ISSN 1067-4136, Russian Journal of Ecology, 2024, Vol. 55, No. 2, pp. 79–88. © Pleiades Publishing, Ltd., 2024.

Structure of Cenopopulations of *Heracleum sosnowskyi* and Mechanisms for Maintaining Their Stability under the North Conditions

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Received August 22, 2023; revised November 1, 2023; accepted November 17, 2023

Abstract—The growth and productivity, rhythm of development, and ontogenetic and spatial structure of cenopopulations of the Sosnowsky's hogweed (*Heracleum sosnowskyi* Manden.) on the territory of the Komi Republic were studied. The duration of the growing season of the *H. sosnowsky*i was 180–190 days due to the early spring germination of seeds and the long autumn growing season of pregenerative individual plants. The studied *H. sosnowskyi* CPs were characterized by left-sided ontogenetic spectra and high recovery indices. These properties characterized them as young and self-renewing plants. The greatest and the lowest numbers per the unit area had the juvenile and the generative plants (710–1700 and 1–3 individuals/m^2, respectively). The average density of the immature and virginile individuals was 4–7 pcs/m^2 and 12–16 pcs/m^2, respectively. The absence of seedlings during the flowering period of the plants was discovered, resulting from of the synchronous germination of mericarps and the rapid passage of the post-emergence development stage. Plants began to flower at the age of 2–6 full years, and the maximum lifespan of the individuals was 7 years. *H. sosnowskyi* plants were characterized by high productivity. They formed up to 15 kg/m^2 of wet phytomass, half of which was produced by generative individuals. The main part of the leaf area of the generative individuals was located in the upper layers (similarly to an "inverted pyramid") and absorbed about 70% of the incoming PAR. The identified mechanisms of the CP self-maintenance mediate the spread and retention of territories which are occupied by *H. sosnowskyi* plants on the northern border of the invaded range.

Keywords: *Heracleum sosnowskyi*, cenopopulations, ontogenetic spectrum, phenology, morphostructure, phytomass, architectonics, the Komi Republic

DOI: 10.1134/S1067413624020024

INTRODUCTION

The life strategy of plants is determined by optimization of the duration of ontogenesis, methods and rates of reproduction, allocation and durability of phytomass, and individual characteristics of growth and development. The basis for an investigation of the life cycle and an identification of the ecological, phytocenotic, and ontogenetic strategies of the species are population studies [1–3]. The study of biology and ecology and the determination of the adaptive abilities of invasive plant species capable of rapid dispersal and naturalization outside their natural area are of significant interest [4, 5].

Tall hogweeds (*Heracleum sosnowskyi*, *H. mantegazzianum,* and *H. persicum*) are aggressive invasive plants that occupy the temperate areas of Europe [6, 7]. In the conditions of the invaded range, these species dominate in the composition of species-poor plant communities that are formed in postagrogenic landscapes and transformed areas. *H. sosnowskyi* maintain high seed productivity, efficiently use environmental resources, and easily recover from damage [8–12]. An assessment of their invasive potential remains relevant, considering the high dissemination rates and the ongoing expansion of plants of the *Heracleum* genus [13–19]. An investigation of the structural and functional characteristics of plants in cenopopulations which determine the self-maintenance and distribution of the species is necessary for a better understanding and control of the distribution of invasive species of the *Heracleum* genus in the invaded range.

The purpose of this investigation is the study of the growth and rhythms of development, productivity, and the ontogenetic and spatial structure of the *Heracleum sosnowskyi* cenopopulations in the conditions of the North. The study is aimed at identifying the mechanisms that ensure the stability of the biological encroachment of invasive species at the organismal and population levels.

MATERIAL AND METHODS

Object of study. The *Heracleum sosnowskyi* Manden. is a perennial, summer-green, herbaceous, taproot, monopodially growing monocarpic plant with semi-rosette erect shoots. Underground part of the *H. sosnowskyi* is represented by a submerged caudex at the top of which the terminal overwintering bud of renewal is formed. The main root branches out up to 3–4 orders; the roots have contractile properties. The reproductive stem is fistular and achieves up to 3 m or more in length. The basal (rosette) and stem leaves are trifoliate or pinnate. Umbrellas are numerous (5–7 pcs.); the central umbrella is the largest [20, 21]. Under the conditions of the European North-East of Russia, a potential seed productivity of the *H. sosnowskyi* is 15–20 thousands of mericarps per one generative plant [8].

