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The impact of disturbance on the site conditions and regeneration of a *Dianthus carthusianorum* population in sand grassland

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Abstract. The impact of disturbance on site conditions and regeneration of *Dianthus carthusianorum* L. in an abandoned patch of sand grassland *Koelerion glaucae* is examined in the paper. Observations were conducted in the years 2013–2016, at a site with phytomass and topsoil artificially removed (NEW PATCH) and a site with untouched vegetation (OLD PATCH). The number and height of vascular plant species, plant and cryptogam cover and soil moisture were lower, while light availability and soil pH were higher in the NEW PATCH. The habitat conditions within an opening in the plant canopy enhanced the recruitment and growth of seedlings in *D. carthusianorum*, whereas variability of individual traits (i.e. number and features of rosette leaves, number and dimensions of generative stems, as well as fruit and seed production) in the studied patches might enable the persistence of a population in a post-disturbed place, as well as its escape from an overcrowded site.

Key words: clonal species, individual and population traits, *Koelerion glaucae*, ramet cluster, regeneration

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Introduction

Literature has extensively confirmed that anthropogenic disturbances, such as overgrazing, deforestation and harvesting of non-timber forest products, overexploitation of minerals, as well as tourism and adventure activities occurring on a large scale, have dramatically changed the species composition, structure, and function of several habitats around the world (Chabanet & al. 2005; Wei & al. 2013; Peng & al. 2013; Malik & al. 2016; Menga & al. 2016). On the other hand, small-scale disturbances may contribute to the origination of gaps considered as 'safe sites for seedling recruitment' (*sensu* Harper & al. 1965), where individuals can germinate spontaneously from propagule reserves stored in the soil bank, or from post-disturbance seed rain. Such phenomenon was observed over a wide range of habitats: from forests (Dzwonko & Gawroński 2002; Gairola & al. 2015), via meadows and grasslands (Falińska 2003; Kostrakiewicz 2007, 2011; Kostrakiewicz-Gierałt 2013a, 2015a, b; Müller & al. 2013; Yuan & al. 2016) to abandoned old fields (Lavorel & al. 1998). Moreover, other observations (Borkowska 2004; Sapkota & Odén 2009; Otoda & al. 2013; Plenzler & Michaels 2015) proved that gaps play the role of 'regeneration niches' (*sensu* Grubb 1977), defined as sets of environmental requirements necessary for germination, establishment and further development of immature plants, leading eventually to replacement of the individuals of one generation by those of the next.

Despite growing interest in this topic, studies combining post-disturbance investigations of the natural recovery of populations are still rather scarce. Such investigations would appear to be especially valuable and desirable in endangered habitats, providing a basis for successful programmes for their restoration. Accordingly, the present studies were performed in abandoned sand grassland of a *Koelerion glaucae* alliance, currently considered among the most endangered habitats in Europe (European Commission DG Environment 2007). The main aim of the investigations was to assess the effect of disturbance on habitat conditions, as well as on population and individual traits of the rare clonal species *Dianthus carthusianorum* L. The specific aims were to assess: (i) biotic and abiotic site conditions; (ii) number and age structure of individuals/ramet clusters of *D. carthusianorum*; (iii) selected traits of vegetative and generative individuals/ ramet clusters of the target species.

Material and methods

Study species

Dianthus carthusianorum (Carthusian Pink) is a herbaceous perennial plant forming rosettes of grass-like leaves up to 7 cm long and 5 mm wide, and from one to several mostly unramified generative stems up to 70 cm high. Several purple fly-pollinated flowers are produced together in a tight flower head. The fruit is an oblong capsule containing numerous light self-dispersed seeds with considerable germination ability (Sychowa 1992; Kleyer & al. 2008; Royal Botanic Gardens Kew 2017). The aforementioned taxon reproduces also in a vegetative way and is classified among root-splitters with slight lateral spreads (Klimešova & Klimeš 2008). *Dianthus carthusianorum* is native to Europe, from Spain in the west, Belgium and Poland in the north, and Ukraine in the east, to Italy, Greece and Turkey in the south (Anderberg & Anderberg 1996). Populations of Carthusian Pink occur in calcareous or sandy soils, mostly in grasslands and at forest edges (Matuszkiewicz 2001). Moreover, several populations are adapted to grow in serpentine soils and wastes (Koszelnik-Leszek & Kasowska 2009), as well as in calamine soils and Zn-Pb waste deposits (Wierzbicka & Rostański 2002); therefore, the chosen ecotypes might be used in remediation of contaminated sites (Muszyńska & Hanus-Fajerska 2016). Carthusian Pink, considered rare in some parts of its range, e.g. in Bulgaria (Petrova & Vladimirov 2009) and Switzerland (Moser & al. 2002), is vulnerable due to abandonment of traditional land use and subsequent successional overgrowing and afforestation of grasslands (Poschlod & al. 1996), and rare occurrence of pollinators (Bloch & al. 2006).

