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FACTORS DETERMINING THE DISTRIBUTION OF *ARONIA PRUNIFOLIA*, AN EMERGING INVASIVE PLANT SPECIES IN LATVIA

Agnese Priede

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The paper presents a study of the non-native invasive shrub *Aronia prunifolia*, a species with a rising number of localities and increasing abundance within invaded areas. This deciduous shrub of North American origin is invading abandoned meadows, pastures and forests in some coastal parts of Latvia. Due to its specific habitat requirements, the species is confined to rather small areas, where it grows on moderately acidic to acidic soils on sand and peat substrates. In order to understand the factors limiting its spread, climatic and soil conditions, vegetation types and the spread of the species were studied. The species appears to be strongly related to the sub-oceanic climate with specific soil conditions, mostly low pH, as the most important limiting factors. In some areas it has become a vigorous invader, causing changes in biologically valuable grassland types and outcompeting local secondary shrub species.

Key words: *Aronia prunifolia*, climatic relevance, distribution, non-native species, soil traits.

Agnese Priede, Ķemeri National Park, Meža māja, Ķemeri, Jūrmala, LV-2012, Latvia, agnese.priede@kemeri.gov.lv

Introduction

Non-native plant invasions are considered a significant part of a biota's change towards homogenization of originally different flora (Gordon 1998). Non-native invaders can perform new functions in the invaded community, e.g. change the community structure and probably cause changes in the soil by nutrient cycles (Parker at al. 1999; Ehrenfeld 2003). Disturbed and fragmented ecosystems are considered to be more prone to invasions than others (With 2004). In forest ecosystems, clearings, fires, high recreation impact and other disturbances, particularly in the vicinity of human settlements, pose a threat to the disturbed system by non-native species invasions. In grasslands where the semi-natural ecosystem diversity is maintained by continuous management, the abandonment and subsequent decline of species diversity may be essential factors for the establishment and expansion of non-native invaders. Recent land abandonment in many parts of Europe has resulted in significant changes in previously managed grasslands and pastures by decreasing the grassland cover and diversity and extension of woodlands (Stampfli & Zeiter 1999). Abandonment is followed by dominance of stronger, ecologically less specific competitors, consequently changing the light availability at the soil surface and producing larger amounts of litter (Berendse 2005), thus causing a decrease of species diversity. The former grassland areas turn into shrub lands, threatening grassland communities and endangered grassland species. The vicinity of donor areas and suitable environmental conditions are significant factors facilitating

establishment of non-native invasive shrub species in overgrowing grasslands and pastures, comprising a significant portion of the newly emerged vegetation type.

In many cases, the initial phases of non-native invasions are poorly documented, thus not allowing proper reconstruction of many common invaders, also in Latvia (Priede 2008). In Latvia, *Aronia prunifolia* represents an example of non-native invasive shrub species in its initial phase of invasion with rising number of localities and increasing abundance in invaded areas. *A. prunifolia* had been found both on shrub lands, in abandoned grasslands and pastures and deteriorated secondary forests and bog margins. The currently known distribution of the species suggests that it is locally invasive, limited to several relatively small areas where it is able to become a vigorous grassland invader and to build mono-dominant or mixed shrub stands. This study is aimed at finding out the current distribution of *A. prunifolia*, currently a rare non-native invader, in Latvia and to identify the specific factors limiting the spread of the species. This article attempts to answer following questions: (1) Is *A. prunifolia* only locally invasive or potentially widely spread invasive species? (2) What is limiting the spread of *A. prunifolia*?

Species

Species of the genus *Aronia* are deciduous shrubs that belong to the family Rosaceae. Three species are known: red chokeberry *Aronia arbutifolia* (L.) Pers., black chokeberry *A. melanocarpa* (Michx.) Elliot. and purple fruit chokeberry *A. prunifolia* (Marshall) Rehder. Most authors consider the purple fruit chokeberry *A. prunifolia* to be an intermediate species, a natural hybrid of *A. arbutifolia* and *A. melanocarpa* (Hardin 1973; Rosell & Kesgen 2003).

