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Ecogeographical Analysis of the *Heracleum persicum*, *H. mantegazzianum*, and *H. sosnowskyi* Distribution at the Northern Limit of Their Secondary Ranges in Europe

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Abstract—This paper analyzes the distribution of *Heracleum persicum*, *H. mantegazzianum*, and *H. sosnowskyi* at the northern limit of their secondary ranges in Europe based on original and published data. The northernmost *H. persicum* occurrences are localized in coastal regions in the northern and central parts of the Scandinavian Peninsula (up to 71° N). In Fennoscandia, *H. mantegazzianum* and *H. sosnowskyi* were noted up to 69° N. The gradient of climatic resources in the subarctic and temperate zones made it possible to identify factors limiting further expansion of these species in northern Europe and determine their tolerance limits to these factors. The duration of the frostless season at the northern boundary of the secondary range of invasive Heracleum species is 80–150 days. The probability of cold damage to vegetating plants in areas located north of 66° N (i.e., in the northern part of Finland and in the continental northern part of European Russia) is high. The biological minimum for the sum of active air temperatures ≥5°C is 1150°C, while the minimum requirement of the studied plants for the sum of active temperatures ≥10°C is over 450°C. If available thermal resources exceed this level, then invasive Heracleum species can naturalize in climatic conditions of subarctic Europe. The presence of a sustainable snow cover more than 25 cm depth in areas where the minimum winter temperatures are less than –30°C prevents the freezing of renewal buds and seedlings, thus, preserving the viability of plants. It is proposed to use climatic indices computed as ratios between the air temperature and the snow cover depth (or the precipitation amount in winter) as climatic markers characterizing wintering conditions for plants. The main factors limiting the spread and naturalization of invasive Heracleum species in northern Europe are lack of heat, soil freezing to temperatures critical for hibernating plant organs, and early autumn frosts.

Keywords: *Heracleum sosnowskyi*, *Heracleum mantegazzianum*, *Heracleum persicum*, invasion, northern distribution limit, climatic conditions

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INTRODUCTION

The spread of alien plant species attracts close public and scientific attention owing to adverse impacts exercised by invaders on native ecosystems and significant costs required to control them (Simberloff, 2009; Pimentel, 2011; Pluess et al., 2012; Dalke et al., 2018). The invasion of *Heracleum mantegazzianum* Sommier & Levier, *Heracleum persicum* Desf. ex Fisch., C.A. Mey. & Avé-Lall., and *Heracleum sosnowskyi* Manden., belonging to the section Pubescentia, genus *Heracleum*, is currently under review since these species became widespread in Europe. On the basis of their similar habits (plant height up to 4–5 m and leaf length up to 3 m), reactions to environmental factors, and high invasive potentials, researchers consider them a single group of invasive Heracleum species (Nielsen et al., 2005; *Ecology and Management*..., 2007). Invasive Heracleum species are difficult to identify (Jahodová et al., 2007) and can hybridize with other species of the genus *Heracleum* (Stewart and Grace, 1984; Rijal et al., 2015), which makes it possible to treat them as a single group for the purposes of their invasive potential assessment and development of control measures (Nielsen et al., 2005).

The history of their introduction has largely determined the modern distribution of these species in Europe. *H. persicum* is widespread in Northern Europe (Norway, Finland, and Sweden) (Nielsen et al., 2005). The expansion of *H. mantegazzianum* is noted in a significant part of the European continent: from the Scandinavian Peninsula in the north to the Apennine Peninsula in the south. The western boundary of the invasive range of the species encompasses the British Isles (Nielsen et al., 2005; *Ecology and Management*..., 2007), while the eastern boundary passes through central Russia (Notov, 2005). *H. sosnowskyi* is more widespread in Eastern Europe: the species is noted from Poland, Bulgaria, and the Baltic states in the west (*Ecology and Management*..., 2007; Vladimirov et al., 2019) to the Ural Mountains in the east (Abramova, 2011). The southern border of the *H. sosnowskyi* distribution range in Russia is located north of 50° N (Afonin et al., 2017), while the northernmost occurrences were registered on the Kola Peninsula (Men'shakova, 2011).

The leading role of climate in the distribution of plants is generally recognized. Results of numerous studies indicate that such factors as temperature regime, amount of precipitation, and content of mineral nutrients in the soil affect the possibility of invasion of alien species and changes in their distribution ranges. Interactions between elements of global climate change that can contribute to biological invasions are of special interest (Dukes and Mooney, 1999; Simberloff, 2000; Clements and Ditommaso, 2011; Allen and Bradley, 2016). A number of studies examined climatic conditions that determine the distribution of species of the genus *Heracleum*. It was found that the key factors for successful *H. mantegazzianum* reproduction in central Europe (Czech Republic) are the temperature regime in the winter period and the amount of precipitation (Pyšek et al., 1998). Experimental studies conducted in the altitudinal gradient in England showed that a decrease in heat supply equal to the reduction of the sum of active temperatures ≥5°C to the level of 1000°C suppresses the biomass accumulation process in *H. mantegazzianum*; the authors believe that the formation of germinable seeds by the plants under such conditions is unlikely (Willis and Hulme, 2002). In the southern part of the *H. sosnowskyi* secondary range in European Russia, the main factor limiting the spread of this species is moisture availability. South of 60° N, the *H. sosnowskyi* occurrence frequency declines as the precipitation amount decreases, and the southern limit of its distribution range in European Russia coincides with the hydrothermal coefficient isoline equal to 1.25 (Afonin et al., 2017).

