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ORIGINAL RESEARCH PAPER

Influence of environmental conditions and crop competition on morphological and biological diversity of *Avena fatua* L. and *Solanum nigrum* L.

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Abstract
This study investigated the effects of climate/soil conditions and crop competition on selected morphological traits, biomass productivity and some other biological aspects of the weedy species *Avena fatua* L. and *Solanum nigrum* L. The species examined came from arable fields differing with respect to soil type and crop species according to the following pattern: *A. fatua* (in maize – brown soil, in spring wheat – podsolic soil), *S. nigrum* (in maize – brown soil, in potatoes – podsolic soil). The investigations included measurements in their original habitats and in a controlled environment. Plants grown on fields with brown soil reached higher values of the evaluated traits as compared to those recorded for plants grown on a podsolic soil. The height of *A. fatua* was similar in both habitats because competitive ability of the crop balanced the soil effect. There were no differences in plant morphology and biomass productivity within the two species when plants were grown in the same soil/climate conditions but on different soils *S. nigrum* exhibited variation in plant height and biomass productivity. Both species similarly responded to reduced light that revealed differences between them in chlorophyll content. Seeds of *A. fatua* and *S. nigrum*, regardless of their origin, germinated better in darkness than in the light and seeds of both species were more able to germinate when they were collected from plants grown in the light conditions from above the crop canopy. All seeds of *S. nigrum* also germinated better under warm conditions (20°C).

Keywords
wild oats; black nightshade; biomass productivity; morphological traits; chlorophyll content index; germination; environment; crop competition

Introduction

Weeds are strong competitors for crops and contribute to yield loss and deterioration in their quality. Different weed species vary in their competitive ability with crops because of their genetic characteristics. Additionally, a weed's competitiveness is strongly modified by the habitat conditions including soil/climate, farming practices, and the ability of the crop to suppress weeds [1,2]. Abiotic factors play a crucial role in modifying plant characteristics such as its height, biomass productivity, leaf and flowers numbers, leaf area, cuticle status, chlorophyll content, etc. However, plant species differ in their responses to habitat conditions. Growth and development of some plant species is only weakly related to individual environmental factors, whereas others are highly responsive to changeable habitat conditions [3,4]. Many plant species have been able to adapt to these, both through phenotypic plasticity and variation in biomass production, and genetic variation and selection at the population level, which can result in the formation of intraspecific variants [5].

The present study focused on two weed species commonly occurring on arable fields in Poland. Wild oats (*Avena fatua* L.) is a one of the main graminaceous weeds in cereals. It is described as the most detrimental annual weed species of temperate agricultural areas all over the world [6–8]. In the latter study by Beckie et al., the economical threshold for *A. fatua* in winter and spring wheat was 13–50 panicles m^{-2}. At a density of 25 panicles m^{-2}, the yield of spring wheat was reduced by 8% and 50 panicles m^{-2}, by 11% [9]. Black nightshade (*Solanum nigrum* L.) is a thermophilic weed, which mainly infests wide-row crops such as maize, sugar beet, and potato. In a study by Sartorato et al. [10], the economic threshold for this species in soybean was >1 plant m^{-2}. Both species exhibit high morphological plasticity and produce several distinct variants. Genetic diversity has been reported within them [11–13].

Complex habitat conditions on arable fields, including soil/climate factors, crop competition, and farming practices, all affect weed growth and development, their reproductive fecundity, and so their occurrence in the crop canopy. They therefore play an important role in diversification within a particular weed species. A detailed knowledge of weed biology, especially the time and requirements for seed germination and responses to variable environmental conditions, can be a useful tool to improve weed management strategies. It can make it possible to adjust agricultural practices to prevailing field conditions. The aim of this investigation was to evaluate the effects of climate and soil conditions on selected morphological traits, biomass productivity, and some other biological aspects of the two weeds, *A. fatua* and *S. nigrum*, originating from arable fields with differing soil conditions and supporting different cultivated crop species.

Material and methods

Two populations of both *A. fatua* and *S. nigrum* were investigated. They originated from arable fields located in the proximity of Wrocław, differing in their soil type and cultivated crop species. The characteristics of these two habitats for each species are presented in Tab. 1.

Tab. 1 Characteristics of the habitats of the *A. fatua*. and *S. nigrum* populations studied.

