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SEED QUANTITY AND QUALITY IN FRUIT HEADS OF *ASTER LANCEOLATUS* WILLD.: IM- PLICATIONS FOR INVASION SUCCESS

Abstract: *Aster lanceolatus* Willd. is a herbaceous perennial that is considered invasive in many European countries. In Serbia, this plant inhabits wet habitats and forms widespread monospecific stands. The objective of this research is to determine whether generative reproduction has an important role in the expansion of this species to new areas. In 13 different localities, fruit heads were collected from lateral and terminal parts of infructescence. Seed quantity and germination parameters were determined for seeds in the fruit heads. The results showed that the position of the fruit heads did not have a major impact on germination parameters. However, germination parameters differed among the localities. The findings of this study suggest that *A. lanceolatus* produces a great amount of viable seeds that germinate in an amount sufficient to ensure a successful spread of this invasive species to new areas.

Key words: *Aster lanceolatus* Willd., invasive plants, generative reproduction

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КОЛИЧИНА И КВАЛИТЕТ АХЕНИЈА НАСТАЛИХ ИЗ ГЛАВИЦА ВРСТЕ *ASTER LANCEOLATUS* WILLD.: ПОСЛЕДИЦЕ НА ШИРЕЊЕ ВРСТЕ

Апстракт: *Aster lanceolatus* Willd. је зељаста перена која се сматра инвазивном у великом броју европских земаља. У Србији, ова биљка насељава влажна станишта и формира широко распрострањене монодоминантне састојине. Циљ овог истраживања је да утврди да ли генеративно размножавање има важну улогу у ширењу ове врсте на нова подручја. Ахеније настале из бочних и терминалних главица су сакупљене на 13 локалитета у Србији. Утврђен је број ахенија насталих из једне главице, као и параметри клијања семена. Резултати су показали да се параметри клијања нису разликовали у односу на место настанка ахенија, већ у односу на локалитет са кога су оне сакупљане. Ово истраживање је потврдило да *A. lanceolatus* ствара велику количину вијабилног семена које клија у количини која је довољна да обезбеди успешно ширење врсте на нова подручја.

Кључне речи: *Aster lanceolatus* Willd., инвазивне врсте, генеративно размножавање

1. INTRODUCTION

Invasive species draw a great deal of attention since they represent a danger to human health and because of their economic and environmental impact (Davis, 2009). Some invasive plants often perform better compared to native ones (Vilà *et al.*, 2007). They become abundant and are likely to have negative effects on the native plant communities and to the diversity of those communities (Vitousek and Walker, 1989; Gurevitch and Padilla, 2004). Species traits such as fast growth rates, broad ecological niches, high seed production or long-distance dispersal are characteristics that should be taken into account when predicting future invasion (Grotkopp *et al.*, 2002; Vilà *et al.*, 2007). In addition, Daehler (2003) found that the success of invasive plants depends on growing conditions. Due to the specific characteristics of each species and habitat, it is difficult to say which plant features and habitat type will have a crucial role in the uncontrollable spread of invasive plants. Nevertheless, it is reasonable to assume that species with great reproductive potential and widespread native distribution could be the cause for invasion success in ecosystems.

Aster lanceolatus Willd. is a herbaceous perennial, native to North America, with a nearly transcontinental distribution (Chmielewski and Semple, 2001). This species is considered invasive in many European countries (Jedlička and Prach, 2006). Because of its competitive nature and the difficulty in controlling the spread of *A. lanceolatus*, it is important to determine which traits contribute to the spread and formation of dense, monospecific stands.

The aim of this paper is to examine whether there are differences in the germination parameters in relation to the position of the fruit heads and among localities, to examine whether there is a tradeoff between seed quantity and quality of *A. lanceolatus*, and to assess the role of generative reproduction in the invasion success of this plant.

2. MATERIALS AND METHODS

2.1 Studied species

The studied species was identified as *Aster lanceolatus* Willd. (Compositae) based on standard floristic methods, using relevant literature Javorka and Csapody (1934), Josifović (1970-1977), Tutin *et al.* (Eds.) (1964-1980), Sarić and Diklić (1986), Sarić (1992) and Online data base of Flora Europaea. This species is an edicator in the *Asteretum lanceolati* community, which is a new type of invasive community (Obratov-Petković *et al.*, 2011). *A. lanceolatus* occupies moist soils on wet habitats or along roadsides and disturbed ground and it forms dense monodominant stands and thus prevents the development of wetlands native species (Obratov-Petković *et al.*, 2009). Clonal growth allows this species to form widespread stands with long and tangled horizontal rhizomes (Jones, 1978). During the first season of growth most resources are allocated in to vegetative parts, specifically rhizomes in opposition to seeds (Chmielewski and Semple, 2001). Overwintering rosettes produce flowering stem the following summer (Peterson and Bazzaz, 1978). Flowering (Figure 1) and fruiting (Figure 2) occurs in late