Aronia shrubs are rhizomatous. The shrubs flower in May-June. Flowers are followed by dark purple to black fruits (Rosell & Kesgen 2003).
The genus *Aronia* is native to North America. In its native region, *A. arbutifolia* is distributed throughout eastern North America, centred in the southeastern Coastal Plain. It ranges from the costal plains on the east coast to inland. The species occurs in bogs, savannahs, low wet woodlands both in lowlands and mountainous areas. A congener native species *A. melanocarpa* is found in similar habitats. Its range is centred in the northeast of the U.S. and Great Lakes area. It had been found also in higher elevation in the Appalachians. The species is absent in coastal plains and occurs further inland (Hardin 1973; Rosell & Kesgen 2003). Andreas & Bryan (1990) mentioned that *A. prunifolia* is a common species on the marginal areas of raised bogs.

In the U.S., *Aronia* species are used in ecological restoration, landscaping and wildlife management, especially in the native regions of the species (Rosell & Kesgen 2003). The rhizome system is suitable for soil fixation. Branches are able to root if touching the ground, therefore in suitable conditions the plant propagates easily. *A. melanocarpa, A. arbutifolia*, and the hybrid species *A. prunifolia* were introduced to central and northern Europe in the 19th century (Lohmeyer & Sukopp 1992; Kukk et al. 2001), where they were cultivated in gardens both as fruit frees and ornamentals. In Latvia, *Aronia* species were introduced in 1821 and reintroduced at the end of the 19th / beginning of the 20th century. After World War II *A. prunifolia* under the name *A. mitschurinii* was brought from Russia, currently known as *A. prunifolia* 'Floribunda' (Cinovskis 1994). Currently all three species of *Aronia* (*A. arbutifolia*, *A. melancarpa* and *A. prunifolia*) are cultivated in Latvia. While the first two are rare, a variety of *A. prunifolia* 'Floribunda' is a common garden ornamental and fruit tree.

The pomes of *Aronia* are edible and highly valuable as a foodstuff and vitamin source. When ripe they are used mainly for producing juice with a specific dark purple colour. The pigments of the juice are used commercially as a natural colour in the food industry (Riekstiņš 1959; Rosell & Kesgen 2003). In temperate and northern Europe, *Aronia* species and cultivars are quite frequently used as ornamental shrubs,

mainly in hedges. In temperate climates, they are able to grow fast and form dense leafage.

In some countries of temperate Europe where the *Aronia* species had been cultivated, they are announced as invasive neophytes (Wiegers 1983, 1984; Kukk et al. 2001; Sżkora & Bergsma 2005; Anonymous 2006b). In the Netherlands, *Aronia* communities classified as DC Aronia prunifolia-[Betulion pubescentis] are accompanied by *Betula pubescens* with rejuvenating *Alnus glutinosa*, while the herbaceous and moss layer is formed by *Aulacomnium palustre* and *Eurhynchium praelongu* (Sżkora & Bergsma 2005). Lohmeyer & Sukopp (1992) mention that in central Europe the species forms *A. prunifolia* communities, and had been found in Caricion fuscae and Alnion glutinosae communities. Wiegers (1990) noted that the species is widespread in the Netherlands in peat land forests. However, there is still little information available on the distribution and ecology of the introduced species in Europe.

Study area

In 2007-2008 a study of the species' distribution and ecology was performed in Latvia on the coastal lowland of the south west coast of the Gulf of Riga in Ķemeri National Park (ĶNP). The coastal lowland is dominated by sandy sediments (Anonymous 2000; Dreimanis & Zelčs 1998). Typical sandy podsols are dominating on higher ground, while gleyic podsols (peat soils) are developed in depressions (Nikodemus, 1998). The neighbourhoods of the studied area are covered by the shallow lagoon lake Kaņieris, while the surroundings of the lake are dominated by calcareous soils. On the lakeshore, which is relatively little affected by human activities, fens on nutrient- and base-rich peat predominate. In the coastal area the partly merged villages Ragaciems (57°01'28'', 23°29'40''), Lapmežciems (57°00'19'', 23°30'45''), and Bigauņciems (56°59'06'', 23°32'21'') are located, while the rest of area is extensively used. Abandoned pastures and grasslands, shrub lands and secondary forests predominate. The study area includes the Kūdra village (part of Jūrmala city) with allotments (56°55'50'', 23°32'46'') approximately five kilometres from the seaside. The village is located on the edge of a raised bog complex that had been used for peat extraction over the last decades. Soils are formed on nutrient-poor peat substrates. Vegetation is dominated by secondary birch and pine forests.