Study area

The studies were carried out in the Kostrze district, on the western border of Cracow (South Poland). The research area was located on the low flood terrace of Vistula River, where arenosols are covered by *Koelerion glaucae* patches (Jędrychowski 2007). Abandonment of the traditional land use for at least a dozen years back has favoured the encroachment of shrubs and trees such as *Berberis vulgaris* L., *Betula pendula* Roth, *Crataegus* sp., and *Robinia pseudacaccia* L., as well as of tall-growing herbaceous plants, e.g. *Erigeron canadensis* L., *Solidago canadensis* L. and *S. gigantea* Aiton. This phenomenon has contributed to fragmentation of the sand grassland patches.

The investigations were conducted in an abandoned sand grassland (50° 1' 28.02" N; 19° 50' 6.59"E) characterised by moderate presence of the grassland taxa (*D. carthusianorum, Calamagrostis epigejos* (L.) Roth, *Corynephorus canescens* L., *Achillea millefolium* L., *Sedum sexangulare* L., *S. acre* L., *Koeleria glauca* (Schrader) DC, *Euphorbia cyparissias* L., *Galium verum* L., *Briza media* L., and *Leucanthemum vulgare* Lam.) and substantial abundance of ruderal taxa (*S. canadensis, Erigeron annuus* (L.) Pers, *Cirsium arvense* (L.) Scop., and *Rubus* sp.). In the early summer of 2013, the plant canopy and topsoil were removed from part of the grassland measuring 8 × 40 m. In August 2013, two permanent square sample plots measuring 200 m^2 were established in an area with removed plant cover (NEW PATCH) and an area with untouched vegetation (OLD PATCH).

Field experiment

Habitat conditions in the study patches were observed during the first week of September in the years 2013–2016. In each plot, the names of taxa represented most abundantly by adult individuals or their ramets were noted. Then, within each plot, 20 measuring points were chosen and marked with plastic pegs. Four points were established systematically in the corners of the permanent plots, while the remaining points were chosen randomly. The marked points served as centres for setting iron rims, 30 cm in diameter, used for evaluation of biotic (number and height of vascular plant species, plant and cryptogam cover) and abiotic habitat conditions (light intensity at soil level, pH and moisture of soil). Light availability was measured using a Voltcraft MS-1300 digital light meter (accuracy ±5 %; range 0.01-50,000 lx). Soil humidity and pH were measured using a BIOWIN sensor with a measuring range of 1-10 (soil humidity 1-3: dry; 4-7: moist; 8-10: wet; soil pH 3-6: acid, 7-10: alkaline). The number of vascular plant taxa within the rim was counted, while the percentage of ground surface covered by vascular plants and cryptogams (moss and lichens) was estimated visually. The mean height of *Dianthus carthusianorum* neighbours was estimated on the basis of height (from soil level to the top) of stem of the lowest and the highest plant growing within the rim.

In terms of opportunity for vegetative growth of *D. carthusianorum*, the individual and the ramet cluster were adopted as the basic demographic units in the presented investigation. An individual (genet) is a plant creating one above-ground unit, while the term 'ramet cluster' is understood as an integral group of above-ground units (generative stems and/or leaf rosettes).

All individuals and ramet clusters occurring within study plots in the years 2013-2016 were counted and assigned to developmental stages: seedling (one rosette of leaves with cotyledons), vegetative (one or more leaf rosettes), or generative (flowering stem or stems with/without leaf rosettes). Detailed observations of the vegetative individuals/ramet clusters included the number of leaf rosettes, number of leaves in each rosette, and length of the longest leaf. Investigations of the generative individuals/ramet clusters involved the number of above-ground units, number of leaves per rosette, length of the longest leaf, height of each flowering stem, and number of capsules. Then, in both sample plots, the seed number in 30 randomly collected fruits was counted. Measurements of the height of generative stems were carried out using a folding tape measure; the dimensions of leaf blades were measured using a LUX-Tools Comfort digital caliper (accuracy +/-0.01; measuring range 0.1-150 mm).