Figure 1. *Aster lanceolatus* during the bloom period, early November 2012

Слика 1. *Aster lanceolatus* током периода цветања, почетак новембра 2012



Figure 2. *Aster lanceolatus* during the fruiting period, late November 2012

Слика 2. *Aster lanceolatus*, у време плодношења крај новембра 2012

summer or early autumn (Chmielewski and Semple, 2001). However, in localities in Serbia, this plant often prolongs the flowering period throughout November. One-seeded, dry, indehiscent fruit of the Asteraceae, although technically a cypsel, is typically referred to as an achene or seed (Chmielewski and Strain, 2007). The development of heads in inflorescences is basipetal and determinate and after pollination achenes mature within 3 to 4 weeks (Chmielewski and Semple, 2001). Achenes with adjoining pappus are wind-dispersed. Seeds in the Asteraceae family have non-deep dormancy, which is broken with low temperature (Baskin *et al.*, 2005).

2.2 Seed collection sites

In order to test the seed germination of *A. lanceolatus*, during the autumn of 2012 seeds were collected in 13 different localities. In Vojvodina, sites along the Danube River, Slankamen, Beška, Sremski Karlovci, Sremska Kamenica and Beočin were selected for this study. In Belgrade and its environs the selected sites were: the Kumodraž area in the valley of the creek of Kumodražki potok; Makiš, Živača and Jakovo on the alluvial plain of the Sava River; Krnjača on the alluvial plain of the Danube; and Košutnjak hill near the Sava. Two islands, Ada Medica (on the Sava) and Veliko Ratno Ostrvo (on the Danube), were selected because island ecosystems are especially susceptible to invasion.

2.3 Germination test

Seed germination was investigated and quantified as germination percentage,

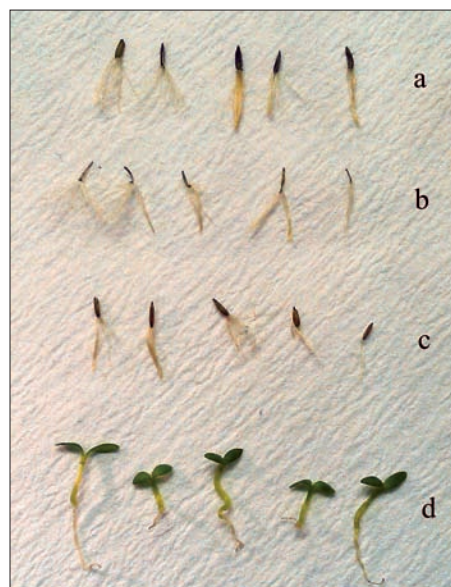


Figure 3. Dead seeds (a), empty seeds (b), fresh ungerminated seeds (c) and seedlings (d)

Слика 3. Труло семе (а), штуро семе (б), свеже неисклијало семе (с) и изглед клијаваца (д)



Figure 4. Fresh ungerminated seeds before (a) and after (b) dissection

Слика 4. Свеже неисклијало семе пре (а) и после (б) пресецања

real germination, germination energy and viability percentage. For this purpose, fifty visually mature fruit heads from top and lateral parts of infructescence were randomly collected in every location and each fruit head was placed in a separate bag. In the laboratory, seeds for testing were obtained at a random sample of 4 fruit heads from each part of infructescence. The achenes were separated from fruit heads and cleaned from other visible impurities and stored at 5°C for after-ripening period of 4 months. Pappus remained attached to achenes since Chmielewski (1999) suggested that in *Aster umbellatus* var. *umbellatus* the key role of the pappus is to facilitate dispersal as opposed to encourage germination. After this period, for all localities, in 4 replications for each terminal and lateral fruit head, achenes from one fruit head were placed in 9 cm Petri dishes lined with moist filter paper. The Petri dishes were incubated in a growth chamber, Type 1291/TPC-1/LP-113 at 20°C (± 2), and a 16-hour photoperiod was applied (Grbić *et al.*, 2011).

The number of germinated seeds (Figure 1, d) and the number of ungerminated seeds, precisely dead seeds (Figure 1, a), empty seeds (Figure 1, b) and fresh ungerminated seeds (Figure 1, c) were counted. Germinative capacity (GC) and real germination (RG) were determined after 14 days, while germinative energy (GE) was calculated on the fourth day (ISTA, 2003). The viability of fresh ungerminated seeds (Figure 2, a) at the end of the germination test was determined by dissection (ISTA, 2003). Seeds with fully developed, white and firm embryo (Figure 2, b) were placed in the category of fresh ungerminated seeds.