On the coastal lowland the climate is mild, influenced by the vicinity of the sea. Mean temperatures in July range between +16.5 to and +17°C. In January the mean temperatures vary from +4.0 to +5.0°C. Annual precipitation ranges from 600 to 650 mm (Krūmiņš 1998). The western part of the Gulf of Riga is characterized by weak continentality (compared with most of the territory of Latvia, snow periods are shorter, and there is a moderate amount of warmth, low amounts of precipitation and moderately cool summers typical for coastal areas) (Laiviņš & Melecis 2003).

Material and methods

In 2007, areas invaded by *A. prunifolia* were surveyed. The exact localities of *A. prunifolia* shrubs and stands within the study area in ĶNP were noted, and accurate distribution of the species was mapped. Areas potentially invaded by *A. prunifolia* were distinguished on the basis of habitat similarity to currently invaded areas. In order to find out the current distribution of the species in Latvia, the herbarium materials of the Institute of Biology, University of Latvia, were revised. Expert notes and personal observations were included.

Relevance to climatic conditions (continentality, precipitation, character of summers, and amount of warmth) was analyzed on the basis of a regular grid of 10×10 km with fixed average climatic parameters, divided in sectors for all the territory of Latvia, prepared by Laiviņš & Melecis (2003). Continentality sectors were defined by average temperatures in January, annual average temperature, absolute minimal temperature, annual average minimal temperature, maximum depth of soil freezing, number of days with snow cover per year, water content in snow cover,

height above the sea level and distance from the sea. Precipitation sectors were distinguished by classifying the average precipitation in the warm months (May to October), the average precipitation in cold months (November to March) and annual average precipitation. On the basis of average July temperatures and absolute maximum temperatures, the character of summers was classified into four groups: cool, moderate, moderately warm and warm. The amount of warmth reflects the biologically active season (vegetation period), which is defined by the sums of air temperature in the periods with the average air temperature above 0°, 5°, 10° and 15°C and the number of days when the temperature is higher than 10° and 15°C (Laiviņš & Melecis 2003). Each 10×10 km quadrate was attributed by climatic variables mentioned above.

In order to understand the characteristics of invaded vegetations types and environmental conditions typical for invaded sites, species composition and covers were used as indicators. Vegetation in 17 randomly chosen plots within the invaded area of size 10×10 m were described, and total cover and cover of all species in each vegetation layer were estimated. Vegetation was described both in grasslands and woodlands in typical situations where *A. prunifolia* was present as a dominating species. The division of relevés was performed by the TWINSPAN program. Mean Ellenberg's values (Ellenberg et al. 1992) for each relevé were calculated. Environmental gradients, such as moisture, light, nutrients and soil traits were selected to analyze the ecology of species. Ordination of relevés attributed by mean Ellenberg's values was performed using DCA (Detrended Correspondence Analysis).

Soil samples were taken from the depth 20 to 30 cm (lower topsoil layer), excluding the litter layer. Two mixed samples in each of five selected localities were taken in September 2007. Sites were selected in well-established and increasing *A. prunifolia* populations. Total nitrogen (TN), total organic matter (TOC), and pH were analyzed. TN was determined by modified Kjeldahl method LV ISO 11261:2002; TOC was determined by LVS EN 13039:2003 (dry combustion), and pH was measured in potassium chloride (KCl) solution.

Results

Distribution

In Latvia, *A. prunifolia* is a recently emerged non-native species and has been found in few localities. Herbarium data from the 1970's and the 1980's suggest that the spread probably began approximately at the end of the 1970's. The farthest know record of a locality, Mērsrags on the west coast of the Gulf of Riga, dates back to 1979. Repeated survey in Mērsrags in 2007 revealed approximately 50 individuals on the coastal meadow. In 2007 and 2008, several areas heavily invaded by *A. prunifolia* were found in ĶNP. In the vicinity of Lake Kaņieris, Kūdra village and Ķemeri the species forms dense stands or were found as scattered individuals. The invaded areas were rather confined, neighbouring with villages, lakeshore, deteriorated peat bogs, or forests. Other localities are scattered in the coastal area in suburban and former peat extraction areas, and in the vicinity of villages and towns, where the species was found mainly in shrub lands, forests and margins of grasslands (Fig. 1). The registered localities are listed in Appendix 1.

