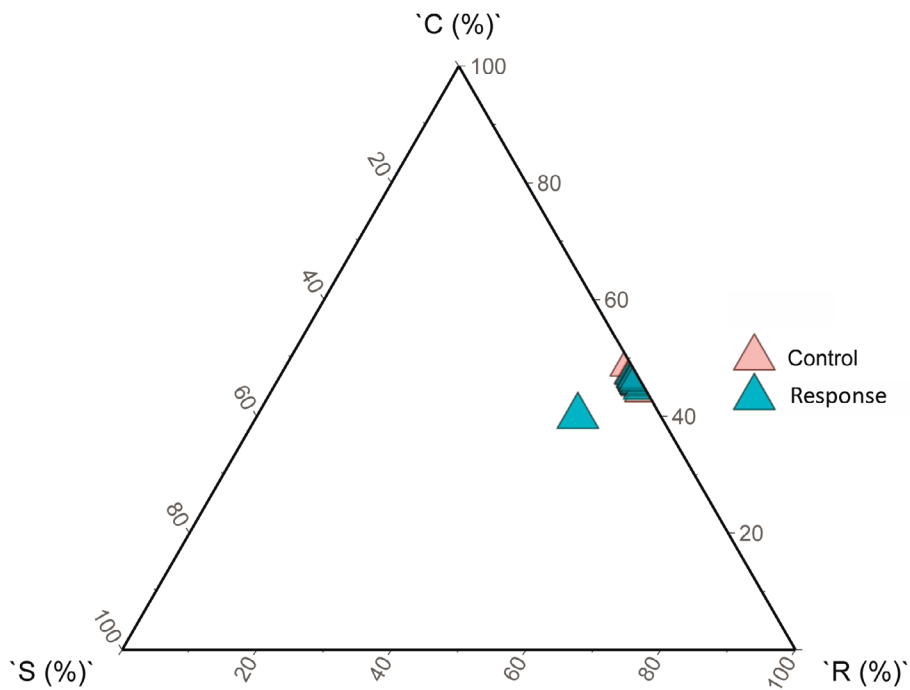


Fig. 5. Life strategy of *C. nobilis* according to the Grime concept: C – competitor, S – stress-tolerant, R – ruderal.

conditions caused by the influence of *H. sosnowskyi* is a stress factor able to shift the parameters of *C. nobilis* life strategy towards stress tolerance. To confirm this hypothesis, a larger sampling and further comprehensive research are required.

Conclusion

The main indicator of a plant vitality in one ontogenetic phase is biomass. Therefore, its 3 times drop in *C. nobilis* (influenced by *H. sosnowskyi*) points to a depressed state of the plant. Another important indicator is reproduction. Vegetative propagation is not typical for *C. nobilis*. Hence, the low mass fraction of generative organs in plants neighboring with *H. sosnowskyi* is evidence for the negative influence of the latter. The chlorophyll dynamics in the specimens is indicative of the stressful effect of the invader on *C. nobilis*. Among its leading negative factors is a reduced illumination under the canopy formed by monodominant thickets of *H. sosnowskyi*.

The revealed changes in morphological and physiological parameters of *C. nobilis* show its reduced viability. Based on the obtained data, one can expect the replacement of *C. nobilis* by *H. sosnowskyi* in the coming years.

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