There are four periods in the life cycle of the *H. sosnowskyi*: latent, virginile, generative, and senile. The dormant period of seeds lasts several months and is caused by underdevelopment of the germ. The after-ripening of the germ occurs at low temperatures (+2°...5°). The seeds are characterized by an aboveground type of germination; field germination is 20–70%. The virginile period lasts from 1 to 5 (or more) years. The first true leaf is formed after a short period of germination and the appearance of a root and hypocotyls with the cotyledons. Further development is associated with the formation of basal leaves and an active growth of aboveground and underground organs. The generative period lasts one growing season. The senile period begins after the fruit ripening and is characterized by the gradual death of above-ground organs and the root system [20].

Area of the investigations and sampling. Data collection was carried out in the southwestern part of the Komi Republic (Syktyvkar and Knyazhpogostsky district). The climate of the territory is cold (continental) without a dry season, with cold summers. Average annual air temperature is about +1°C. The average daily temperatures of the warmest (July) and the coldest (January) months are about 17°C and –16°C, respectively. The annual precipitation is 600–700 mm. The appearance of snow cover is observed in mid-October, stable snow cover is formed in the first ten days of November and melted in late April–early May. The spring and autumn transitions of average daily temperature through 0°C occur in the second ten days of April and in early October, respectively. The duration of the frost-free period is 180–190 days [22].

Experimental areas with cenopopulations (CP) of the *H. Sosnowskyi* were localized on fallow lands (CP 1, CP 4, and CP 5) or on the territory of deserted vegetable gardens (CP 2, CP 3, and CP 6) and confined to watersheds or floodplain terraces. The automorphic soils existed in the soil cover of the areas under consideration before the start of an agricultural development. The vegetation cover is represented by grass-forb communities with a dominance of the *H. sosnowskyi*; species of herbaceous plants with high constancy included *Urtica dioica, Poa pratensis, Symphytum asperum, Chamaenerion angustifolium, Elytrigia repens, Calamagrostis epigejos, Artemisia vulgaris, Festuca pratensis,* and *Chrysosplenium alternifolium*. Their abundance was about 5–10%. Geographic coordinates of the areas were: CP 1 – 61.645695° N, 50.731816° E; CP 2 – 61.638128°N, 50.832044°E; CP 3 – 61.650820° N, 50.841117° E; CP 4 – 61.607331° N, 50.735631°E; CP 5 – 62.268674° N, 50.661795° E; CP 6 – 61.702186° N, 50.818812° E. The CP area of the *H. sosnowskyi* varied from 0.3 to 6 ha and averaged 1 ha.

The examined areas were not subjected to alienation of phytomass, treatment with herbicides, and other measures of the weed control. We determine the age of the studied CPs of the *H. sosnowskyi* to exceed 10 years on the basis of the results of our own route research and the analysis of spatially referenced images of the earth's surface, that were available in the terrain panorama mode of the Google Maps (https://www.google.ru/maps) and Google Earth Pro (https://www.google.com/intl/ru/earth/versions) mapping services.

Phenological observations of the *H. sosnowskyi* plants were performed from April to October in 2021 and 2022. Studies of the CP structure were carried out during the flowering period of generative individuals (June–July). In CP 1 and CP 5, counting areas (1 × 1 m) were laid. All the plants of these areas with the exception of juveniles were dug up. A cylindrical soil sampler with an internal diameter of 10.5 cm and a height of 3.5 cm was used for a selection and count of the juvenile individuals and the seeds. The number of seeds and juvenile plants in soil samples was determined, and their number per unit area was calculated.

The ontogenetic states of the plants were evaluated according to the shape and the degree of segmentation of the leaf blade [9, 21]. We identified the following seedlings: (*p*), single-shoot individuals with two oblong cotyledons and/or one simple rounded leaf; (*j*), juvenile single-shoot individuals with 1–2 (3) trifoliate leaves; (*im*), immature individuals with 1–2 (3) trifoliate leaves which lobes had an unevenly serrate-toothed edge; (*v*), virginile individuals with several rosette shoots with trifoliate or pinnately compound leaves; and (*g*), generative individuals with reproductive and rosette shoots.

The ontogenetic spectra of CP were compared using the similarity index (*r*) based on taking into account the frequencies of common ontogenetic conditions. Index of the cenopopulation recovery (I_{IN}) was calculated based on the number of descendants per one generative individual [3].