		A. fatua		*S. nigrum*	
		Habitat 1	**Habitat 2**	**Habitat 1**	**Habitat 2**
Location		Zagródki	Warkocz	Brzezina	Laskowice
Crop plant		Maize	Spring wheat	Maize	Potatoes
Soil type		Brown soil	Podsolic soil	Brown soil	Podsolic soil
$C_{org.}$ content (%)		3.0	1.3	3.4	1.2
$pH_{1M\ KCl}$		5.9	5.6	6.2	5.3
P_2O_5 content	per 100 mg of soil	16.4	11.7	19.0	9.6
K_2O content		18.0	8.9	20.2	11.5

Biometric assessments were carried out in the original habitats during two growing periods (2014–2015), after the end of inflorescence growth stage. They included the following measurements: plant height, leaf number on the main shoot, panicle length (for *A. fatua*), number of flowers in the inflorescence (for *S. nigrum*), leaf length, fresh and dry weights of a single plant. Fifty plants were measured from each habitat.

Seeds of the two species from untreated plots at each site were collected in 2014 and stored at room temperature. They were used for glasshouse and climate chamber experiments carried out in 2015 in the Department of Weed Science and Tillage Systems, Wrocław, which is part of the Institute of Soil Science and Plant Cultivation – State

Research Institute in Puławy. Two separate series of experiments were carried out with four replications. The glasshouse study investigated morphological traits and biomass productivity under the following conditions: (***i***) the same climate and soil conditions and (***ii***) the same climate but different soil conditions. In the first type, seeds were sown into pots filled with a mixture of peat and sand (2:1 w/w). The temperature in the glasshouse ranged from 20°C to 24°C and the photon flux density range was 450–500 μmol m^{-2} s^{-1} with a 14-h day and 10-h night. For the second study, soil was collected from the habitats and then seeds were sown into pots filled with soil from their site of origin. Thus, for example, seeds of *A. fatua* collected from the maize field were sown into soil coming from this parent location. The soil was prepared by removing any stones and large plant residues. It was then dried at 105°C for 24 h in an oven to achieve a water content <2%. Dry soil was then thoroughly mixed with the amount of water needed to achieve 60% soil moisture content. Each pot was weighed and watered daily by adding the amount of water to maintain the initial pot weight. Temperature and light conditions were the same as for the first experiment. For both, 10 seeds of each species were sown per pot and after seedling emergence, seedlings were thinned to six plants/pot, which remained to the end of the experiments. Plant measurements were performed 8 weeks after planting.

The controlled environment study was used to investigate the effect of light intensity on biomass productivity and chlorophyll content. Pots were placed in controlled environment chambers at temperature 20°C/10°C (day/night), with a photoperiod of 14 h day / 10 h night. One chamber was set up to obtain a maximum light intensity (10,000 lx), whereas in the second chamber, the light intensity was reduced by 30% (7,000 lx). Eight weeks after planting, biomass productivity and chlorophyll content indices (CCI) using a chlorophyll meter (model CCM-200; Plus Opti Sciences, USA) were determined. The CCI was recorded for five of the youngest but fully-expanded leaves on each plant.

The examination of germination capacity was assessed in climate chambers under varied thermal and light conditions. It was carried out in three replications, in two separate series. Fifty seeds collected at each locality were transferred onto water-soaked filter paper placed in Petri dishes and covered with another sheet of filter paper to prevent evaporation of water. The dishes were placed in climate chambers with two different thermal regimes, 20°C and 10°C. The same temperature treatments were applied to seeds that had no access to light. The experiments were conducted with three replicates of each treatment. Germinated seeds on each dish were counted after 10 days.

The experimental design for all parts of the study was a completely randomized one. Mean values of each trait were calculated for each species and habitat separately, and then compared using Student's *t* test to identify significant differences between means.

Results

Assessments carried out at the parent environments showed differences in morphological traits and biomass productivity within and between the two weed species. Plants of *A. fatua* differed with respect to length of leaves and panicles as well as their biomass productivity. Individuals grown in Habitat 1 (maize, brown soil) had leaves and panicles longer by 30% and 26%, respectively, and produced biomass 22% greater compared to plants grown in Habitat 2 (spring wheat, podsolic soil) (Tab. 2). In the case of *S. nigrum*, differences were observed in stem height, number and length of leaves, number of flowers in the inflorescence, and biomass productivity. More expressive in these parameters were plants grown on the more fertile brown soil. The greatest differences for leaves and flower number (per inflorescence) were 31% and 33%, respectively. Biomass productivity for individuals grown in the more fertile habitat was 18% greater than for plants grown in the other habitat (Tab. 2).