However, the available data on the role of environmental factors in the distribution of the invasive Heracleum species group in Europe (Pyšek et al., 1998; Willis and Hulme, 2002; Afonin et al., 2017) and North America (Page et al., 2006) are insufficient and do not make it possible to assess the effect of climatic conditions on the northward expansion of the invasive range of these species.

A characteristic feature of invasive species is their ongoing expansion. It is believed that most naturalized neophytes have not reached the equilibrium state yet and will continue to expand their ranges for at least 150 years (Williamson et al., 2009). Modern climatic changes can affect the distribution ranges of invasive species (Dukes and Mooney, 1999; Clements and Ditommaso, 2011). Therefore, it is important to determine the potential limits of their invasive ranges and factors affecting the distribution of these plants, both for the purposes of fundamental science and for practical control of alien species (Willis and Hulme, 2002; Simberloff, 2009; Pluess et al., 2012).

The purpose of this study was to assess environmental conditions at the northern limit of modern invasive ranges of *H. persicum*, *H. mantegazzianum*, and *H. sosnowskyi*, identify factors limiting their further expansion in northern Europe, and determine the tolerance limits of the studied plants to these factors.

MATERIALS AND METHODS

Data Collection: Occurrences of Invasive Species of the Genus Heracleum

Data on the *H. persicum* and *H. mantegazzianum* distribution in the northern part of Europe were obtained from the literature (Pyšek et al., 2010; Gederaas et al., 2012; Rijal et al., 2015, 2017). The geographic coordinates of giant hogweed discovery points (Table 1) were obtained from the Global Biodiversity Information Facility (GBIF) database (GBIF..., 2020). A critical analysis of the invasive Heracleum species occurrence data accumulated in the GBIF was performed; preference was given to occurrences previously mentioned in the literature and/or verified by us through a visual assessment of spatially referenced photographs available in the Google Street View (2021).

Some data on *H. sosnowskiy* occurrences in the northern part of European Russia were also obtained by analyzing spatially referenced Yandex.Maps (2021) and Google Maps photographs. Using built-in tools of the cartographic services, the geographical coordinates and survey dates were recorded for locations where the presence of *H. sosnowskyi* plants was visually confirmed. This data collection approach made it possible to specify the geographical coordinates of *H. sosnowskyi* occurrences in the cities of Murmansk, Arkhangelsk, and Apatity. In addition, field studies were conducted in 2016 and 2018 in the northern part of European Russia (north of 66° N). The Inta and Vorkuta urban districts in the Komi Republic (settlements of Meskashor and Sivomaskinsky), where *H. sosnowskyi* used to be cultivated as a fodder crop (Khantimer, 1974), were surveyed. The total mileage of field survey routes in the vicinity of the city of Inta was 120 km; in the vicinity of the settlements of Meskashor and Sivomaskinsky, 22 km. All data on *H. sosnowskyi* occurrences collected by the authors in the course of field studies and by analyzing Google Maps and Yandex.Maps images have been published in GBIF (Dalke et al., 2019).

Table 1. Heracleum invasive species occurrences at the northern limit of their secondary ranges and the closest weather stations (WS)

No.	Species and GBIF occurrences identifier	Settlement and occurrences geographic coordinates, °N, °E	Closest WS (distance to the closest Heracleum occurrences)	Station ID in GHCNd*	WS coordinates, °N, °E	Elevation above sea level, m
1	*H. persicum* gbifid = 2332845068	Gamvik 71.0833, 28.1857	SLETTNES FYR (3 km)	NOE00109777	71.0839, 28.2178	8
2	*H. persicum* gbifid = 2400590081	Vardø 70.3722, 31.0963	VARDOE (1 km)	NOE00105494	70.3703, 31.0990	14
3	*H. persicum* gbifid = 1323758612	Tromsø 69.6418, 18.9249	TROMSO (1 km)	NO000001026	69.6539, 18.9281	100
4	*H. persicum* gbifid = 2400590081 *H. mantegazzianum* gbifid = 1603087669	Muonio 67.9562, 23.6833 Kittilä 67.7888, 25.2541	MUONIO_ALAMUONIO *H. persicum* (1 km) *H. mantegazzianum* (70 km)	FIE00146423	67.9681, 23.6803	254
5	*H. mantegazzianum* gbifid = 1323856589	Sodankylä 67.4190, 26.5872	SODANKYLA_AWS (6 km)	FI000007501	67.3678, 26.6328	179
6	*H. mantegazzianum* gbifid = 2876124595	Kandalaksha 67.1514, 32.4060	KANDALAKSA (2 km)	RSM00022217	67.1692, 32.3542	26
7	*H. sosnowskyi* gbifid = 2236595237	Murmansk 68.9601, 33.0756	MURMANSK (1 km)	RSM00022113	68.9667, 33.0497	57
8	*H. sosnowskyi* gbifid = 1316549054	Inta 66.0499, 60.1657	PETRUN (54 km)	RSM00023324	66.4715, 60.7541	58
9	*H. sosnowskyi* gbifid = 2236595238	Arkhangelsk 64.4592, 40.6447	ARHANGELSK (6 km)	RSM00022550	64.5042, 40.7269	8

* Station code in the Global Historical Climatology Network daily (GHCNd) database, National Centers for Environmental Information (USA) (Menne et al., 2012).