We measured the mass of aboveground and underground organs, the length and the diameter (at the base) of the reproductive shoot, the longest length of

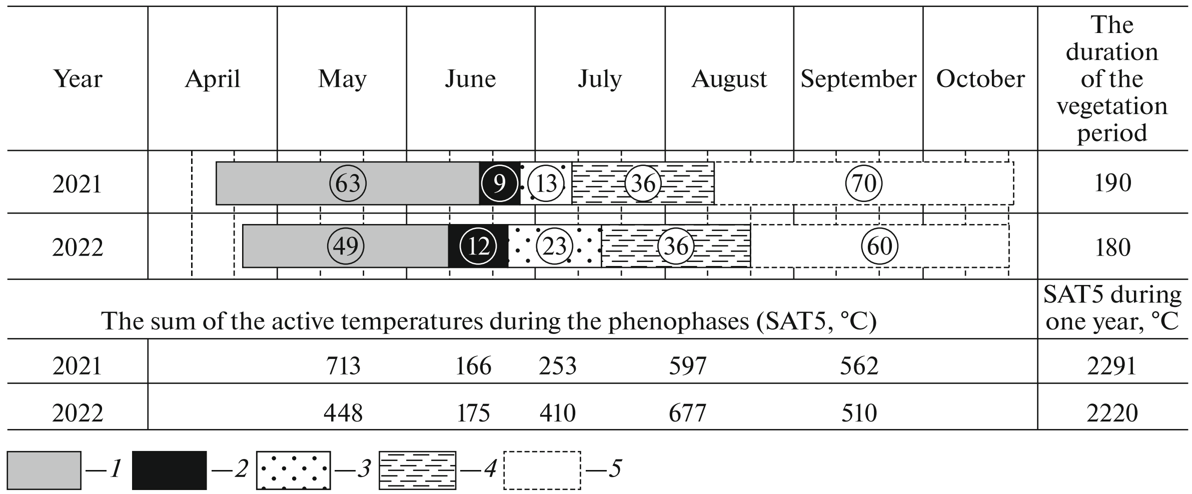

Fig. 1. Phenophase duration of *Heracleum sosnowskyi* plants and the sum of active temperatures >5°C (SAT5, °C): *1*, emergence of seedlings and vegetative growth of the plants; *2*, budding; *3*, flowering; *4*, fruiting; *5*, dispersal of fruits and death of the aboveground parts of the plants. The numbers in circles indicate the duration of the phenophases in days. Data are presented for CPs 1–6.

leaves with petioles, and the depth of the regeneration bud in order to determine the morphometric characteristics of plants and the spatial structure of the *H. sosnowskyi* cenopopulation. Reproductive effort was calculated as the proportion of the mass of inflorescences from the total mass of the generative individual [2].

The leaf area was determined on the basis of the analysis of photographs of leaf blades using the ImageJ program [23]. The angles of inclination of leaf petioles and leaf blades were measured from photographs of plant thicket profiles using the same ImageJ program [23]. Calendar age of the *H. sosnowskyi* plants were evaluated according to the number of annual increments on a longitudinal section of the caudex [19].

The input of photosynthetic active radiation (PAR) was measured using a Li-190SA quantum sensor (Licor Inc., United States). The sum of active temperatures (SAT) was calculated from the information on the average daily air temperature on the basis of data from the Syktyvkar weather station (WMO index 23804) that was obtained from the Weather Schedule resource (https://rp5.ru).

Means and standard deviations are given in the text, tables, and figures.

RESULTS

Rhythm of a seasonal development. Phenological observations showed that the *H. sosnowskyi* plants were ahead of native herbaceous species in terms of the start of the growing season by 10–15 days. Emergence of seedlings and beginning of regrowth of the juvenile and immature individuals of the *H. sosnowskyi* were noted in mid-April—early May after the melting of the snow cover (Fig. 1). After 7–10 days, the rosette leaves of the virginile and generative plants unfolded. 49–63 Days after regrowth, the plants began to bud. Mass flowering was observed in the first ten days of July when the accumulated sum of average daily temperatures of more than 5°C exceeded 1000°C. Fruiting began in mid-July. In the second ten days of August, the basal and stem leaves of generative individuals began to die, and seeds began to fall. The bulk of the seeds fell from the inflorescences in September. The pregenerative individuals remained viable until autumn frosts and the appearance of snow cover in the second or third ten days of October. Total growing season of the *H. sosnowskyi* was 180–190 days.

The ontogenetic and age states of cenopopulations. Study of ontogenetic states of the *H. sosnowskyi* plants during the flowering period of the generative individuals (June–July) revealed the absence of seedlings in CP (*p*) (Table 1). The number of juveniles plants (*j*) reached 1699 pcs/m^2. Average plant density in the immature (*im*) state was 4–7 pcs/m^2 and that of the virginile plants (*v*) was 12–16 pcs/m^2. The minimum number in CP was observed for the generative individuals (*g*). It was 1–3 pcs/m^2. The absolute density (the number of individuals per one unit of an area) for plants of different age states was characterized by significant variability. Thus, the variation coefficient (*CV*) of this parameter reached 78% for the juveniles in CP 1. The recovery indexes (I_{IN}) of CP were rather high (1718 for CP 1 and 365 for CP 2).