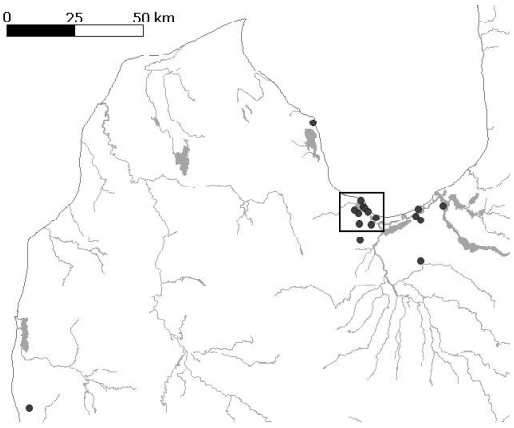


Fig. 1 Distribution of *Aronia prunifolia* in Latvia. The study area is marked with a frame.

Invaded habitat complexes

Within the studied area, two heavily invaded habitat complexes were distinguished. Using TWINSPAN division, two major vegetation groups invaded by *A. prunifolia* were differentiated.

On the coastal lowlands to the southwest of the Gulf of Riga, most *A. prunifolia* shrubs were found on moderately humid grasslands on sandy, peat and/or sandy-peaty soils, dominated by *Deschampsia cespitosa* and *Festuca ovina, Nardus sticta* and/or *Sieglingia decumbens*, typically accompanied by *Potentilla erecta, Holcus lanatus, Luzula multiflora* and *Rumex acetosa* (Group I). *Nardus stricta*, *Sieglingia decumbens* and *Calluna vulgaris* predominated on shallow slopes and declines. Over the previous decades, most of these grasslands in the surroundings of the coastal villages were used as pastures and hay meadows. It is likely that the increasing abundance of *D. cespitosa* is related to accumulation of nutrients due to the absence of previously practiced grazing management. Due to abandonment, the expansion of *Calamagrostis epigeios* was observed. Currently, rapid overgrowing both by secondary local shrub species *Frangula alnus, Betula sp., Salix sp.* and non-native *A. prunifolia* is observed. On more humid, slightly acidic peat soils, higher abundance of *Alnus glutinosa* was observed. Consequently, continuous lack of management will lead to formation of dense shrub land followed by *Alnus glutinosa* dominated forest.

Large *A. prunifolia* stands were found on the margins of a former peat extraction site, where the population of the invader was limited to a rather small area where the species grew in a species poor secondary *Betula pubescens* dominated forest with dominating *Molinia caerulea* on the herbaceous layer, partly disturbed by several forest fires. The shrub layer was dense, dominated by *A. prunifolia* and *Frangula alnus*. *Salix myrsinifolia, S. cinerea, Sorbus aucuparia, Amelanchier spicata, Populus tremula, Corylus avellana* and *Quercus robur* were found as frequent accompanying species with lower density (Group II). In the vicinity, *A. prunifolia* had been planted as a hedge ornamental around several summer cottages. *A. prunifolia* was found also on the margins of peat extraction ponds in plant communities typical for deteriorated raised bogs dominated by dwarf shrubs *Calluna vulgaris, Ledum palustre, Vaccinium uliginosum, Vaccinium vitis-idaea* and *Andromeda polifolia*. Recently the invasive species was found on the margins of the former peat milling field, a deteriorated raised bog, on the east part of the Great Ķemeri Mire, which is perhaps a suitable habitat for formation of *A. prunifolia* shrub land. A few isolated *A. prunifolia* shrubs were found in other localities within ĶNP on the margins of ditches and drained *Alnus glutinosa* dominated forests on the lakeshores, in glades in secondary birch forests, in mixed pine-alder forests on a lakeshore, and on sand dunes with lichen and moss dominated vegetation.