Collection and Processing of Meteorological Data

Long-term (1989–2019) meteorological data with a daily resolution were obtained for occurrences of invasive species of the genus *Heracleum* in Northern Europe from the Global Historical Climatology Network daily (GHCNd) database, National Centers for Environmental Information (USA) (Menne et al., 2012). The geographic coordinates of weather stations whose data were used in this study and their distances from invasive Heracleum species occurrences are provided in Table 1.

The source GHCNd data were transformed into a tabular format with observation dates in rows and meteorological data in columns. The following variables were used: TMAX (maximum daily temperature, °C), TMIN (minimum daily temperature, °C), PRCP (precipitation amount, mm), and SNWD (snow depth, cm). In addition, the TAVG (average daily temperature, °C) variable was computed for each day. A script written in the Python programming language was used to automate the data transformation procedure (Chadin, 2021a).

The climatic parameters and indices (ratios between parameters) were used to characterize environmental conditions in invasive Heracleum species locations. The sums of active temperatures ≥5°C (SAT_5) and ≥10°C (SAT_{10}) (Selyaninov, 1937) were used to estimate heat accumulation throughout the year. In addition, the number of calendar days with TAVG ≥5°C ($DAYS\_SAT_5$ variable) and the number of calendar days with TAVG ≥10°C ($DAYS\_SAT_{10}$ variable) were computed. The TDIF variable was calculated as the difference between the highest and lowest air temperatures in the year.

Wintering conditions for plants were assessed according to the absolute minimum air temperature during the year (AMAT, °C) and a parameter proposed by P.I. Koloskov: average snow cover depth in the last third of February (SNDP, cm) (Sinitsyna et al., 1973).

The winter severity index (WSI) proposed by A.M. Shulgin was computed using the formula

$$\mathrm{WSI} = \frac{T_{\text{mean min}}}{H_{\text{mean snow}}}, \quad (1)$$

where $T_{\text{mean min}}$ is the mean of the absolute daily air temperature minimums in January and February and $H_{\text{mean snow}}$ is the mean snow cover depth for the same period (Sinitsyna et al., 1973).

The data source used in this study provides data on the snow cover depth not for all weather stations. Therefore, an additional index, ID^w, equal to the reciprocal value of the dryness index D^w (Kaverin et al., 2019) was used to assess the severity of winter:

$$\mathrm{ID}^{w} = \frac{\mathrm{FDD}}{\mathrm{R}^{w}}, \quad (2)$$

where FDD is the sum of below-zero temperatures throughout the year (°C) and R^w is the amount of precipitation in the cold period of the year (i.e., the period used to calculate FDD) (mm).

Another technique used to assess the severity of the winter period was based on the air temperature and duration of cold weather (Urban et al., 2018). The winter severity index (WOW) was calculated as follows:

$$\mathrm{WOW} = (1 - 0.25\mathrm{Tw}) \times 0.8325 + 0.0144\mathrm{NDw} + 0.0087\mathrm{NDf} + 0.0045\mathrm{NDvf} \times 0.0026\mathrm{ST}, \quad (3)$$

where Tw is the average air temperature in winter (°C), NDw is the number of winter days (i.e., days with average daily temperatures ≤0°C), NDf is the number of cold days (maximum temperatures <0°C), NDvf is the number of very cold days (minimum temperatures <–10°C), and ST is the sum of average daily temperatures <0°C.

The last date before July when TMIN dropped below 0°C was taken as the last frost of the year. The first date after July when TMIN dropped below 0°C was taken as the first frost of the year. The duration of the frostless period was calculated as the number of days between the last and first frosts in the year.

Statistical analysis of the meteorological data was performed using the R environment (R Core Team, 2017). Samples were described using the mean value, the standard deviation, and the minimum and maximum values. Box plot charts constructed using the boxplot function of the R environment were used to process, group, and rank climatic indices. The source code of the R program used to perform the computations and the source data set have been published in the public domain (Chadin, 2021b).

RESULTS

Invasive Heracleim Species Occurrences at the Northern Limit of Their Secondary Range

According to the published data (Pyšek et al., 2010; Gederaas et al., 2012; Rijal et al., 2015, 2017), the northernmost *H. persicum* occurrences are localized in coastal areas of northern and central Norway (up to 71° N) and in northern Finland (up to 68° N). The northern *H. mantegazzianum* distribution limit encompasses the southern and central parts of the Scandinavian Peninsula (Norway, Sweden, and Finland) (Table 1, Fig. 1).

H. mantegazzianum plants have been discovered up to 69° N. Invasive Heracleum species occurrences identified in the course of the visual analysis of Google Maps panoramic images are localized in anthropogenically transformed areas, in settlements, and along roads.

The northernmost *H. sosnowskyi* occurrences were described on the Kola Peninsula close to 68° N (Avrorin et al., 1964; Men'shakova, 2011). In addition,