Studying the calendar age of the *H. sosnowskyi* plants of various ontogenetic groups demonstrated that the majority of the juvenile individuals (more than 95% of the plants of a small height with 1–

Table 1. Density and calendar age of the plants of the different ontogenetic states in cenopopulations (CP) of the *Heracleum sosnowskyi* (June–July 2021)

Parameter	Ontogenetic state					
	se	*p*	*j*	*im*	*v*	*g*
Number of plants in CP 1, pcs/m^2	161 ± 124	0	1699 ± 1329	7 ± 3	16 ± 2	1 ± 1
Number of plants in CP 5, pcs/m^2	192 ± 129	0	709 ± 506	4 ± 2	12 ± 7	2 ± 1
Calendar age, completed years*	0 (this year life)		0–1	1–5	2–7	3–4

se—seeds, *p*—seedlings, *j*—juvenile, *im*—immature, *v*—virginile, *g*—generative individuals; *—minimum and maximum.

Table 2. Morphophysiological characteristics of the *Heracleum sosnowskyi* plants (June–July 2021 and 2022)

Parameter	Generative plant (*N* = 29)	Immature and virginile plants (*N* = 335)
Total length of caudex and roots, cm	63 ± 15	25 ± 12
Caudex diameter (maximum), cm	8 ± 1	2 ± 2
Regeneration bud depth, cm	14 ± 5	7 ± 3
Leaf length (maximum), cm	200 ± 25	97 ± 53
Reproductive shoot length, cm	295 ± 34	–
Number of leaves, pcs/individual	7 ± 2	2 ± 1
Leaf area, dm^2/individual	138 ± 61	13 ± 25
Total phytomass, g/individual	4526 ± 2959	265 ± 530

Data are presented for CPs 1–6.

2 rounded or separate leaves) were represented by the plants of the current year of development or at the age of one full year of their life (see Table 1). Other ontogenetic groups (*im*, *v*, and *g*) in CP included the plants at the age from 1 to 7 full years. The average calendar age of generative individuals was 3 full years.

The morphostructure of the aboveground and underground organs. In the summer, the generative individuals formed the appearance of herbaceous communities with a dominance of the *H. sosnowskyi*. During the flowering period, the length of the reproductive shoot of the generative individuals reached 3–3.5 m (Table 2). The total number of basal (rosette) and stem leaves was 7 pieces on average. The length of the basal leaves (leaf blade and leaf petiole) in the generative individuals was 200 cm, and the total leaf area was 138 dm^2/individual. Each generative individual accumulated 4.5 kg of wet mass an average, and aboveground organs contained approximately 80% of the phytomass. The shares of inflorescences in the total mass and in the underground part were 11% and 18%, respectively. Renewal buds were immersed in the soil to a depth of about 14 cm.

In the middle of the growing season, pregenerative individuals of the *H. sosnowskyi* were characterized by significant variability in morphological parameters. The leaf length varied in the range from 43 to 155 cm for the immature plants and from 57 to 230 cm for virginile ones. Significant variation in the absolute values was also typical for other quantitative characteristics (see Table. 2). Average values of the longest leaf length for this group (*im* and *v* plants) were 97 cm, and the leaf area of one individual was 13 dm^2. The plants accumulated 265 g of the wet weight, 75% of which was in above-ground organs. The average length of the roots was 25 cm, and the diameter of the caudex was 2 cm. Renewal buds were immersed in the soil to a depth from 2 to 18 cm.

The juveniles plants were characterized by small sizes. The leaf length did not exceed 10 cm, the length of the root system was 5–8 cm, and the total leaf area was less than 10 cm^2. The mass of a juvenile individual did not exceed 0.5 g. It should be noted that a significant part of the juvenile plants did not have leaf blades and petioles and were in a state of paradormancy in the summer (June–July). The proportion of juvenile plants in the dormant state ranged from 39% in CP 6 to 48% in CP 1.

An accumulation of the phytomass and a growth of the leaf area. The accumulation of phytomass was observed from the beginning of the unfolding of leaves by the *H. sosnowskyi* wintering plants (April–May)