Ellenberg indicator values

In most cases, slight differences in mean Ellenberg values of both vegetation types invaded by *A. prunifolia* were found. As the most important, the continentality factor was stronger in grassland communities (Group I) with *A. prunifolia* than in woodland (Group II). Average values of soil reaction and nutrients show that communities of species-poor birch forests grow on acidic and nutrient-poor soils, while those of *Nardus* grasslands tolerate slightly less acidic soil with higher nutrient levels. In both groups most species are adapted to moderately warm soils and grow in half-light to half-shaded conditions (Fig. 2).

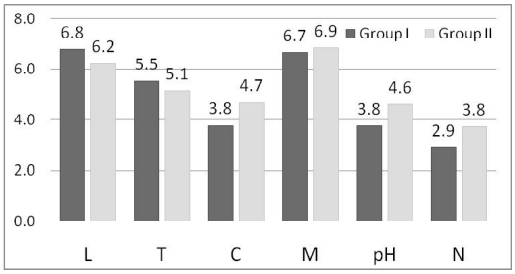


Fig. 2 Comparison of mean Ellenberg values for Group I and Group II.

DCA ordination distinguished two groups of relevés. The positions of relevés in ordination space suggest the same distribution pattern along the ecological gradients as described above (Fig. 3a). DCA Axis 1 explained 46% of the variance in the distribution of the relevés, while Axis 2 explains only 18%.

Soil traits of invaded areas

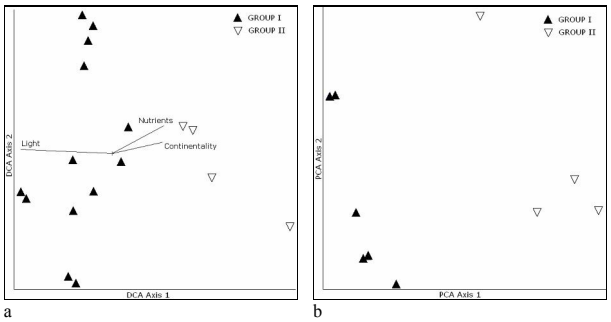
High variability was found in all soil parameters (Table 1). PCA Axis 1 distinguishes two major groups, differentiating by significant differences in TN, TOC and pH (Fig. 3b). Group I represent deteriorated peat bog and lakeshore meadow on acidic to slightly acidic peat soils with high nitrogen content and high content of poorly decomposed organic matter. Group II shows the soil characteristics of *Deschampsia cespitosa* and *Nardus stricta* grasslands on sandy soils with low nitrogen and TOM content, and slightly acidic to acidic reaction.

Correlation with climatic variables

Among the climatic variables, low winter air temperatures, low minimum temperatures in January and probably also the length of the soil freezing period (factors comprised under continentality) seem to be the most important factors influencing the distribution of *A. prunifolia*. The majority of invaded quadrates fall into the zone of weak continentality (Fig. 4a). Differences in other climatic factors, such as precipitation, character of summer, and length of vegetation season (Fig. 4b - 4d) seem to have less effect on the distribution of *A. prunifolia*.

Table 1. Soil sampling sites and chemistry results

Sample No.	Group	Soil type	Dominating vegetation type	N tot. (g/kg)	Org. matter (%)	pH KCl
1	I	Peat soil	Lakeshore *Nardus stricta* grassland	17.3 ± 0.7	46 ± 1	4.57 ± 0.05
2				12.7 ± 0.5	65 ± 2	3.15 ± 0.03
3	I	Sandy soil	*Sieglingia decumbens* dominated grassland	1.15 ± 0.05	2.65 ± 0.08	3.77 ± 0.03
4				0.7 ± 0.03	1.73 ± 0.05	3.78 ± 0.03
5	I	Sandy soil	*Deschampsia cespitosa* dominated grassland	2.8 ± 0.1	6.7 ± 0.2	4.97 ± 0.04
6				1.11 ± 0.04	22 ± 1	5.01 ± 0.04
7	I	Sandy soil	*Deschampsia cespitosa* dominated grassland	1.19 ± 0.04	5.7 ± 0.2	4.11 ± 0.24
8				2.2 ± 0.1	9.5 ± 0.3	3.45 ± 0.03
9	II	Peat soil	Deteriorated peat bog, sparse birch forest	14.0 ± 0.6	92 ± 3	3.21 ± 0.03
10				15.0 ± 0.6	96 ± 3	2.88 ± 0.03
11	II	Sandy soil	*Deschampsia cespitosa* dominated grassland	1.19 ± 0.04	5.7 ± 0.2	4.11 ± 0.24
12				2.2 ± 0.1	9.5 ± 0.3	3.45 ± 0.03