The study carried out under the same soil/climate conditions did not show differences in plant morphology or biomass productivity between both populations of either *A. fatua* or *S. nigrum*. However, plants of *S. nigrum* obtained from seeds collected from individuals grown on brown soil tended to be more leafy as compared to individuals collected from the site with podsolic soil (Tab. 3).

Tab. 2 Morphological traits and biomass productivity of *A. fatua* and *S. nigrum* grown in different habitats.

Habitat*	Plant height (cm)	Leaf number	Leaf length (cm)	Panicle length (cm)[1] or number of flowers / inflorescence[2]	Biomass productivity / single plant (g)	
					Fresh weight	Dry weight
			A. fatua			
1	140.2 [a]	9 [a]	29.1 [a]	42 [a]	148.5 [a]	35.3 [a]
2	140.6 [a]	8 [a]	20.5 [b]	31 [b]	130.3 [b]	26.2 [b]
			S. nigrum			
1	75.8 [a]	78 [a]	7.9 [a]	9 [a]	116.7 [a]	25.5 [a]
2	61.6 [b]	54 [b]	6.7 [b]	6 [b]	96.0 [b]	23.6 [a]

* Habitat characteristics are given in Tab. 1. Mean values of particular traits marked by the same letter do not differ significantly at the $p < 0.05$ probability level.
[1] For *A. fatua*.
[2] For *S. nigrum*.

Tab. 3 Morphological traits and biomass productivity of *A. fatua* and *S. nigrum* grown under the same climate and soil conditions.

Habitat*	Plant height (cm)	Leaf number	Leaf length (cm)	Biomass productivity / single plant (g)	
				Fresh weight	Dry weight
			A. fatua		
1	50.3 [a]	7 [a]	23.8 [a]	21.3 [a]	3.66 [a]
2	52.5 [a]	7 [a]	22.2 [a]	18.9 [a]	3.53 [a]
			S. nigrum		
1	29.6 [a]	56 [a]	9.2 [a]	24.2 [a]	4.05 [a]
2	26.1 [a]	45 [a]	7.7 [a]	22.2 [a]	3.66 [a]

* Plants obtained from seeds collected from the habitats described in Tab. 1. Mean values of particular traits marked by the same letter do not differ significantly at the $p < 0.05$ probability level.

The results of the study with plants grown under the same climate conditions but on different soils collected from relevant habitats showed a pronounced response of *S. nigrum* to soil conditions. Plants grown on brown soil were 17% taller than those grown on podsolic soil, possessed 25% more leaves and produced 26% more biomass (Tab. 4). Plants grown on brown soil featured higher plant heights, longer leaves, greater numbers of leaves, and higher biomass productivity. Plants of *A. fatua* only showed differences between soils with respect to biomass productivity. Plants grown in the more fertile habitat produced greater biomass (by 24%) than plants from the other habitat.

Light intensity considerably affected chlorophyll content and biomass productivity of the two species (Tab. 5). Plants of *S. nigrum* produced more chlorophyll and biomass than did *A. fatua*. The traits measured were significantly reduced by 30% light intensity. However, both species responded similarly to light reduction. There were no differences within particular species under full light conditions, whereas reduced light intensity resulted in variation in CCI values for *A. fatua* and *S. nigrum*, as well as biomass productivity in *A. fatua*. Plants obtained from seeds collected from fields with brown soil produced more chlorophyll (*A. fatua* 18% and *S. nigrum* 9%) and biomass (*A. fatua* 17% and *S. nigrum* 7%).

Temperature and light exerted strong effect on germination capacity (Tab. 6). For *S. nigrum*, a substantially lower number of seeds germinated at the lower temperature

Tab. 4 Morphological traits and biomass productivity of *A. fatua* and *S. nigrum* grown under various soil conditions.

Habitat*	Plant height (cm)	Leaf number	Leaf length (cm)	Biomass productivity/single plant (g)	
				Fresh weight	Dry weight
			A. fatua		
1	46.6 [a]	7 [a]	21.7 [a]	20.5 [a]	3.53 [a]
2	42.4 [a]	7 [a]	21.0 [a]	17.4 [b]	3.21 [a]
			S. nigrum		
1	23.0 [a]	52 [a]	9.0 [a]	22.9 [a]	3.92 [a]
2	19.1 [b]	39 [b]	7.1 [b]	17.0 [b]	3.50 [a]

* Plants obtained from seeds collected from the habitats described in Tab. 1. Mean values of particular traits marked by the same letter do not differ significantly at the $p < 0.05$ probability level.