Statistical analysis

Normal distribution of the untransformed data concerning habitat conditions, as well as production of seeds of *D. carthusianorum* in an individual sample (from a particular patch and year), was tested using the Kolmogorov-Smirnov test, while homogeneity of variance was tested using the Levene test at the significance level of $P<0.05$. As the values of individual characteristics in some groups were not consistent with normal distribution and variance was not homogeneous, the Mann-Whitney U test was applied to check for variability between patches in terms of habitat conditions. Moreover, it was also used to test whether the number of seeds per fruit differed remarkably between the sample plots, while the Kruskal-Wallis H test was applied to check whether this number presented significant temporal variability.

The chi-square statistics was applied to test whether significant differences existed between plots and years in terms of: (i) age structure of individuals (ramet clusters); (ii) contribution of vegetative individuals (ramet clusters) characterised by various features of leaf rosettes; (iii) contribution of generative individuals (ramet clusters) characterised by various features of leaf rosettes, as well as by different numbers and traits of flowering stems. Statistical analyses were performed with STATISTICA 10 software (StatSoft, Inc. 2010).

Results

Habitat conditions

The observed patches differed in terms of species composition of standing vegetation. In the NEW PATCH, the dominant species differed in the consecutive years. In 2013, ramets of the clonal species *A. millefolium* from the undisturbed adjacent vegetation started to encroach on the plot surface; in the subsequent seasons *C. canescens*, *Poa annua* L., and *Briza media* L. prevailed in the plant cover; and in the final year of observation, *Trifolium arvense*, *Euphorbia cyparissias* L. and *Thymus serpyllum* occurred most frequently. In the OLD PATCH, *A. millefolium*, *Leucanthemum vulgare*, *S. canadensis*, *E. annuus*, and *Rubus* sp. dominated during the entire study period. The number of vascular plant species, plant and cryptogam cover, height of standing vegetation, and soil moisture were significantly higher in the OLD than in the NEW PATCH, while soil pH and light availability at ground level presented an inverse tendency (Table 1).

Table 1. Habitat conditions in the study plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) in 2013–2016.

Year	The abiotic or biotic parameter	Mean value (±SD) recorded in:		The value of U Test
		NEW PATCH	OLD PATCH	
2013	Number of plant species	4.3 (±2.2)	12.8 (±2.4)	Z = 4.98***
	Plant and cryptogam cover [%]	10.7 (±4.4)	79.3 (±9.1)	Z = 5.41***
	Height of plant [cm]	10.5 (±6.2)	40.3 (±16.9)	Z = 5.18***
	Soil moisture (range 1-10)[1]	1.2 (±0.4)	2.3 (±0.8)	Z = 3.93***
	Light availability [Lx]	47300.0 (±2830.3)	42400.0 (±2764.1)	Z = -4.04***
	pH of soil (range 1-10)[2]	7.5 (±0.5)	7.0 (±0.4)	Z = -2.28*
2014	Number of plant species	7.5 (±2.7)	14.3 (±2.5)	Z = 5.22***
	Plant and cryptogam cover [%]	15.4 (±10.6)	81.5 (±8.8)	Z = 5.39***
	Height of plant [cm]	11.9 (±8.0)	44.7 (±19.7)	Z = 4.89***
	Soil moisture (range 1-10)	1.2 (±0.4)	2.4 (±0.8)	Z = 2.82**
	Light availability [Lx]	47000.0 (±2704.3)	43050.0 (±2355.3)	Z = -3.44***
	pH of soil (range 1-10)	7.5 (±0.5)	6.9 (±0.4)	Z = 4.17***
2015	Number of plant species	10.6 (±3.2)	15.5 (±1.6)	Z = 4.61***
	Plant and cryptogam cover [%]	21.0 (±10.6)	82.2 (±8.4)	Z = 5.31***
	Height of plant [cm]	14.1 (±8.0)	47.5 (±20.6)	Z = 4.92***
	Soil moisture (range 1-10)	1.4 (±0.3)	2.6 (±0.8)	Z = 3.92***
	Light availability [Lx]	46550.0 (±2704.3)	42150.0 (±2833.3)	Z = -3.81***
	pH of soil (range 1-10)	7.6 (±0.5)	6.9 (±0.5)	Z = -3.50***
2016	Number of plant species	13.3 (±4.8)	17.1(±2.6)	Z = 2.48*
	Plant and cryptogam cover [%]	26.6 (±11.5)	83.0 (±8.4)	Z = 5.39***
	Height of plant [cm]	19.1 (±8.6)	48.6 (±22.8)	Z = 4.31***
	Soil moisture (range 1-10)	1.2 (±0.4)	2.5 (±0.9)	Z = 4.21***
	Light availability [Lx]	45400.0 (±3377.9)	42650.0 (±2666.9)	Z = -2.63***
	pH of soil (range 1-10)	7.7 (±0.7)	6.9 (±0.4)	Z = -3.42***