2.4 Data analysis

The difference between seed quantity and the germination parameters of the seeds from terminal and lateral parts of infructescence and the difference between localities were tested using the one-way analysis of variance (ANOVA) followed by Fisher's LSD test ($p < 0.05$). The numbers of germinated seeds were expressed as a mean percentage of the number of seeds of four replicates. Viable seeds were calculated as the sum of fresh ungerminated and germinated seeds and were also expressed as a mean percentage of the number of seeds of four replicates. Because of the small share of dead seeds, those data were not shown.

3. RESULTS

3.1 Seed quantity in fruit heads

As shown in Table 1, the number of achenes ranges between 48.50 and 68.00 per fruit head. Taking into account all the collection sites and both parts of infructescence, the average number of achenes was 56.14 per fruit head. The differences in the number of seeds in one fruit head across all locations were not significant ($p > 0.05$).

Table 1. Mean number of seed production and germination parameters of *A. lanceolatus*. Each value represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$ **Табела 1.** Средња вредност броја семена и параметара клијања врсте *A. lanceolatus*. Свака вредност представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

Location/Локалитет	FN/ПГ	N/N	GC/ТК	RG/АК	GE/EK	V/B
Ada Međica/Ада Међица	L	55,00 ^{bcde} \pm 1,472	14,95 ^{bcde} \pm 5,958	23,75 ^{bcde} \pm 8,940	14,95 ^{bcde} \pm 5,958	63,38 ^{abcde} \pm 4,49
	T	53,50 ^{bcde} \pm 0,645	43,44 ^a \pm 9,587	60,81 ^a \pm 0,815	17,79 ^{ab} \pm 5,604	72,14 ^{abc} \pm 6,66
Beočin/Беоћин	L	57,00 ^{bcde} \pm 2,972	5,53 ^{cd} \pm 2,111	9,74 ^{ef} \pm 3,723	1,77 ^{cde} \pm 0,098	65,66 ^{abcde} \pm 9,520
	T	51,00 ^{cde} \pm 2,273	10,93 ^{bcde} \pm 2,972	15,72 ^{cdef} \pm 3,114	7,59 ^{cd} \pm 2,733	65,71 ^{abcd} \pm 5,865
Beška/Бешка	L	61,75 ^{abc} \pm 5,808	16,97 ^{bc} \pm 4,595	21,40 ^{bcde} \pm 4,919	2,51 ^{cde} \pm 0,556	72,24 ^{abc} \pm 4,212
	T	50,25 ^{de} \pm 1,377	25,22 ^b \pm 8,954	34,24 ^b \pm 11,260	0,00 ^e \pm 0,000	67,43 ^{abcde} \pm 4,776
Јаково/Јаково	L	56,25 ^{bcde} \pm 5,089	7,97 ^{ab} \pm 0,251	11,07 ^{def} \pm 1,133	7,97 ^{bcde} \pm 0,251	74,08 ^{abc} \pm 9,268
	T	57,25 ^{abcde} \pm 5,822	5,12 ^{cd} \pm 1,305	6,72 ^{ef} \pm 1,787	5,12 ^{cde} \pm 1,305	58,39 ^{bcde} \pm 3,823
Кошутњак/Кошутњак	L	59,00 ^{abcde} \pm 4,262	45,98 ^b \pm 13,860	70,31 ^a \pm 15,170	0,35 ^e \pm 0,352	63,64 ^{abcde} \pm 6,502
	T	53,50 ^{bcde} \pm 1,848	44,23 ^a \pm 10,890	65,55 ^a \pm 11,750	0,45 ^e \pm 0,447	63,62 ^{abcde} \pm 6,156
Крпјаца/Крпјаца	L	53,00 ^{bcde} \pm 4,708	4,88 ^{cd} \pm 0,769	6,06 ^{ef} \pm 1,250	0,00 ^e \pm 0,000	81,81 ^a \pm 7,208
	T	62,00 ^{ab} \pm 5,701	4,83 ^{cd} \pm 1,440	9,05 ^{ef} \pm 4,003	1,39 ^{de} \pm 1,390	60,02 ^{bcde} \pm 11,849
Крњача/Крњача	L	53,25 ^{bcde} \pm 1,652	3,31 ^{cd} \pm 0,509	5,24 ^{fg} \pm 0,824	1,38 ^{de} \pm 0,852	49,72 ^{def} \pm 5,155
	T	58,00 ^{abcde} \pm 4,916	4,79 ^{cd} \pm 1,228	6,07 ^{ef} \pm 1,340	0,57 ^e \pm 0,567	65,52 ^{abcde} \pm 4,849
Кумодраж/Кумодраж	L	61,25 ^{abc} \pm 5,25	11,95 ^{bcde} \pm 1,868	15,91 ^{cdef} \pm 1,852	3,59 ^{cde} \pm 2,191	71,00 ^{abc} \pm 1,718
	T	61,00 ^{abcd} \pm 4,916	24,14 ^b \pm 5,833	30,76 ^b \pm 7,132	24,14 ^a \pm 5,833	77,20 ^{ab} \pm 8,031
Сланкамен/Сланкамен	L	55,00 ^{bcde} \pm 1,354	23,25 ^b \pm 7,529	36,88 ^b \pm 11,610	5,88 ^{cde} \pm 1,660	57,90 ^{cde} \pm 2,558
	T	53,75 ^{bcde} \pm 2,658	14,77 ^{bcde} \pm 3,836	32,56 ^{bc} \pm 9,789	1,76 ^{cde} \pm 0,681	44,43 ^{ef} \pm 1,856
Stemska Kamеница/Stemska Kamеница	L	61,00 ^{abcd} \pm 2,345	17,73 ^{bc} \pm 4,599	28,66 ^{bcde} \pm 6,921	0,00 ^e \pm 0,000	58,14 ^{def} \pm 6,675
	T	48,50 ^a \pm 2,598	6,44 ^{cd} \pm 2,729	9,99 ^{ef} \pm 4,094	0,00 ^e \pm 0,000	55,75 ^{cde} \pm 6,923
Stemski Karlovgi/Stemski Karlovgi	L	51,25 ^{bcde} \pm 2,175	7,08 ^{cd} \pm 3,184	9,55 ^{ef} \pm 3,702	7,08 ^{cd} \pm 3,184	43,90 ^g \pm 16,215
	T	68,00 ^{ab} \pm 4,950	5,06 ^{cd} \pm 0,751	6,83 ^{ef} \pm 0,816	5,06 ^{cd} \pm 0,751	73,50 ^{abc} \pm 2,307
Veliko Ratno Ostrvo/Veliko Ratno Ostrvo	L	54,00 ^{bcde} \pm 2,273	2,80 ^{cd} \pm 1,603	4,53 ^{fg} \pm 2,628	2,80 ^{cde} \pm 1,603	63,14 ^{abcde} \pm 1,744
	T	61,00 ^{abcd} \pm 5,115	13,40 ^{bcde} \pm 6,666	18,88 ^{bcde} \pm 7,933	4,19 ^{cde} \pm 1,840	63,99 ^{abcde} \pm 5,201
Živača/Живача	L	54,25 ^{bcde} \pm 4,328	1,79 ^{cd} \pm 1,061	2,71 ^{fg} \pm 1,676	0,00 ^e \pm 0,000	57,80 ^{cde} \pm 2,197
	T	50,00 ^a \pm 4,021	0,58 ^{cd} \pm 0,583	0,83 ^{fg} \pm 0,832	0,58 ^a \pm 0,583	60,27 ^{bcde} \pm 7,888