a b

Fig. 3 Ordination of relevés and soil samples. DCA ordination of relevés along environmental gradients (a); PCA ordination of soil samples (b).

Fig. 4 Distribution of *A. prunifolia* in climatic zones of Latvia.

The intensity of colouration of the grids indicates the strength of each

factor from weak (white) to strong (medium dark to dark grey).

Although the statistical evidence for the effect of certain climatic factors is rather weak, the results suggest that the zone of weak continuality, low to moderate precipitation, moderately warm summers and medium to high amount of warmth is the most suitable for the growth and spread of *A. prunifolia* (Table 2).

Table 2. Frequency of occurrence of *Aronia prunifolia* within the zones defined by climatic variables.

Factor	**Strength**	**Frequency**
Continentality	Weak	8
	Moderate	1
	Medium	0
	Strong	0
Precipitation	Low	4
	Moderate	4
	Medium	0
	High	1
	Very high	0
Character of summers		Cool 1
	Moderately cool	1
	Moderately warm	7
	Warm	0
Amount of warmth		Slight 0
	Moderate	1
	Medium	4
	High	4

Discussion

A. prunifolia has been widely cultivated in Latvia since the second half of the 20th century. Nevertheless, its spread outside cultivation is confined to rather small areas in coastal regions only, while there is no evidence of its spreading outside cultivation in more continental regions of central and/or eastern Latvia. Analysis of the current distribution reveals that most probably the spread of *A. prunifolia* is limited by climatic and soil conditions. Distances of all known *A. prunifolia* localities do not exceed 25 km from the seaside, which suggests that it is a sub-oceanic species limited by low air temperatures and long cold periods. The species is able to tolerate oligotrophic to medium rich peat soils and light, and poor sandy or peaty-sandy soils ranging from low to medium low pH. Mean Ellenberg's values derived from the vegetation types invaded by *A. prunifolia* suggest suitability to certain environmental conditions, where light and soil nutrients differentiate the vegetation composition, while *A. prunifolia* tolerates both major types of growing conditions. Soil samples taken in five established populations form two easily distinguishable groups and the same pattern is demonstrated by the analysis of Ellenberg's values. However, at present the species is a recently emerged, rare non-native, thus the current distribution pattern may be coincidental. Experimental study could prove or reject the hypothesis of the climatic and edaphic limitations for successful spread of the species in more continental situations.

Mostly the species grows on moderately humid soils. In very few cases *A. prunifolia* had been found on extremely dry sandy soils in sand dunes. No *A. prunifolia* shrubs were found in the neighbouring grasslands on calcareous soils dominated by *Sesleria caerulea* because the species do not tolerate high calcium levels (Sżkora & Bergsma 2005). This suggests that soils conditions are significant constraint limiting the spread of *A. prunifolia*, thus not allowing establishment in certain habitat types. Mostly *A. prunifolia* have been found on drained soils, suggesting that also hydrological changes followed by peat extraction and consequent removal of the former vegetation promotes the establishment and spread of *A. prunifolia*. Wiegers (1984; 1990) and Sżkora & Bergsma (2005) note that in the Netherlands *A. prunifolia* grows in former peat-cutting areas on birch woodlands in nutrient poor marshes or on deteriorated peat bogs on nutrient poor, acidic peat and peaty-mineral soils with a high groundwater level, low calcium contents (<0.1%) and pH below 5.0. The results of this study are in accordance with previous studies in the