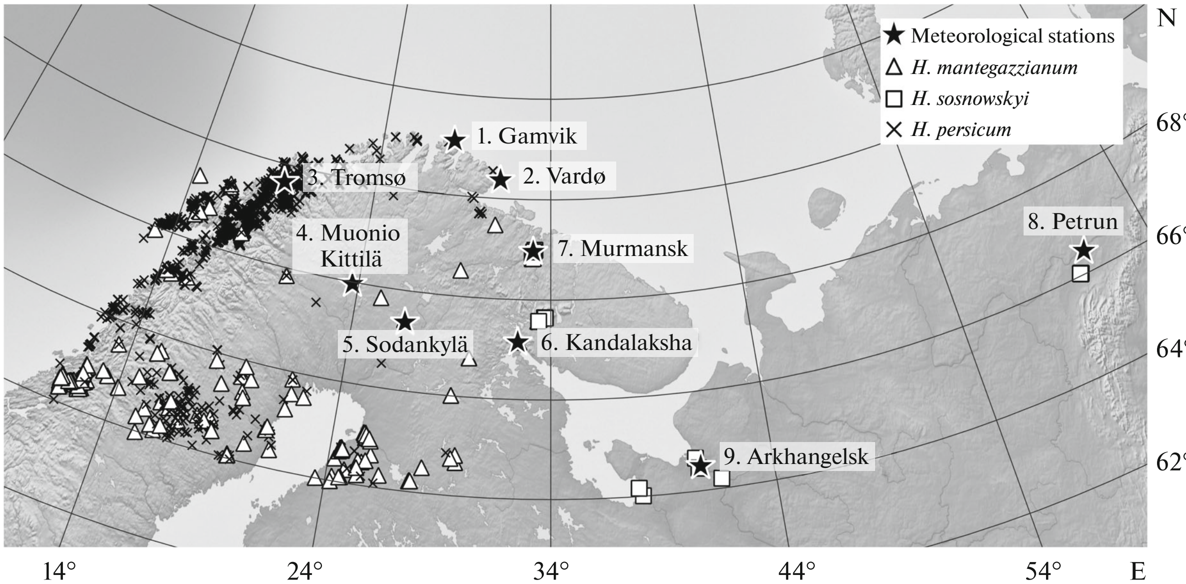

Fig. 1. *Heracleum mantegazzianum*, *Heracleum persicum*, and *Heracleum sosnowskyi* occurrences at the northern limit of the secondary range of the species and location of meteorological (weather) stations (marked by asterisks). The occurrences are plotted in accordance with GBIF.org (2020).

the plants were found north of 64° N in Arkhangelsk Region (Dalke et al., 2019). Using Google Maps and Yandex.Maps, we determined the geographic coordinates of *H. sosnowskyi* populations in Murmansk, Apatity, and Arkhangelsk with an accuracy of 30–100 m (Table 1). Analysis of images showing *H. sosnowskyi* thickets in Murmansk and Arkhangelsk oblasts indicates that the plants are confined to residential areas or localized on disturbed lands.

In the course of field studies conducted in the continental northern part of European Russia, *H. sosnowskyi* was found north of 66° N in the vicinity of the city of Inta (66.0499° N, 60.1657° E). The active spread of *H. sosnowskyi* was noted within the boundaries of the city, in abandoned gardens, and on roadsides. The plants localized on fallow lands occupied the largest areas. Plants representing all age stages were present: seedlings, juvenile, vegetative, and generative individuals. The plants bear fruit in climatic conditions of this region, and their populations are self-maintained.

In addition, searches for *H. sosnowskyi* were performed north of Inta: in the settlements of Meskashor (66.6095° N, 62.5291° E) and Sivomaskinsky (66.6755° N, 62.5777° E); back in the 1950s, attempts were made to introduce *H. sosnowskyi* there as a silage crop with the purpose to improve floodplain meadows (Khantimer, 1974). Data collected in the course of route surveys indicate that plant communities in the study area currently do not include *H. sosnowskyi*.

Comparison of Climatic Conditions in Locations of Invasive Heracleum Species

In 1989–2019, the average number of days in a year with average daily air temperatures ≥5°C ($DAYS\_SAT_5$) at the northern limit of the range of invasive Heracleum species varied from 116 to 150 days (Table 2).

The lowest heat supply was registered on the northeastern coast of the Scandinavian Peninsula (Gamvik and Vardø, Norway) where average SAT_5 values do not exceed 1200°C. Deeper into the peninsula, the heat supply to plants increases, and the SAT_5 value reaches 1400–1500°C. On the Kola Peninsula and in the continental northern part of European Russia, SAT_5 values are at the same level. The average numbers of days in a year with average daily air temperatures ≥10°C ($DAYS\_SAT_{10}$) are significantly smaller: from 37 (Gamvik and Vardø, Norway) to 101 days (Arkhangelsk, Russia). In the course of the growing season, plants receive from 454 to 1538°C SAT_{10}. The heat supply to plants varies significantly over the years. Significant SAT_5 and SAT_{10} deviations from the average values were observed throughout the entire area under study (Table 2).

A characteristic feature of climatic conditions in the northern part of the Scandinavian Peninsula is a significant (75–94 days) difference between the numbers of days with average daily air temperatures ≥5°C and ≥10°C. As the climate continentality increases, this difference is halved. The difference between these two periods determines a significant discrepancy

Table 2. Climatic parameters at invasive Heracleum species occurrences on the northern limit of their secondary ranges (1989–2019)