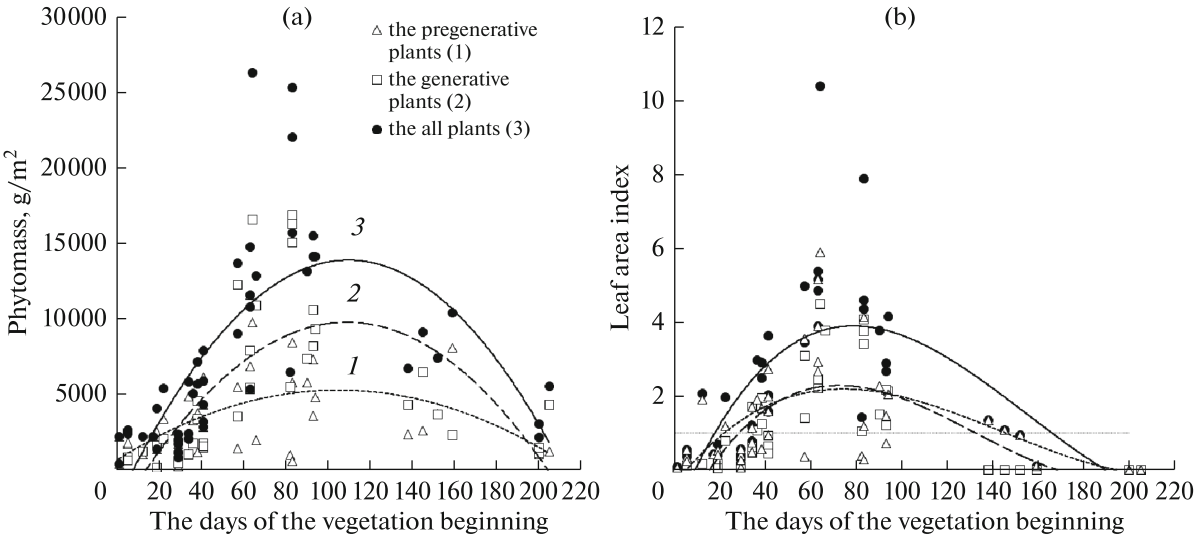

Fig. 2. Dynamics of (a) phytomass accumulation and (b) leaf area index in the *Heracleum sosnowskyi* cenopopulations during the growing season ($N = 50$, 2021–2022). Data are presented for CPs 1–6.

before the fruiting period in July (Fig. 2). During the period of the maximum plant development, the phytomass reserves averaged 15 kg/m^2. Moreover, this parameter reached 25 kg on separate recording sites (see Fig. 2). The contribution of the generative individuals to the total phytomass was 50–65% in average. Most part (over 60%) of the organic substance that was formed by the generative individuals was in the stems of reproductive shoots and leaf petioles. The share of leaves in the total phytomass was 15%.

The leaf area of the plants was changed synchronously with the accumulation of the phytomass (see Fig. 2). In July, the leaf area of the generative plants varied from 30 to 245 dm^2/individual and was one order of magnitude higher than that of the pregenerative individuals (see Table 2).

Architectonics of communities and a radiation regime. Study of the CP spatial structure was carried out during the period of maximum accumulation of phytomass (June–July), and resulted in an identification of several horizontal layers in herbaceous communities with a dominance of the *H. sosnowskyi*. The leaves of juvenile specimens were located in the bottom ground layer (0–50 cm above the soil surface). Two upper layers (50–100 cm and 100–150 cm), were predominantly formed by leaves of the immature and virginile plants. Basal and stem leaves of the generative individuals were dominated in the top layer (>150 cm above the soil surface). We observed a significant change in the area of assimilation organs (from 6 to 388 dm^2/m^2) and leaf lighting conditions within the identified layers, (Fig. 3). The distribution of the total mass of the leaves (leaf blade and leaf petiole) that were formed one or another layer was also asymmetrical (from 13 to 1844 g/m^2) with a minimum in the ground canopy layer and a maximum in the upper part of the canopy.

In July, the assimilation organs of virginile and generative individuals were maximum developed, the leaf CP index was increased to 4–6 (see Fig. 2), and 10–20 μmol/m^{2}s of PAR entered the ground layer. This value was less than 2% of the total luminous flux intensity. During this period, no more than 1% of the CP total leaf area was localized in the lower part of the canopy. The leaf blades of the juvenile plants were located almost parallel to the soil surface, the deviation from the horizontal was 17° (see Fig. 3).

In the middle layers (50–150 cm), the saturation of a space with a leaf mass ranged from 5 to 11%. At this level, the illumination varied from 30 to 300 μmol/m^{2}s, corresponding to 3–30% of the total influx of PAR., Plants oriented their leaf blades at angles of 35–40° to the horizontal under moderate shade conditions.

The upper layer (>150 cm) was occupied by the assimilation organs of the generative and most developed virginile individuals. The saturation of a space with the leaf mass was 83%. The leaf blades were located at angles of about 45° to the horizontal and absorbed approximately 70% of the incoming PAR.