Legend: FN - fruit head position, L - lateral, T - terminal, N - number of achenes in fruit head, GC - germinative capacity, RG - real germination, GE - germinative energy, V - viability

Легенда: ПГ - положај главица из којих су настале ахеније, L - бочне, T - терминалне, N - број ахенија насталих из једне главице, ТК - техничка клијавост, КА - апсолутна клијавост, ЕК - енергија клијања, В - вијабилност

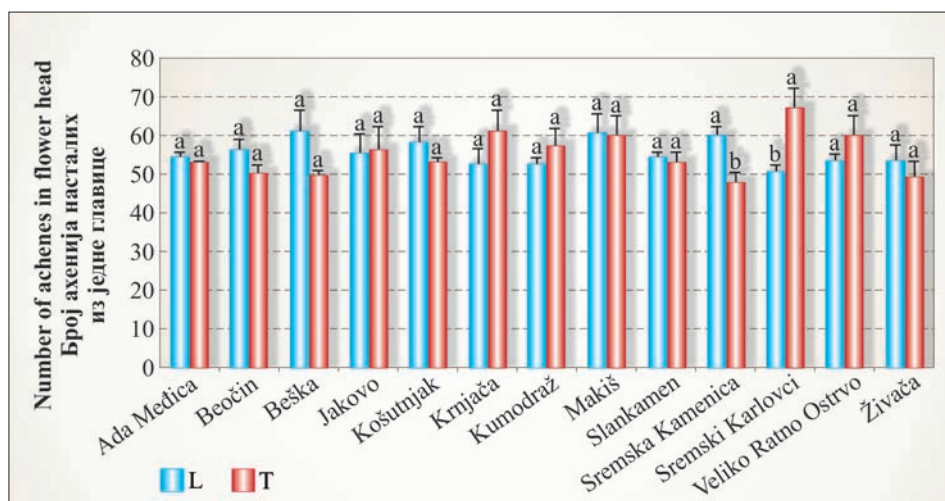


Diagram 1. Number of achenes in fruit head - differences between seeds from lateral (L) and terminal (T) parts of infructescence. Each bar represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$

Графикон 1. Број ахенија насталих из једне главице – разлике између ахенија насталих из бочних (L) и терминалних (T) главица. Сваки стуб графикана представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

Furthermore, the seed (achene) number per fruit head did not differ with respect to the part of infructescence from which they were sampled, except for the seeds from Sremska Kamenica and Sremski Karlovci localities, where there were significant differences ($p < 0.05$) among seed sets in lateral and terminal fruit heads (Diagram 1).