No.	HMS name	Settlement	SAT_5, °C	$DAYS\_SAT_5$, days	SAT_{10}, °C	$DAYS\_SAT_{10}$, days	AMAT, °C	AVG_SNWD, cm
1	SLETTNES_FYR	Gamvik	1157 ± 164 816–1556	131 ± 15 100–170	454 ± 174 151–1004	37 ± 13 13–78	–15.0 ± 2.2 –20.9 to –11.8	N/A
2	VARDO	Vardø	1172 ± 194 730–1601	131 ± 17 92–168	494 ± 218 187–1185	41 ± 17 16–94	–14.5 ± 2.4 –21.5 to –10.5	N/A
3	TROMSO	Tromsø	1499 ± 160 1232–1882	147 ± 14 122–186	929 ± 186 578–1339	72 ± 13 48–100	–13.8 ± 1.8 –18.3 to –10.7	62 ± 30 18–154
4	MUONIO_ ALAMUONIO	Muonio Kittilä	1438 ± 168 1051–1743	126 ± 12 101–144	1062 ± 185 678–1520	76 ± 12 50–109	–36.0 ± 3.7 –46.2 to –28.0	60 ± 10 43–84
5	SODANKYLA_ AWS	Sodankylä	1465 ± 169 1072–1732	125 ± 12 95–153	1111 ± 182 786–1392	78 ± 12 55–98	–36.9 ± 3.6 –49.5 to –30.6	59 ± 10 41–76
6	KANDALAKSA	Kandalaksha	1576 ± 175 1287–1900	136 ± 12 114–157	1180 ± 177 887–1543	84 ± 11 64–104	–32.4 ± 3.8 –40.3 to –27.4	50 ± 10 36–75
7	MURMANSK	Murmansk	1469 ± 207 1095–1899	134 ± 15 108–163	1006 ± 224 658–1670	73 ± 15 48–113	–28.7 ± 3.9 –39.4 to –21.0	26 ± 12 10–58
8	PETRUN	Inta	1392 ± 204 1057–1950	116 ± 14 94–143	1031 ± 223 643–1674	68 ± 13 42–101	–44.1 ± 3.8 –52.4 to –37.3	47 ± 15 24–73
9	ARHANGELSK	Arkhangelsk	1907 ± 297 681–2309	150 ± 20 60–174	1538 ± 282 507–1942	101 ± 17 35–126	–34.8 ± 3.3 –41.3 to –27.8	39 ± 10 20–54

* Station code in the Global Historical Climatology Network daily (GHCNd) database, National Centers for Environmental Information (USA) (Menne et al., 2012).
SAT_5 is the sum of active temperatures ≥5°C, SAT_10 is the sum of active temperatures ≥10°C, SAT_5_DAYS is the number of days with SAT_5, SAT_10_DAYS is the number of days with SAT_10, AMAT is the minimum air temperature during the year, and AVG_SNWD is the average snow cover depth. Above the line is the mean value ± standard deviation; below the line are the minimum and maximum values of climatic parameters.

between the parameters reflecting the heat supply to plants at the SAT_5 and SAT_{10} levels.

The duration of the frostless season in the area under study varies widely (Zakhozhiy et al., 2021). The greatest values for the period from the last spring frost to the first autumn frost are 140–150 days (Gamvik, Vardø, and Tromsø, Norway). Most often, the last frost is registered there in the second ten days of May, and the probability of frost in June is less than 6%. Autumn frosts usually begin in late September–October. As the distance from the seacoast increases, the frostless period duration significantly decreases. The most unfavorable conditions in terms of the probability of cold damage to vegetating plants are observed in the northern part of Finland (Muonio, Kittilä, and Sodankylä) and in the continental northern part of European Russia (Inta). The values of the duration of the frostless season in these areas vary from 80 to 92 days; deviations observed in various years amount to 50–126 days. Concurrently, the probability of frosts in June is 29–77%, and first frosts occur as early as August. In terms of dates of first frosts and the frostless season duration, locations of invasive Heracleum species on the Kola Peninsula and in Arkhangelsk Region (Russia) occupy an intermediate position between values of these climatic parameters registered in the northern coastal part of the Scandinavian Peninsula and in the continental northern part of European Russia (Zakhozhiy et al., 2021).

The periphery of the northern distribution limit of invasive Heracleum species is very heterogeneous in terms of the temperature regime in the winter period. The values of the absolute minimum air temperature (AMAT) in coastal sites of invasive Heracleum species in Norway never drop below −15°C (Table 2). Deeper into the Scandinavian Peninsula, the AMAT value decreases to −35 to −37°C (Muonio, Kittilä, and Sodankylä, Finland). The lowest average values of the absolute minimum air temperature in winter were registered in the continental northern part of European Russia (Inta). The TDIF value reflecting the difference between the maximum and minimum air temperatures during the year and characterizing the climate continentality varies from 27°C in the coastal northwestern part of Norway to 64°C in the continental northern part of European Russia (Fig. 2).

Except for the northeastern coastal regions of the Scandinavian Peninsula (Gamvik, Vardø, and Tromsø, Norway), the winter period in the area under study is distinguished by the presence of a sustainable snow cover more than 25 cm deep. In the coldest regions where absolute minimum winter temperatures are below –30°C, the average snow cover depth in January–February is 39–60 cm. According to the data collected at the SLETTNES_FYR and VARDO stations (Norway), the average AMAT values amount to −12 to −13°C (Table 2).

The WSI and WOW indices indicate a significant geographical differentiation in the severity of the winter season in the northern part of the secondary range of invasive Heracleum species; this differentiation can be clearly traced along the line going from the Barents Sea coast to internal regions of the Scandinavian Peninsula and to the continental part of Europe (Fig. 2).

The WSI index computed as the ratio between the air temperature and the snow cover depth varies widely in the area under study. At Heracleum species occurrences in Norway and Finland, its values do not exceed 0.4. In Russia, the severity of the winter season increases, and average WSI index values reach 0.55–0.57 in Inta and Murmansk. Analysis of climatic conditions in the winter period performed on the basis of the ID^w index representing the ratio between the sum of below-zero air temperatures and the amount of precipitation in the winter period reveals a similar climatic pattern (Fig. 2).