DISCUSSION

Successful adaptation of invasive species to the soil and climatic conditions of the invaded territories is one of the important mechanisms of their naturalization. A significant gradient of ecological conditions of

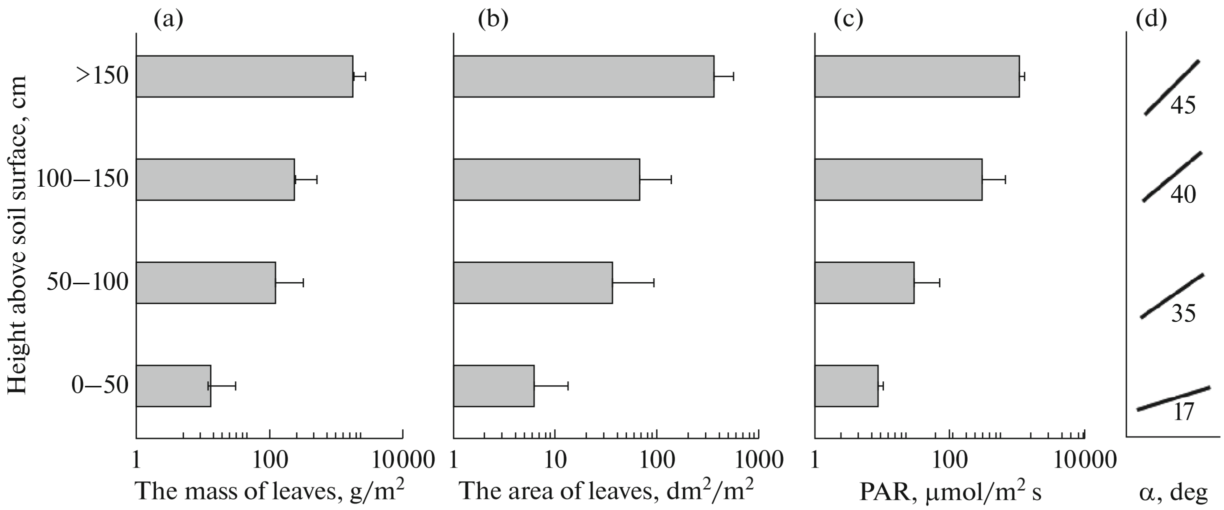

Fig. 3. The leaves mass (a) and leave area (b), photosynthetically active radiation (c), and the inclination of the plane of the leaf blade (d) at noon in the *Heracleum sosnowskyi* CP. The ordinate axis is presented in the form of a logarithmic scale ($N = 18$, June–July, 2021–2022). Data are presented for CPs 1–6.

habitats in the invaded range indicates a high adaptive potential of the *H. sosnowskyi*.

The results of the study showed that this species is characterized by a long (180–190 days) growing season in the natural climatic conditions of the North. The seed germination and the regrowth of the juvenile and immature individuals are noted immediately after the melting of the snow cover. This fact allows the *H. sosnowskyi* plants using the heat and light resources available in the spring. When the soil is warmed to a greater depth, the active regrowth of the virginile and generative individuals begin. Increase in leaf area of these individuals leads to a shading of plants in the ground canopy layer and has an inhibitory effect on an accumulation of their phytomass.

The cold resistance and ability of the pregenerative individuals to actively grow until mid-October, when the average daily air temperature reaches near-zero values, determine the efficient use of environmental resources in the autumn period. It was previously shown [24] that the *H. sosnowskyi* plants exhibited a resistance to low temperatures in spring and autumn due to a shift in the temperature optimum of growth in accordance with changes in thermal environmental conditions. This peculiarity allows the plants that live on the periphery of the northern border of the invaded range functioning at low positive air temperatures at the beginning and the end of the growing season [18, 25].

Duration of a growing season of the *H. sosnowskyi* is associated with the peculiarities of the rhythm of a seasonal development. It that by mid-July, up to half of the juvenile plants has been shown to turn into a state of the paradormancy as a result of a decrease in light supply below a critical level. The vegetation resumption of the juveniles was noted in the autumn, after the leaves of the generative plants died off and the flow of PAR into the ground canopy layer was increased. Similar data were obtained for the deciduous forest zone, where the *H. sosnowskyi* juvenile plants went into a dormant state in the summer and resumed growth processes in the autumn [9].

Revealed features of the rhythm of development of the *H. sosnowskyi* ensure the CP self-maintenance and the dominance of this species in herbaceous communities throughout the entire growing season of plants. For northern territories, the duration of the growing season of the *H. sosnowskyi* was almost equal to the number of days in a year without a snow cover.

The studied *H. sosnowskyi* CPs were characterized by left-sided ontogenetic spectra with a high level of similarity ($r = 0.98$). Individuals in the pregenerative state were dominated in CP (see Table. 1), characterizing CP as normal and young. The average density of the immature and virginile plants was 4–7 pcs/m^2 and 12–16 pcs/m^2, respectively. The generative individuals had a significantly lower density (1–3 pcs/m^2). Based on quantitative parameters of the ontogenetic structure of CP, recovery indices were calculated (I_{IN}) of CPs the values of which were $\geqslant 2$. The obtained values point to the high efficiency of the maintenance and recovery of the *H. sosnowskyi* CP.