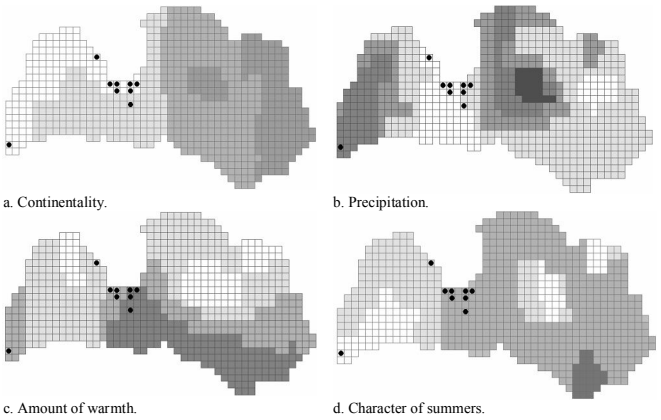


Fig. 4. Distribution of *A. prunifolia* in climatic zones of Latvia

Netherlands. Since the amount of nitrogen and organic matter in soil samples is highly variable (0.7 – 17.3 g/kg and 1.73 – 96 %, respectively), these factors are considered of low importance in limiting the establishment and spread of *A. prunifolia*. The most significant soil variable limiting the spread of the species is soil pH, in this case varying in comparatively smaller range (pH2.88 – 5.01).

A. prunifolia has spread over a wide range of habitats. The species can grow in open areas, sparse shrub lands or disturbed sparse secondary deciduous and mixed deciduous-pine forests, glades and margins of former peat-cutting areas. The species is rather tolerant to shade, although it decreases the pome production (Riekstiņš 1959) and consequently curtail its spread. Several studies (Knight & Reich 2005; Mandryk & Wein 2006) show that undisturbed forest structure and species composition reduce the possibility of establishment of non-native invaders, and native species richness is negatively correlated with covers and richness of non-native invaders. Most of known *A. prunifolia* localities in Latvian forests are found on ~~in~~ various levels of disturbance, suggesting that no threats for neighbouring natural forest communities may be expected. For instance, the secondary birch forest in Kūdra had been lately disturbed by fire. Fire disturbance allows the establishment of *A. prunifolia* by temporal clearing of other native shrubs, thus creating suitable light conditions for the emerging invaders.

As an illustration for the local situation on the coastal lowland to the southwest of the Gulf of Riga, potentially invaded habitats were distinguished on the basis of similarity to currently invaded habitats. Habitat invasibility and the potential occurrence were estimated by the suitability of the invasive species to certain grassland, shrub land and forest types observed in the particular area, and the vicinity of donor areas. Since no *A. prunifolia* populations or few scattered individuals were found in calcareous grasslands, dry or swampy pine forests, and rich deciduous forests, they are assumed to be relatively resistant again invasions, while moderately humid, nutrient rich grasslands, particularly in the surroundings of coastal villages are highly vulnerable (Fig. 5).

From the viewpoint of nature conservation, the spread of *A. prunifolia* within semi-natural grasslands on the coastal area is not desirable. Firstly, it causes degradation of highly valuable species-rich *Nardus* grasslands, a rather rare

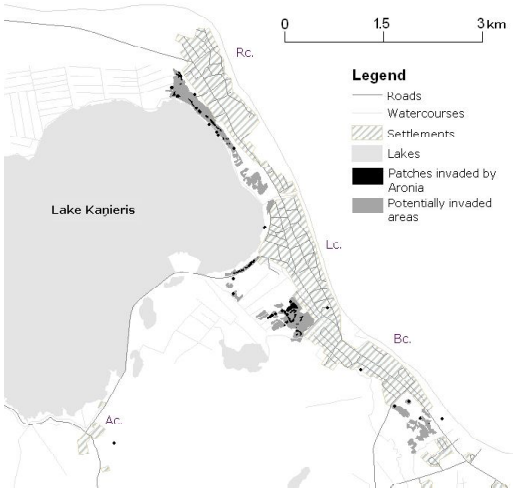


Fig. 5 Invaded and potentially invaded areas in the vicinity of Ragaciems (Rc.), Lapmežciems (Lc.), Bigauņciems (Bc.) and Antiņciems (Ac.) villages.

grassland type in Latvia. Secondly, the management measures needed for its eradication are rather intricate in comparison with native secondary shrubs and trees. Grassland restoration and control measures used for eradication of shrub layer create suitable conditions for establishment of fast growing *A. prunifolia* stands. Rhizomatous growth, ability to resprout from upper branches and spreading by seeds renders the species a specific status among the other shrub species invading abandoned grasslands. In some overgrown grasslands where shrubs had been cleared in late autumn 2006 fast regrowth of *A. prunifolia* stumps was observed that exceeds the regeneration rate of native shrub species. After cutting, *A. prunifolia* outcompetes native species such as *Frangula alnus* and *Salix cinerea*. In order to eradicate the *A. prunifolia* stands, repeated cutting and uprooting should be performed.