Analysis of the WOW index confirms the above-described trend. According to the WOW values, the severity of the winter period at the northern limit of the secondary range of invasive Heracleum species increases with distance from the seacoast of Norway to European North-East Russia from 4 to 11 in the following order: Tromsø–Gamvik–Vardø < Murmansk < Sodankylä–Arkhangelsk–Kandalaksha < Muonio < Inta. The greatest WOW index variability (from 8 to 14) was registered in Inta (Fig. 2).

DISCUSSION

Occurrences of Invasive Hogweed Species at the Northern Limit of Their Secondary Range

The periphery of the northern limit of the secondary range of invasive invaded species encompasses vast areas in the subarctic and temperate zones with contrasting climatic conditions. At present, all three species occur north of 68° N. *H. mantegazzianum* and *H. persicum* are described as part of the adventitious component of the flora of the Scandinavian Peninsula (Norway, Finland, and Sweden); the northernmost *H. sosnowskyi* occurrences are located on the Kola Peninsula (Russia).

At the northern limit of the secondary range of invasive Heracleum species, their occurrences are usually confined to transformed areas. The most favorable conditions for the spread and self-reproduction of these plants are formed on abandoned agricultural lands, in settlement areas, along roads, and on lands of private households (*Ecology and Management…*, 2007; Chadin et al., 2017). Apparently, microclimatic and edaphic conditions of habitats formed as a result of anthropogenic transformations of the soil and vegetation cover play a significant role in the naturalization of invasive Heracleum species in a cold climate. Such factors as less intense phytocoenotic competition with native plant species, changes in physicochemical soil