Given in Table 1 population densities and distribution of individuals according to their ontogenetic states turned out to be comparable with data on the demographic structure of the *H. sosnowskyi* CP in other parts of the invaded range. In the conditions of the southeastern part of the Kamchatka Peninsula, the pregenerative individuals predominated in the CP

(450–681 pcs/m^2), and 3–4 generative plants were grown at 1 m^2 of this region [26]. A slightly lower density of the plants was observed on the territory of the Republic of Bashkortostan (41–92 pcs/m^2) and in the Primorsky Territory (78 pcs/m^2). The pregenerative individuals dominated in the CP composition; 2–4 reproductive plants were found at 1 m^2 [16, 27].

We found that distinctive features of the structure of the *H. sosnowskyi* CPs were an extremely small number of viable seeds in the soil, the absence of seedlings, and a high density of the juveniles (see Table. 1). In April–May, almost simultaneous germination of most of the seeds and a rapid development of seedlings were observed. In summer (June–July), some of the seedlings died off, and the remaining part of the plants passed into the juvenile state. Subsequently, we detected the growth inhibition of the juvenile plants in the ground canopy layer with the development of the leaf apparatus. Some individuals of this ontogenetic group entered a state of the paradormancy, which was accompanied by the death of the aboveground shoot. This fact explained the absence of seedlings in the *H. sosnowskyi* CP and high density of the juveniles plants.

An assessment of the CP age structure revealed that the average calendar age of the virginile and generative individuals was 3 full years. The *H. sosnowskyi* plants started flowering at the age of 2–6 years, and the maximum lifespan of the individuals was 7 full years. The tame *H. sosnowskyi* plants reached the calendar age of 14–16 years [28], whereas the closely related *H. mantegazzianum* species lived 12 years in the conditions of the invaded range [14].

The *H. sosnowskyi* plants reached significant sizes under the North conditions (see Table 2). The *H. sosnowskyi* plants formed communities with a low abundance of other herbaceous species due to the large size and productivity. The maximum accumulation of the *H. sosnowskyi* phytomass (about 15 kg/m^2) was observed by the middle of the growing season. The generative individuals formed more than 60% of the total phytomass during periods of the flowering and the beginning of fruiting. The pregenerative individuals produced approximately 5 kg/m^2 of the phytomass. This value corresponded to only a third of the total plant mass in the cenopopulations. The obtained values of the phytomass accumulation by the *H. sosnowskyi* plants corresponded to the productivity of this species cultivation [21, 29].

Estimate a preproductive effort (the amount of the reproductive organs relatively to the total mass of the generative plants) showed its low values (11%). The small reproductive effort provided sustainable seed regeneration, retention of occupied territories, and dispersal of the species owing to maintenance of a stable density of generative individuals in the CP (1–3 pcs/m^2) [11].

We classify the *H. sosnowskyi* plants as a geophytes [19], because their underground part consists of a submerged caudex at the top of which the terminal overwintering bud of renewal is formed. Generative plants at the age of 3–5 years are characterized by the most developed underground part (see Table 2). A distinctive feature of the *H. sosnowskyi* is a significant immersion of the caudex and the renewal buds into a soil with an increase in the calendar age and the size of the plants. The caudex deepening is achieved due to a contractile system of roots the length of which can reach 90 cm. This life strategy protects the renewal buds from mechanical damage and freezing. Freezing of soils to critical temperatures for wintering plant organs is one of the factors that limit the spread and naturalization of invasive *Heracleum* species in northern latitudes [18].

The rhythm of a development of the plants and their morphological structure determined the architectonics of the communities with a dominance of the *H. sosnowskyi*. In the first 2–3 weeks of the growing season (April–May), the seedlings and the juvenile plants received from 25% to 100% of incident photosynthetically active radiation (up to 1000 μmol/m^2c), which ensured their active growth. Subsequently, the spatial distribution of leaf area and light levels were significantly changed with a development of the assimilation organs of the immature, virginile, and generative plants.

The type of a vertical distribution of the assimilation area that is observed for herbaceous communities with a participation of the *H. sosnowskyi* in summer (see Fig. 2) is known as "inverted pyramid" [13, 29]. A distinctive feature of this method for placing the leaf apparatus is a significant increase in the area of the assimilation area in the vertical profile. This type of a placement of the assimilation organs has been shown to be the most optimal for communities with few species. The "inverted pyramid" provides a higher level of daily CO_2 fixation by a plant community in comparison with other types of vegetation architecture ("broad base pyramid" and "narrow base pyramid"). At the same time, the highest photosynthetic productivity is observed when the grass canopy reaches a leaf index in the range from 5 to 6. We found the value of the leaf index for the CPs to be 4.4. This value is close to the those of this parameter for highly productive communities with *H. sosnowskyi* in the Caucasus [13].