[1,2] range 1–10 (soil moisture 1–3:dry, 4–7:-moist, 8–10: wet; soil pH 3–6: acid, 7–10: alkaline). The level of statistical significance: *-P<0.05, **-P<0.01, ***-P<0.001.

Abundance and age structure of individuals/ ramet clusters of *D. carthusianorum*

During the entire study period, the abundance of individuals and ramet clusters of *Dianthus carthusianorum* was greater in the NEW PATCH with removed plant cover and topsoil, than in the OLD PATCH with untouched plant canopy (Table 2). In both sample plots, seedlings, vegetative individuals and generative ramet clusters were observed, while no vegetative ramet clusters or generative individuals were found. In the NEW PATCH, in the first season of observation only seedlings and vegetative individuals were recorded; in the following years, the number of recruits diminished and domination of generative ramet clusters gradually increased. In the OLD PATCH, moderate seedling recruitment occurred in the years 2013-2014 only, while generative ramet clusters prevailed during the entire study period (Fig. 1).

Table 2. Abundance of individuals and ramet clusters of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2013–2016.

Year	NEW PATCH	OLD PATCH
2013	96	78
2014	88	80
2015	104	64
2016	114	66

Traits of vegetative and generative individuals/ ramet clusters of *D. carthusianorum*

The number of leaves per rosette in vegetative individuals was constant throughout the study period in both sites, reaching significantly greater values in the NEW PATCH (Fig. 2). The length of the longest leaf increased in consecutive years in both sites, achieving greater values in the OLD PATCH (Fig. 3). A much greater number of ramets creating generative ramet clusters were noted in the NEW PATCH. Moreover, ramet clusters showed a significant temporal increase in the number of above-ground units (Fig. 4).

The number of rosette leaves in generative ramet clusters remained constant in the consecutive seasons and was much greater in the NEW PATCH (Fig. 5), whereas the length of the longest leaf increased in subsequent years and was much greater in the OLD PATCH (Fig. 6). The height of flowering stems showed only spatial variability and was significantly greater in the OLD PATCH (Fig. 7). The number of capsules per flowering stem (Fig. 8) and number of seeds per fruit (Table 3) showed only spatial variability and achieved greater values in the OLD PATCH.

TTable 3. Average number of seeds per capsule (±SD) of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. The level of statistical significance is as in Table 1.

Year	NEW PATCH	OLD PATCH	The value of U Test
2014	132.7 (±38.8)	143.4 (±49.4)	Z = -0.90
2015	140.8 (±20.7)	161.4 (±40.1)	Z = -3.35***
2016	148.6 (±41.4)	175.9 (±47.7)	Z = -2.37***
The value of H Test	H = 5.68	H = 5.17	