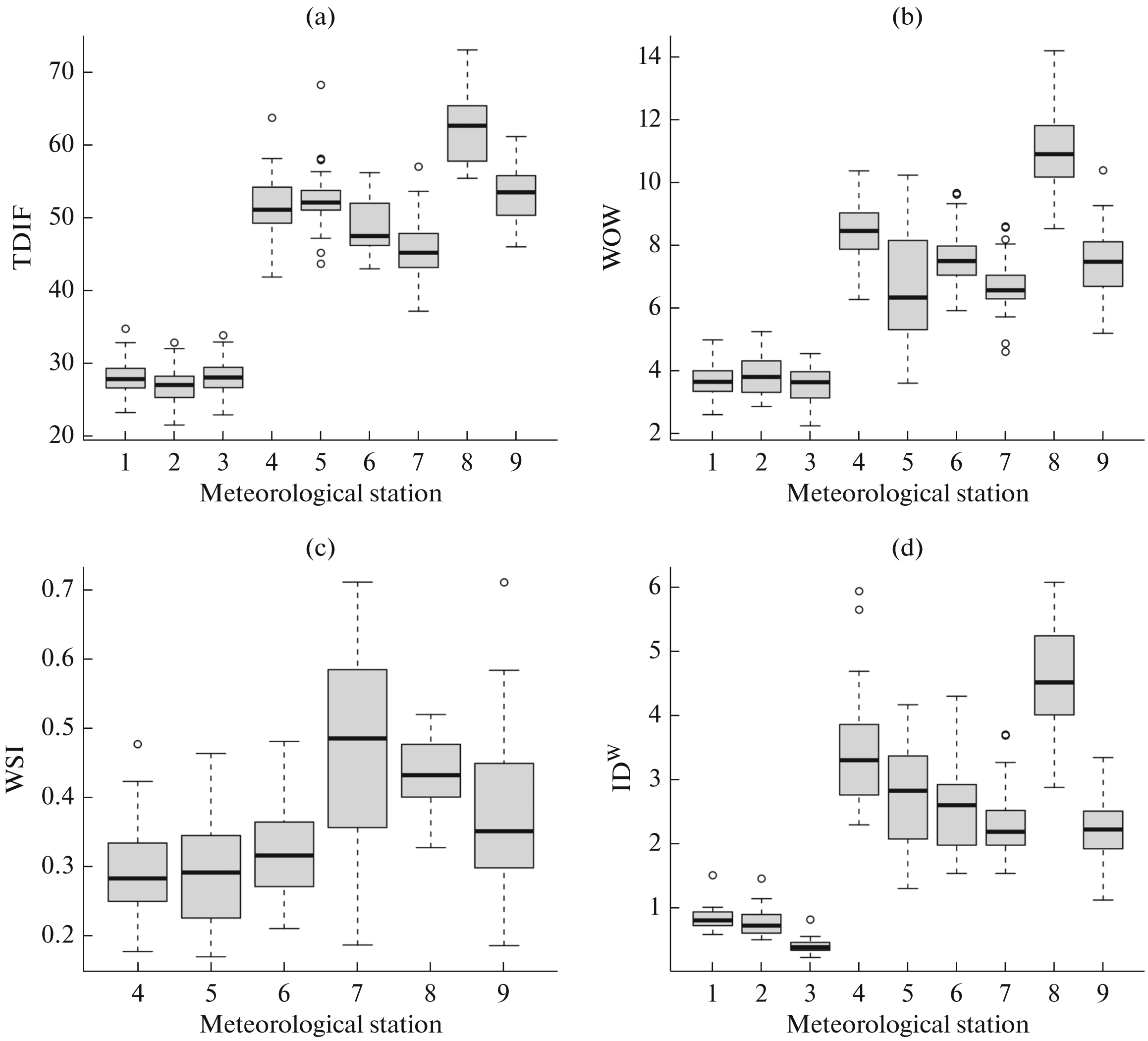

Fig. 2. Climatic indices at *Heracleum mantegazzianum*, *Heracleum persicum*, and *Heracleum sosnowskyi* occurrences located near the northern limit of their secondary range in Europe: (a) TDIF (difference between the highest and lowest air temperatures in the year), (b) WOW (winter severity index), (c) WSI (winter severity index), and (d) ID^W (winter severity index). The indices have been computed for the period of 1989–2019 on the basis of GHCNd meteorological data with a daily resolution, National Centers for Environmental Information (USA) (Menne et al., 2012). Meteorological (weather) stations: (1) SLETTNES_FYR, (2) VARDO, (3) TROMSO, (4) MUONIO_ALAMUONIO, (5) SODANKYLA_AWS, (6) KANDALAKSA, (7) MURMANSK, (8) PETRUN, and (9) ARHANGELSK.

properties, and higher availability of mineral nutrition elements as a result of human economic activities can facilitate the intrusion of Heracleum species into existing biocenoses. In addition, it cannot be ruled out that the warming impact of aboveground and underground structures (buildings, heat supply networks, and engineering and technical communications) in urban areas can affect seasonal changes in thermal regimes of soils and air, thus exercising a positive effect on the naturalization of alien plants.

Analysis of Climatic Parameters at the Northern Limit of the Invasive Range

Climate is the most important natural factor determining the possibility for a specific species of plants to successfully exist in a given area. Analysis of environmental conditions in locations of invasive Heracleum species in the subarctic and temperate zones shows significant differences in heat supply to plants during the growing season. Within the Scandinavian and Kola peninsulas, the average annual number of days with average daily air temperatures ≥10°C varies in a wide range, and SAT_{10} heat amounts received by plants differ by more than a factor of two (Table 2). Taking the relatively large number of days with average daily air temperatures ≥5°C and larger amounts of heat received by plants on such days (SAT_5 varies from 1157°C in Gamvik, Norway, to 1907°C in Arkhangelsk, Russia), one of the adaptation strategies for plants at the periphery of the northern border of their secondary range can be to extend the temperature range suitable for their growth and development toward low above-zero temperatures. Earlier, we showed that the metabolic activity of *H. sosnowskyi* seedlings and terminal buds is maintained at a relatively high level at temperatures down to 5°C, which ensures its adaptation to low temperatures and high growth rates in early spring (Dalke et al., 2020). In autumn, vegetating *H. sosnowskyi* plants can maintain photosynthesis rates in the range of 4–10 μmol/(m^2 s) at temperatures of 5–10°C (our unpublished data), which is comparable to the CO_2 assimilation rate in leaves in the summer period (Tappeiner and Cernusca, 1998; Dalke et al., 2015). Phenological data collected in Central Europe indicate that *H. mantegazzianum* grows in spring at an average air temperature of 5°C (Otte and Franke, 1998). In England, a decrease in the SAT_5 level to 1100°C suppresses the accumulation of biomass, but does not completely stop the growth and development of the plants (Willis and Hulme, 2002).

In a temperate climate, representatives of the section Pubescentia of genus *Heracleum* complete the full development cycle, including the formation of seeds, when the SAT_{10} level exceeds 1500°C (Aleksandrova, 1971; *Introduktsiya borshchevikov*..., 1980). However, regular fruiting of *H. sosnowskyi* was also noted on the Kola Peninsula (Murmansk), where the average annual SAT_{10} value is less than 1010°C (Avrorin, 1964; Men'shakova, 2011). In the course of field studies, we detected fruiting plants in Inta, Russia, where SAT_{10} varies in the range from 643 to 1674°C. Numerous occurrences of *H. persicum* up to 71° N in Norway (SAT_{10} varies in the range from 151 to 1339°C) also indicate that invasive Heracleum species could adapt to flowering and fruiting at lower heat supply levels in the subarctic zone (Alm, 2013). The extension of the temperature range suitable for their growth and development, as well as faster passage of individual phenological phases by the plants, can represent a general strategy implemented by species of the section Pubescentia of genus *Heracleum* in the course of their adaptation to the cold climate.

We believe that the minimum thermal resources required for the growth and development of invasive Heracleum species are sums of active temperatures above 5 and 10°C equal to 1200 and 450°C, respectively. Heat supply values below these levels can be considered one of the key factors limiting the distribution of *H. mantegazzianum*, *H. persicum*, and *H. sosnowskyi* at the northern boundary of their secondary range.

Adverse meteorological phenomena whose intensity, duration, and time of occurrence pose threats to plants include, inter alia, severe cold weather and morning frosts. According to the published data, cultivated *H. sosnowskyi*, *H. lehmannianum*, and *H. ponticum* plants can be killed in dry winters with long thaws (Aleksandrova, 1971). Morning frosts and extremely unfavorable weather conditions in the autumn period (lack of snow cover and air temperatures below −15°C) caused the death of *H. sosnowskyi* crops in the forest-tundra zone of the Komi Republic (Khantimer, 1974).