Tab. 5 Influence of light intensity on chlorophyll content and biomass productivity of *A. fatua* and *S. nigrum*.

Habitat*	Full light			30% of full light		
	CCI	Fresh weight (g)	Dry weight (g)	CCI	Fresh weight (g)	Dry weight (g)
			A. fatua			
1	1.27 [a]	23.6 [a]	3.38 [a]	0.96 [a]	21.1 [a]	2.92 [a]
2	1.16 [a]	22.5 [a]	3.02 [a]	0.79 [b]	17.6 [b]	2.64 [b]
			S. nigrum			
1	1.89 [a]	26.4 [a]	3.65 [a]	1.53 [a]	18.2 [a]	2.35 [a]
2	1.97 [a]	25.1 [a]	3.55 [a]	1.40 [b]	17.0 [a]	2.04 [a]

* Plants obtained from seeds collected from the habitats described in Tab. 1. Mean values of particular traits marked by the same letter do not differ significantly within light intensity at the $p < 0.05$ probability level. CCI – chlorophyll content index.

(10°C). At a temperature of 20°C, light access affected the germination capacity of seeds collected from *A. fatua* grown in the less fertile habitat (podsolic soil). Seeds germinated considerably better (by 22% at 20°C) in darkness than with light access. Germination of *S. nigrum* seeds was greater at 20°C than at 10°C, regardless of light conditions and seeds origin. Similarly to *A. fatua*, seeds of *S. nigrum* germinated better in terms of light absence as compared to light access. Different germination capacity was also noted for seeds of *S. nigrum* between the different parental environments. Seeds collected from the habitat with podsolic soil germinated better than those obtained from the field with a brown soil.

Discussion

In this study, we investigated *A. fatua* and *S. nigrum* grown on arable fields with different soil/climate conditions and cultivated crops. The measurements made on location showed clear differences in plant morphology in the two weed species, which varied between habitats. These differences resulted from both soil properties as well as from the competitive ability of different crop species. Brown soil ensured greater nutrient supplementation for crops and hence greater potential productivity. Plants of *S. nigrum* grown on brown soil showed stronger morphological traits and biomass productivity than on the podsolic soil. For *A. fatua*, plant height and leaf number attained similar

Tab. 6 Germination capacity (%) of *A. fatua* and *S. nigrum* seeds under different temperature and light conditions.

	20°C		10°C	
Habitat*	**Light**	**Darkness**	**Light**	**Darkness**
		A. fatua		
1	50 [b]	64 [a]	40 [b]	62 [a]
2	55 [b]	70 [a]	62 [a]	65 [a]
		S. nigrum		
1	66 [c]	72 [b]	42 [b]	46 [b]
2	74 [b]	86 [a]	46 [b]	58 [a]

* Seeds collected from the habitats described in Tab. 1. Mean values marked by the same letter do not differ significantly within temperature at the $p < 0.05$ probability level.

values in both habitats. This was probably due to different morphologies, growth rate, and the agronomy employed for the particular crop grown. These properties are likely the main determinants of crop competitive ability with respect to weeds. In this study, the height of *A. fatua* was similar at both soil sites although it was expected that taller plants would be grown on the brown soil. In wheat, *A. fatua* overtops the crop canopy, whereas in maize it is suppressed by the crop. In this case, competitive ability balanced differences in responses to soil properties.

Individuals belonging to the same species can be genetically diversified which can result in a difference in biomass production between populations [14]. Individuals within the same plant population can also variously respond to environmental conditions. In the study conducted by Krstić et al. [5], *S. nigrum* showed variation in anatomical structure of leaves. For plants grown on cultivated soil, the majority of the traits we examined reached a higher level of expression than for plants grown on ruderal sites. The authors have also shown greater variation between individuals from ruderal habitats attributed to more variable environmental conditions.

Chlorophyll content is a useful measure in the evaluation of plant responses to light deficit. Reduced light intensity results in a decrease in leaf area, chlorophyll content, and consequently, biomass productivity [3,8]. In the present study, both species responded to lower light intensity with a poorer chlorophyll content and biomass production. However, it was observed only for plants obtained from seed collected from fields with the podsolic soil.