3.2 Germinative capacity

In order to assess potential for germinative reproduction of species *A. lanceolatus*, germinative capacity was determined. The results showed significant differences ($p < 0.05$) between germination capacities of seeds from different localities. As can be seen from Table 1, the mean germination percentage varied between 0.58% and 45.98%. The seeds from lateral and terminal parts of infructescence collected in the Košutnjak locality had the highest mean germination percentage, 45.98% and 44.23%, respectively. In addition, the mean germination percentage of the seeds from the terminal part of infructescence collected in Ada Medica belongs to the same homogeneous group. The seeds from both parts of infructescence collected in Živača showed the lowest mean germination percentage. As shown in Diagram 2, there were no significant differences between the mean germination percentages of seeds with respect to the part of infructescence from which they were sampled, except for the seeds collected on the Ada Medica site.

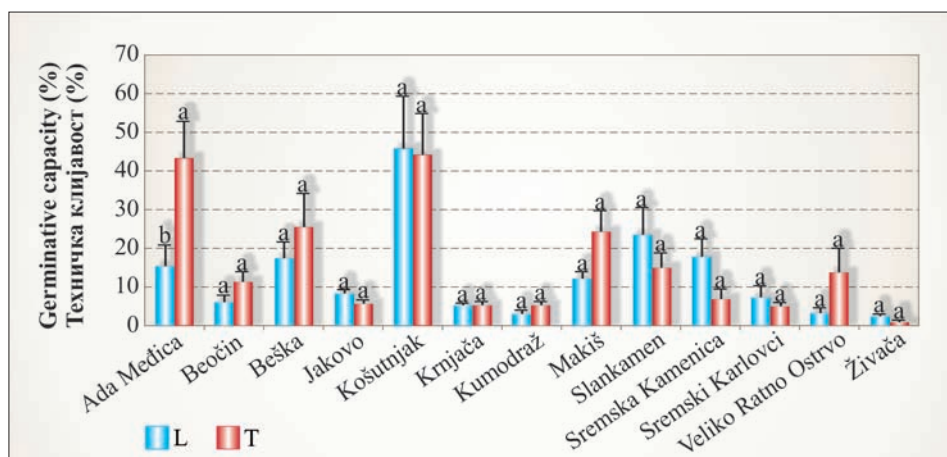


Diagram 2. Germinative capacity - differences between seeds from lateral (L) and terminal (T) parts of infructescence. Each bar represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$

Графикон 2. Техничка клијавост – разлике између ахенија насталих из бочних (L) и терминалних (T) главица. Сваки стуб графикана представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

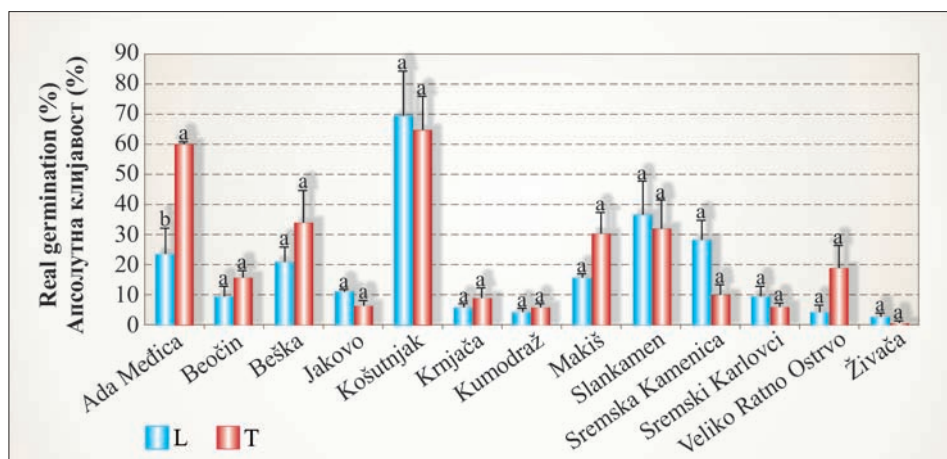


Diagram 3. Real germination - differences between seeds from lateral (L) and terminal (T) parts of infructescence. Each bar represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$

Графикон 3. Апсолутна клијавост – разлике између ахенија насталих из бочних (L) и терминалних (T) главица. Сваки стуб графикана представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