The data presented in Table 2 and Fig. 2 (Zakhozhiy et al., 2021) indicate that invasive Heracleum species can exist in a wide range of abiotic environmental factors. The minimum duration of the frostless season required for plant growth and development is 80–90 days. The plants are resistant to frequent recurring frosts at the beginning of the growing season and to early frosts in autumn. In locations of invasive Heracleum species in the northern part of Finland and in the continental northern part of European Russia, the probability of last frosts persists until the second ten days of June, while first frosts are noted as early as the first half of August. According to data collected at the PETRUN weather station, frosts can reach in some years −5°C both in June and in August. In Finland (according to data collected at the MUONIO_ALAMUONIO and SODANKYLA_AWS weather stations), air temperatures can drop to −3 and −4°C in June and August, respectively. It can be assumed that, at the northern boundary of their modern secondary range, invasive Heracleum species exist at the limit of their adaptive potential. Deterioration of weather conditions during the growing season, including a higher frequency, severity, and duration of frosts, can inflict damage to the plants or cause their death.

Wintering conditions for plants depend on many factors, including air temperature and snow cover depth, that determine the thermal regime and seasonal soil freezing depth. According to the obtained data, invasive Heracleum species habitats with minimum temperatures below −28°C had a sustainable snow cover 26–60 cm depth (Table 2). The WOW, WSI, and ID^w indices were examined as potential climatic markers reflecting the severity of the winter season for hibernating plant organs. The climatic indices computed as ratios between the air temperature (WOW) and the snow depth (WSI) (or the precipitation amount in winter (ID^w)) made it possible to assess the geographical differentiation of the severity of the winter period in the area under study. The most severe conditions during the winter period (WOW > 10) are observed in the continental part of the area under study (Inta, Russia), where the average annual values of the absolute minimum air temperature are around −44°C. Inner regions of the Scandinavian and Kola Peninsulas also feature severe conditions in winter. By contrast, plant occurrences near the seacoast of Norway feature fairly mild winters: long-run average annual values of the minimum air temperature never drop below −15°C, while the WOW index does not exceed 4.

Analysis of the WSI and ID^w indices confirms the above conclusions. The most unfavorable conditions for wintering plants are observed in the continental part of the northern boundary of the secondary range of invasive Heracleum species (Inta, Russia) and on the northern coast of the Kola Peninsula (Murmansk, Russia). In some years, the WSI index is close to 1 there (Fig. 2), which indicates severe conditions for wintering plants (Sinitsyna, 1973). In inner regions of the Scandinavian and Kola Peninsulas, winter conditions are somewhat milder. On the basis of the values of the WSI and ID^w climatic indices registered at the seacoast of Norway, the freezing risk for hibernating plant organs there is low.

Analysis of experimental data presented in the study by Dalke et al. (2019) theorizes the possibility to use the WSI index to assess the winter season severity and freezing risks for hibernating plant organs. From the information provided by the authors, even if the air temperature drops below −20°C, a snow cover over 20 cm depth maintains the soil temperature at the depth where terminal and auxiliary *H. sosnowskyi* buds are hibernating at a level not lower than −3°C, thus preserving the meristem viability. If the snow cover is removed at an air temperature of −31°C, then the soil temperature at a depth of 15 cm drops to −6°C causing death of underground organs of wintering *H. sosnowskyi* plants. Similar situations resulting in damage to plants can be caused by abnormally cold weather in spring or autumn in the absence of snow cover (Aleksandrova, 1971; Khantimer, 1974; Mishurov et al., 1999).

Overall, areas where the WSI climate severity index is close to 1 or exceeds 1 feature unfavorable wintering conditions for invasive Heracleum species. Apparently, the presence of a sustainable snow cover that is thick enough to stabilize the soil temperature at a level preventing damage to renewal buds and seedlings is an extremely important factor contributing to the survival of invasive Heracleum species in areas featuring low below-zero air temperatures in winter.

CONCLUSIONS

The geographical position of the northern limit of the secondary range of invasive Heracleum species in Europe reflects the significant adaptive potential of these plants to cold climate. They occur in areas featuring short growing seasons, low supply of thermal resources to plants, and a significant variability (instability) of the growing season conditions over the years. The minimum average annual duration of the frostless season at the periphery of the northern border of their secondary range is 80–90 days, and the probability of frosts remains high even in June. The biological minimum for the sum of active temperatures ≥5°C is 1150°C, while the minimum requirement of the studied plants to the sum of active temperatures ≥10°C is over 450°C. It is believed that the observed increase in cold tolerance and extension of the temperature range suitable for the growth and development of invasive Heracleum species toward low above-zero temperatures can manifest an important adaptation strategy that ensures their survival in climatic conditions of the subarctic zone. The presence of a sustainable snow cover over 25 cm depth in areas where the minimum winter temperatures are less than −30°C preserves the viability of plants by preventing the freezing of their renewal buds and seedlings. Climatic indices computed as ratios between the air temperature and the snow cover depth (WSI) (or the precipitation amount in winter (ID^w)) can be used as climatic markers reflecting the severity of the winter season and characterizing wintering conditions for plants.

The main factors limiting the distribution of invasive Heracleum species are as follows: insufficient heat supply, soil freezing to temperatures critical for wintering plants, and late spring and early autumn frosts.

Factors hindering the further expansion of areas currently occupied by invasive Heracleum species in northern Europe include inter alia the lack of lands with suitable edaphic conditions due to the low degree of anthropogenic transformation in the subarctic zone. In addition, natural geographical barriers (i.e., waters of the Norwegian and Barents seas and mountain systems in Fennoscandia and in the Urals) prevent the further spread of these plants in Northern Europe.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement of the welfare of animals. The article does not contain any studies involving animals in experiments performed by any of the authors.

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