The establishment and spread of *A. prunifolia* is also greatly facilitated both by continuous cultivation and birds. A combination of these factors allows the species to become a successful invader of overgrowing abandoned moderately humid grasslands and pastures on coastal lowlands. Pasture abandonment, absence of traditional livestock grazing and mowing, peat land drainage and consequent changes in dominating vegetation types and access to light and soil nutrients promotes the spread of the species. The grasslands within the study areas are mostly private owned. Due to economic changes most of lands were abandoned. Unless the grasslands are regularly mown or grazed, they are exposed to expansion of shrubs, both native and non-native, including *A. prunifolia*.

In summary, this study gives an insight into the spread of invasive shrubs limited by certain environmental conditions. *A. prunifolia* represent a case when an introduced species may become a vigorous invader under particular environmental conditions, while being absent or rare in other areas in the same region. Since the 1970's, *A. prunifolia* has been a rare invader in coastal areas with mild climate conditions and specific habitat conditions. Although no large-scale invasions outside coastal areas may be expected in the near future, the species is a strong competitor significantly contributing to the overgrowing process in semi-natural grasslands.

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	Moderate	4
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	High	1
	Very high	0
Character of summers	Cool	1
	Moderately cool	1
	Moderately warm	7
	Warm	0
Amount of warmth	Slight	0
	Moderate	1
	Medium	4
	High	4

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APPENDIX 1

Registered localities of *Aronia prunifolia*

Information sources: LATV – herbarium of the Institute of Biology (University of Latvia); BI GL – Institute of Biology, Laboratory of Geobotany; ĶNP – database of Ķemeri National Park; M – data obtained in personal communication; P – personal observation.

Locality	Habitat	Number of individuals	Year of registration	Author	Information source
Mērsrags	Coastal meadow	unknown	1979	V.Šulcs	LATV
			2003	Ģ.Gavrilova	LATV
		~ 50	2007	A.Priede	P
Rīga, Beberbeķi	Pine forest	unknown	1987	H.Zariņa	LATV
		~ 50	2007	A.Priede	P
S from Olaine	Drained pine forest on peat soil	unknown	1991	M.Laiviņš	BI GL
Rucava	Pine forest	unknown		Ģ.Gavrilova	M
Rīga, Krēmeri	unknown	unknown	2006		Anonymous 2006
Ragakāpa (Jūrmala)	Wooded dunes	1	2002		Anonymous 2002
Lapmežciems	Abandoned meadows, shrub lands, mixed forests	~ 500	2007	A.Priede	ĶNP
Bigauņciems	Abandoned meadows, shrub lands	~ 10	2007	A.Priede	ĶNP
Ragaciems	Abandoned meadows, shrub lands, dry pine forest	~ 350	2007	A.Priede	ĶNP
Kūdra (Jūrmala)	Margins of former peat extraction fields, drained birch forest	~ 260	2007	A.Priede	ĶNP
Antiņciems	Birch forest, glade	1	2007	A.Priede	ĶNP
W from Kauguri (Jūrmala)	Shrub land, margin of peat extraction ponds	1	2007	A.Priede	ĶNP
W from Babīte	Shrub land	~ 10	2008	A.Priede	P
N from Ķemeri	Bog woodland	~ 500	2008	A.Priede	ĶNP
S from Ķemeri	Mixed deciduous forest	~ 10	2008	A.Priede	ĶNP
E of Great Ķemeri Mire	Former peat milling field, drained birch forest on bog margin	~ 30	2008	A.Priede	ĶNP
SW coast of Kaņieris lake	Shrub land	3	2008	A.Priede	ĶNP

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