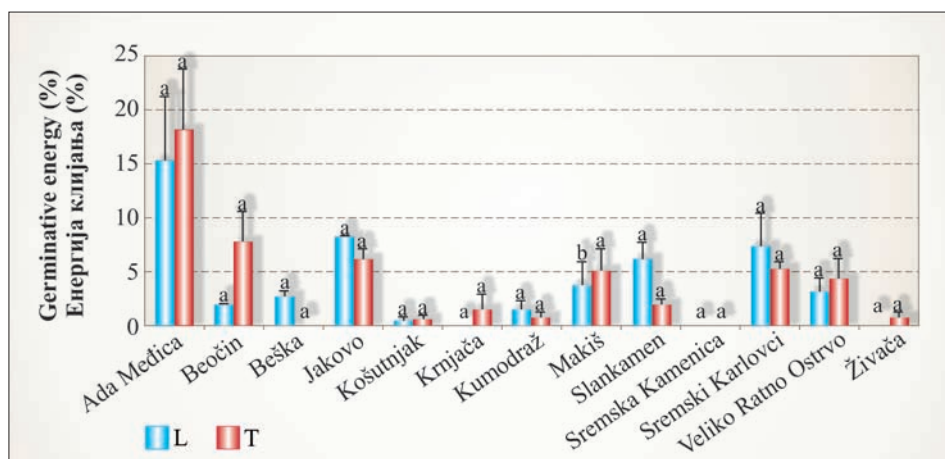


Diagram 4. Germinative energy - differences between seeds from lateral (L) and terminal (T) parts of infructescence. Each bar represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$

Графикон 4. Енергија клијања – разлике између ахенија насталих из бочних (L) и терминалних (T) главица. Сваки стуб графикана представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

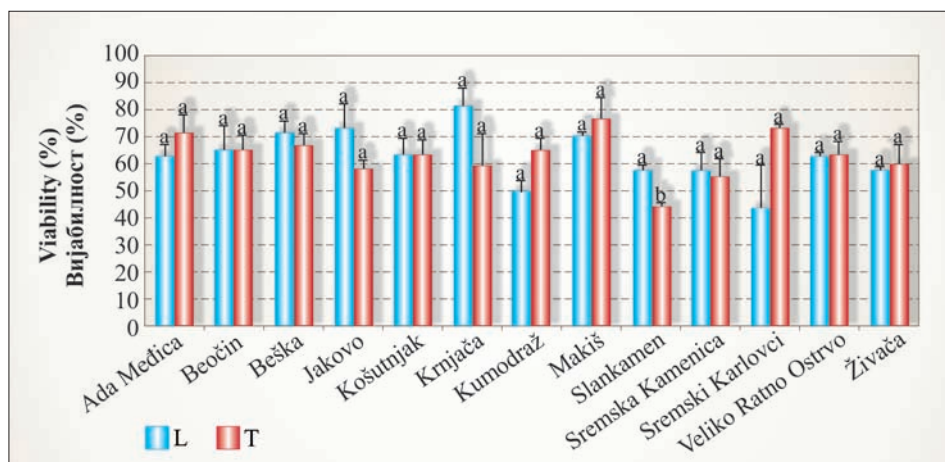


Diagram 5. Seed viability - differences between seeds from lateral (L) and terminal (T) parts of infructescence. Each bar represents the mean (\pm SE) of four replicates. Final means with different letters are significantly different at $\alpha = 0.05$

Графикон 5. Вијабилност семена – разлике између ахенија насталих из бочних (L) и терминалних (T) главица. Сваки стуб графикана представља средњу вредност (\pm SE) четири понављања. Средње вредности са различитим словима се значајно разликују, $\alpha = 0.05$

3.3 Real germination

Real germination or the percentage of sound seeds that germinated ranged between 0.83% and 70.31%. There were significant differences between the real germination of seeds from different localities. The seeds collected in Košutnjak, from both parts of infructescence, show the highest real germination percentage (Table 1). The seeds from the terminal part of infructescence collected in Ada Međica also showed a high real germination (60.81%). Real germination for all other localities was between 4.53% and 36.88%, except for the seeds collected in Živača, where the percentage of sound seeds that germinated was the lowest, 2.71% and 0.83% for seeds belonging to the lateral and terminal parts of infructescence, respectively. While real germination showed differences between seeds from lateral and terminal parts of infructescence in Ada Međica, there were no significant differences in the real germination percentages of seeds in other localities with respect to the part of infructescence (Diagram 3).

3.4 Germinative energy

Seeds of *A. lanceolatus*, from both parts of infructescence, exhibited slow germination. Germinative energy ranged from 0 to 24.14% and there were significant differences between locations (Table 1). Beška, Košutnjak, Krnjača, Kumodraž and Živača are sites with the lowest germinative energy. Germinative energy and germinative capacity were equal for the seeds, from both parts of infructescence, collected in Jakovo and Sremski Karlovci. Also, these parameters were equal for the seeds collected from the lateral part of infructescence in Ada Međica and Veliko Ratno Ostrvo and in the seeds collected from the terminal part of infructescence in Makiš and Živača. Germinative energy showed significant differences between seeds from lateral and terminal parts of infructescence only on the Makiš site (Diagram 4).