Germination capacity is largely determined by the extent of seed dormancy and the prevailing environmental conditions, especially temperature and light. Species with a wide range of adaptive abilities show diversity in germination of seeds collected from plants grown in different habitats and subjected to differing environmental conditions [15,16]. The habitats investigated in our study differed with respect to soil/climate conditions and crop species with differing competitive ability which determined light access to weeds. Lehnhoff et al. [17] found that *A. fatua* that grew beneath the crop canopy produced a reduced amount of seeds that were germinable as compared to those plants producing seeds above the canopy. This finding suggests that light deficit limits the germination of *A. fatua* seeds, which is inconsistent with our observation of better germination in darkness irrespective of temperature. However, comparing germination of seeds obtained from different habitats, there was a slightly better germination of seeds collected from plants grown in the wheat field, because they overtopped the crop canopy and were exposed to more light than plants grown in the maize field. A similar relationship was found in *S. nigrum*; seeds obtained from plants grown in the potato field germinated better than those collected from plants grown in the maize field. Greater germination capacity of *A. fatua* in darkness was also found in the study of Stokłosa [18]. This author also reported a positive effect of higher temperatures on germination capacity. According to Martinez-Ghersa et al. [19], variation in dormancy and germination of *A. fatua* seeds from different agricultural systems promotes population expansion in changing environments. As with *A. fatua*, seeds of *S. nigrum* tended to germinate better in darkness than with good light access. This observation is inconsistent with the report by Barakat [20] that darkness is a factor limiting the germination of *S. nigrum*. The present investigation showed that temperature affected seed germination of *S. nigrum* to a higher degree than it affected germination of *A. fatua*. Germination capacity was greater under warmer conditions at both light levels. A similar result was obtained in the study by Manoto et al. [21] who found that significantly more seed germinated at 10°C/20°C than at lower temperatures (10°C/15°C and 5°C/15°C).

Conclusions

Plants of *A. fatua* and *S. nigrum* grown on fields with brown soil (more fertile) reached higher values of the evaluated traits as compared to those recorded for plants grown on the less fertile podsolic soil. The height attained by *A. fatua* was similar for both sites because the competitive ability of maize balanced the influence of the differing soil properties. There were no differences in plant morphology and biomass productivity within species when plants grown with the same soil/climate conditions, whereas in the same climate but on different soils, *S. nigrum* did exhibit variation in plant height and biomass productivity. Low light intensity produced differences in chlorophyll content index. Seeds of the both weed species germinated better in darkness than in light regardless of their origin. Seeds collected from plants grown with light access, above the crop canopy (*A. fatua* in wheat, *S. nigrum* in potato) were more germinable.

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Wpływ warunków środowiskowych i konkurencji rośliny uprawnej na zróżnicowanie morfologiczne i biologiczne *Avena fatua* L. i *Solanum nigrum* L.

Streszczenie

Przedmiotem przeprowadzonych badań była ocena wpływu warunków klimatyczno-glebowych oraz konkurencyjności rośliny uprawnej na wybrane cechy morfologiczne, produktywność biomasy oraz niektóre aspekty bilogiczne *Avena fatua* L. oraz *Solanum nigrum* L. Badane rośliny pochodziły z pól uprawnych o zróżnicowanych warunkach glebowych i roślinach uprawnych według schematu: *A. fatua* (kukurydza – gleba brunatna oraz pszenica jara – gleba płowa), *S. nigrum* (kukurydza – gleba brunatna, ziemniak – gleba płowa). Badania obejmowały pomiary w badanych siedliskach oraz doświadczenia w warunkach kontrolowanych. Rośliny rosnące na polach z glebą brunatną osiągnęły wyższe wartości odnośnie ocenianych parametrów w porównaniu do osobników rosnących na glebie płowej. Wysokość roślin *A. fatua* była taka sama dla obu siedlisk ponieważ zdolności konkurencyjne rośliny uprawnej zrównoważyły wpływ gleby. Nie zaobserwowano różnic w morfologii roślin i produktywności biomasy w obrębie gatunku, jeśli rośliny rosły w tych samych warunkach klimatyczno-glebowych. *Solanum nigrum* rosnąca w takich samych warunkach klimatycznych, lecz na różnych glebach wykazała zmienność w wysokości roślin i produktywności biomasy. Oba gatunki podobnie zareagowały na zmniejszoną intensywność światła, która ujawniła różnice w obrębie gatunku pod względem indeksu zawartości chlorofilu. Bez względu na pochodzenie, nasiona *A. fatua* i *S. nigrum* lepiej kiełkowały w ciemności niż przy dostępie światła. Nasiona *S. nigrum* lepiej kiełkowały w wyższych temperaturach (20°C)

bez względu na pochodzenie nasion. Nasiona badanych gatunków posiadały większą zdolność kiełkowania, gdy były zebrane z roślin rosnących w warunkach dostępu światła, przerastających roślinę uprawną.