Leaves of the *H. sosnowskyi* plants were characterized by a diffuse distribution from almost horizontal in the ground canopy layer to plagiophilic in the upper layer (see Fig. 3d). Such distribution provided an effective absorption of a solar radiation (see Fig. 3c). The distribution of leaves in the CP vertical profile determined the specific functional characteristics of the *H. sosnowskyi* assimilation organs. Under shading conditions, plants in the ground canopy layer had a low leaf density, a high content of chlorophylls in the light-harvesting complex of the photosynthetic apparatus, and a high efficiency of the light use during photosynthesis [8].

In autumn (August–September), the death of leaves of the generative individuals resulted in the 25–50% increase in light supply in the middle and ground canopy layers of communities with a dominance of the *H. sosnowskyi*. The vegetative individuals preserved their leaf area 30–40 days longer (until October) than that of the generative plants (see Fig. 2). At the beginning and the end of the vegetation, the plants from the ground and middle canopy layers received one order of magnitude more light energy than in the summer period, under conditions of strong shading by the generative individuals.

Thus, the specificity of the radiation regime characteristic of communities with the *H. sosnowskyi* regulates periods of the growth activity and the rest of the individuals of different age states, suppresses the vital activity of competing greenery, and promotes the sustainable development of species-poor communities. A shadowing of the ground canopy layer is one of the mechanisms of environmentally forming influence of the *H. sosnowskyi* during its invasion into native plant communities [9, 10, 17].

CONCLUSIONS

Mechanisms of the sustainable growth and reproduction of the species in the North have been identified as a result of a complex study of the structural and functional organization of plants in the *H. sosnowskyi* cenopopulations.

Observations on the rhythm of seasonal development demonstrate that duration of growing season of the *H. sosnowskyi* is 180–190 days. This phenomenon is due to an early date of the spring regrowth and the long autumn vegetation of the pregenerative individuals, which is a competitive advantage in the course of the *H. sosnowskyi* invasion into natural and transformed phytocenoses.

The studied *H. sosnowskyi* CPs showed a high density of the juveniles (1700 pcs/m^2) and the number of the immature, virginile, and generative individuals of 4–7 pcs/m^2, 12–16 pcs/m^2, and 1–3 pcs/m^2, respectively. The majority of the juveniles (more than 95% of the plants) were represented by plants at the age of one full year of life. Other ontogenetic groups (*im*, *v*, *g*) in CP included plants at the age from 1 to 7 full years. The average calendar age of the generative individuals was 3 full years.

The *H. sosnowskyi* cenopopulations were characterized by the left-sided ontogenetic spectra. The individuals in the pregenerative state were dominated in CP, characterizing them as normal and young. High values of the recovery indices ($I_{IN} \gg 2$) indicated the effectiveness of the processes of maintenance and restoration of the *H. sosnowskyi* CP. A distinctive feature of the CP structure during the flowering period of the generative individuals (June–July) was a small amount of viable seeds and the absence seedlings, which is a consequence of a synchronous germination of mericarps after the melting of a snow cover and rapid passing of the post-emergence development stage.

The *H. sosnowskyi* plants were a high productivity. They formed up to 15 kg/m^2 of a raw phytomass, half of which consisted of the generative individuals. The main part of the assimilating area of the generative individuals was located in the upper canopy layers of CP according to the type of the "inverted pyramid" and absorbed about 70% of the incoming PAR. The phytogenic field of generative plants had an inhibitory ecological-cenotic effect, i.e. regulated the periods of a growth activity and a dormancy of the pregenerative *H. sosnowskyi* individuals and suppressed the activity of competing vegetation.

One of the important characteristics of the *H. sosnowskyi* is an ability of its caudex and the caudex-located renewal buds to penetrate into the soil. This property provides the preservation of the plant viability and is an important factor of the survival of the species in areas with low negative air temperatures in winter.

The identified mechanisms of the structural and functional organization of the *H. sosnowskyi* at a level of one plant and the whole cenopopulation can become the basis for developing a sustainable strategy for alien invasive plant management.

ACKNOWLEDGMENTS

The authors thank E.V. Ivanov (Pitirim Sorokin Syktyvkar State University) for his assistance in collecting material.

FUNDING

The work was carried out within the framework of the topic of State Budget Research, Development and Technological Work "Photosynthesis, Respiration, and Bioenergetics of Plants and Phototrophic Organisms (Physiological-Biochemical, Molecular-Genetic, and Ecological Aspects)" (reg. no. 122040600021-4). No additional grants were received to conduct or direct this specific study.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This article does not contain any studies involving human or animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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