3.5 Seed viability

Analyses of variance indicated that there were significant differences ($p < 0.05$) in mean seed viability among localities. The highest mean percentage of viable seeds was recorded on the Krnjača site (81.81) in lateral parts of infructescence (Table 1). Seeds from Košutnjak (43.90) in lateral parts of infructescence had one of the lowest percentages of viability. In addition, on the Slankamen site, there were significant differences in seed viability between seeds from lateral and terminal parts of infructescence while in other localities differences were not significant (Diagram 5).

4. DISCUSSION

Attributes that promote reproduction and dispersal are one of the key indicators of a successful invader (Rejmánek *et al.*, 2005). Plants with small seeds usually produce more seeds relative to biomass because of the tradeoff between seed number and mean

seed mass (Poschlod *et al.*, 2005). Furthermore, parameters which impact dispersal potential are height of infructescence, seed production and time and duration of seed release (Poschlod *et al.*, 2005).

The seed ripening period and the surrounding vegetation are important for wind dispersal since weather, especially wind speed and changes during the year, and different environments influence this event (Poschlod *et al.*, 2005). On the investigated sites *A. lanceolatus* flowered from late August to late November and its clones were with highly branched inflorescences. The time of flowering could favor *A. lanceolatus* over other native plants since in that time a small number of plants flower and the competition for pollinators is not large. Along the river banks and on the forest edge in wet habitat on 1 m², the number of individuals of *A. lanceolatus* ranges from 60 to 2,700 and 700 to 1,200, respectively (Obratov-Petković *et al.*, 2009). In this study, some plants consisted of 200, sometimes even more fruit heads in infructescence. With the average number of achenes being 56.14 (Table 1) in one fruit head, this species produces a great amount of potentially germinative seeds from one shoot only. *A. lanceolatus* is a tall perennial plant that in some localities reaches a height of more than 2m and usually inhabits open vegetation communities. The weight of 1000 pure seeds of *A. lanceolatus* is 0,127g (Chmielewski and Semple, 2001). Large quantities of small seeds, adapted to wind dispersal, which ripen during the season of windy weather, and the previously mentioned traits are features that could favor *A. lanceolatus* over other native plants in communities.

This study set out with the aim of assessing the potential for generative reproduction of *A. lanceolatus*, since earlier research (Nesic *et al.*, 2012) showed that the potential for generative reproduction of *A. lanceolatus* is restricted. However, the findings of the previous study are inconsistent with some published studies (Jones, 1978; Schmid and Bazzaz, 1987; Jedlička and Prach, 2006), which have determined a high percentage of germinated seeds in the clones of *A. lanceolatus*. The findings of the current study showed a much higher germinative capacity that reaches a value of 45.98% of germinated achenes per fruit head. Real germination was even higher, reaching 70.31%. Since real germination is the percentage of sound seeds that germinate (Grbić *et al.*, 2011), it is clear that *A. lanceolatus* produces a considerable amount of empty seeds. The average amount of empty seeds was 31.50% per fruit head. According to Chmielewski and Semple (2001), selfing could be the primary source of the few achenes produced by *A. lanceolatus*. However, seed quality could be influenced by environmental conditions prevailing during seed formation (Valencia-Díaz and Montaña, 2005).

Both germinative capacity and real germination had the greatest value in Ada Medica and Košutnjak. Compared to other locations, on these two sites flowering occurred last. In addition, *A. lanceolatus* clones on the Kumodraž site were the first ones to flower and the germination percentage was among the lowest in comparison with the germination percentage of seeds from other locations. Chmielewski and Semple (2001) point out that in rhizomatous asters flowering initiation, seed maturation, seed dispersal and germination are fairly synchronized. Jones (1978) suggests that the flowering time of asters is genetically fixed adaptations to climatic and light conditions. Also, substantial phenotypic plasticity was observed in the *Aster* genera across different environments

(Schmid and Bazzaz, 1990; Chmielewski and Semple, 2001). It is complicated to explain this variation in the percentage of germinated seeds, but it might be related to climatic conditions occurring during the time of seed maturation and to the genetic construction of *A. lanceolatus* plants.

Schmid and Bazzaz (1990) reported that the germination percentage in *A. lanceolatus* differed for populations grown on compact inorganic and loose organic soil. There is much evidence of the importance of plasticity in plants undergoing climate change since plants can adjust to these novel conditions through phenotypic plasticity (Franks and Weis, 2008). The extension of the growing season through climate change is important for the spread of the *A. lanceolatus* (Obratov-Petković *et al.*, 2011). It is reasonable to assume that persistent climate change will encourage further expansion of *A. lanceolatus* populations.

Since the percentage of viable seeds was high and the germination percentage low, it is possible that germination was affected by temperature. Specifically, *A. lanceolatus* seeds show a much higher germination rate at 30 and 35°C than at 20°C (personal observation). This could be related with seed imbibition since temperature influences the rate of imbibition with low temperatures causing slow imbibition (Murphy and Noland, 1982; McDonald, 2005). These ecological characteristics need not be a disadvantage in wetland ecosystems, since in those habitats the moisture level of the substrate should not be a limiting factor for seed germination, even during late spring when temperatures are higher. Hence, this quantity of fresh ungerminated seeds could be considered potentially germinable.

Germinative energy is a measure of the germination speed and it points to the vigor of a seed and the seedling it produces (Willan, 1985). The mean germinative energy of *A. lanceolatus* seeds was low (4.53%). This result could be ecologically significant given that the speed of germination could be important for seedling success in a dynamic plant community. Nevertheless, the temperature during the experiment could have been the reason for slow germination.

Flowers within the same inflorescence may have different probabilities of reproductive success since the first opened flowers have a higher probability of setting fruit than the later ones, which implies that the plant allocates more resources to the early opened flowers (Gutián and Navarro, 1996). In the current study, the position of the fruit heads did not have a major impact on the parameters of germination since the differences between seeds from lateral and terminal parts of infructescence were sporadic and without an obvious pattern.

5. CONCLUSIONS

The present study was designed to determine a balance between *A. lanceolatus* seed quantity and quality and to assess the importance of generative reproduction for the spread of this invasive species. This research has shown that with an average achene

number of 56.14 per fruit head and an average of 200 fruit heads per plant, *A. lanceolatus* produced a great amount of seeds that is dispersed by wind. Although there were some empty achenes in the fruit heads and the percentage of seed germination in the fruit heads was not high, considering the amount of seeds per shoot and the number of individuals in the stands, it is reasonable to assume that this amount of germinated seeds is enough for the spread of this plant to new sites. This is probably the way in which *A. lanceolatus* reaches new areas. After this phase, *A. lanceolatus* is able to quickly colonize available space since it has a great vegetative propagation ability. *A. lanceolatus* seeds showed slow germination and since germination energy points to the vigor of a seed and its seedling this could be a limiting factor in the reproductive ecology of *A. lanceolatus*. Still, it is possible that germination energy was influenced by temperature and that with a rise in temperature and a sufficient amount of moisture, germination energy would increase. Yet, since *A. lanceolatus* has a high growth rate, delayed germination in the field would probably not be a problem for the survival of seedlings.

Germination parameters differed among localities. The current study was unable to analyze causes of these variables. These differences could be due to the genetic construction of individuals, phenotypic plasticity or they could be attributed to specific conditions in each locality.

Taken together, these findings suggest that *A. lanceolatus* produces a great amount of viable seeds that germinate in an amount sufficient to ensure a successful spread of this invasive species to new areas. Future research should investigate the influences of temperature and other climatic parameters on germination in *A. lanceolatus* and try to predict how this species will react to unremitting climate change. In addition, the results could be compared and correlated to others parameters of invasion that would explain how biological traits of invader and environmental factors affect the process of invasion.

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КОЛИЧИНА И КВАЛИТЕТ АХЕНИЈА НАСТАЛИХ ИЗ ГЛАВИЦА ВРСТЕ *ASTER LANCEOLATUS* WILLD.: ПОСЛЕДИЦЕ НА ШИРЕЊЕ ВРСТЕ

Резиме

Aster lanceolatus Willd. је северноамеричка врста која се сматра инвазивном у великом броју европских земаља. Због комутативности коју испољава и тешкоће у контроли ширења, важно је утврдити које особине доприносе експанзији врсте. Ово истраживање

има за циљ да одреди количину и квалитет семена врсте *A. lanceolatus*, као и да испита да ли постоје разлике у параметрима клијања у зависности од положаја главица из којих су настале ахеније и локалитета. У оквиру истраживања се анализира и улога генеративног размножавања у процесу ширења врсте.

Резултати су показали да *A. lanceolatus* ствара велику количину семена које се расејава анемохорно. Утврђена је одређена количина штурог семена, а проценат клијања ахенија насталих из једне главице није био висок. Ипак, с обзиром на велику количину семена по једној биљци и броју индивидуа у једној популацији, може се рећи да је ова количина клијалог семена довољна за ширење врсте на нове локације. Управо на овај начин, *A. lanceolatus* доспева на нове територије, а након ове фазе, захваљујући великој способности за вегетативно размножавање коју поседује, за кратко време успева да освоји слободан простор. Семе је показало малу енергију клијања и то може бити ограничавајући фактор у репродуктивној екологији врсте *A. lanceolatus*. Ипак, могуће је да је на енергију клијања утицала температура током клијања семена и да би са порастом температуре и енергија клијања била већа. Параметри клијања су се разликовали у односу на локалитете. Ове разлике се могу приписати различитој генетској структури и фенотипској пластичности индивидуа врсте *A. lanceolatus* као и различитим микроклиматским условима локалитета.