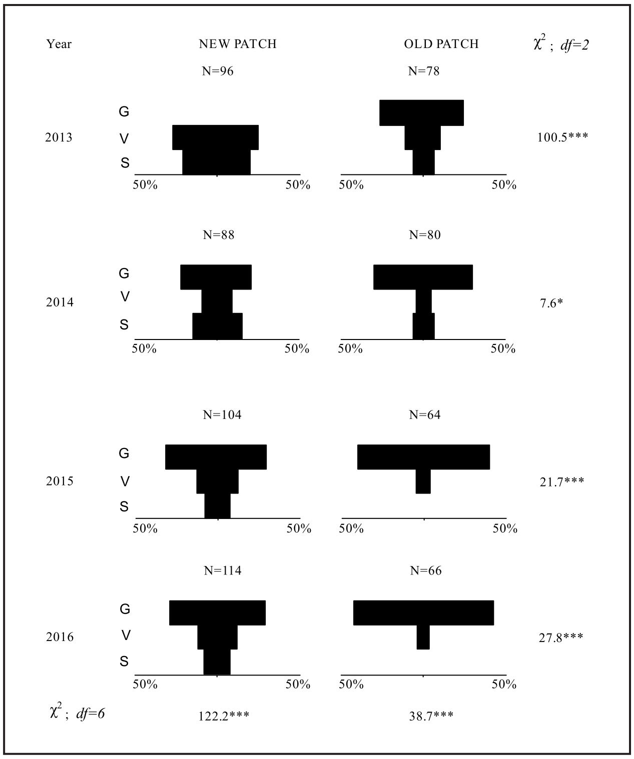

Fig. 1. Structure of developmental stages of the individuals and ramet clusters of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September of 2013–2016. Abbreviations: S- seedlings, V- vegetative individuals/ramet clusters, G-generative individuals/ramet clusters; N= number of individuals and ramet clusters; χ2 – the value of chi-square test; *df*= degree of freedom; the level of statistical significance is as in Table 1.

Discussion

Habitat conditions

The observed considerable post-disturbance encroachment of ramets from the undisturbed adjacent vegetation, as well as the recruitment of seedlings from soil seed reserves or seed rain, contributed to bridging the gap in the percentage of plant cover between the NEW and the OLD PATCH at the conclusion of the observations. The results correspond to the findings of Schnoor & al. (2015) showing a rapid colonisation of degraded sand grasslands subjected to experimental ploughing or rotavation. Furthermore, the significantly lower height of vascular plants in the NEW PATCH is in accordance with the observations of Ónodi & al. (2008), showing that the height of standing vegetation is significantly greater in the unmanaged sand grasslands than in the grazed ones.

The lower degree of soil moisture observed in post-disturbed sites supports the observations showing augmented water stress as an effect of mowing in

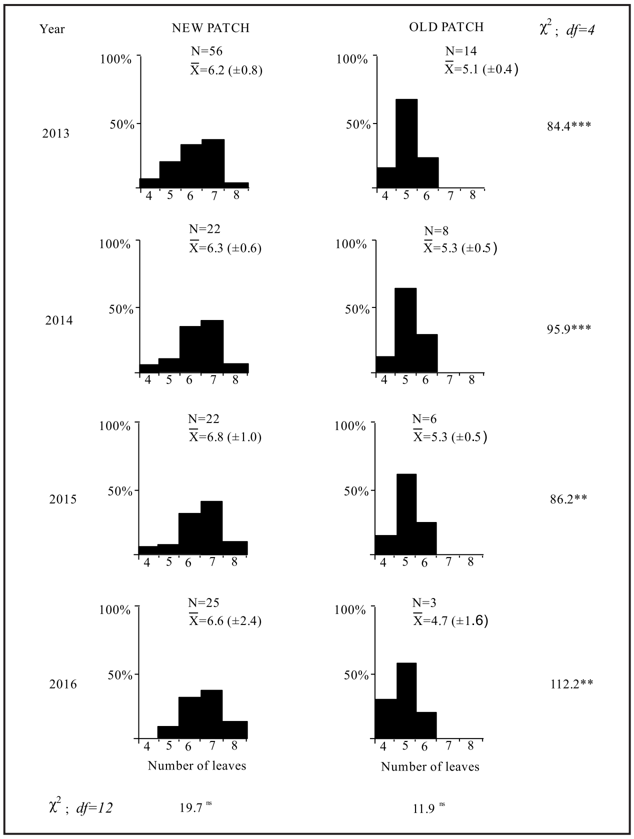

Fig. 2. The number of leaves in rosettes in vegetative individuals of *Dianthus carthusianorum* at the plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September of 2013–2016. Abbreviations: $\bar{X}$ mean value (±standard deviation). Other abbreviations are as in Fig. 1.

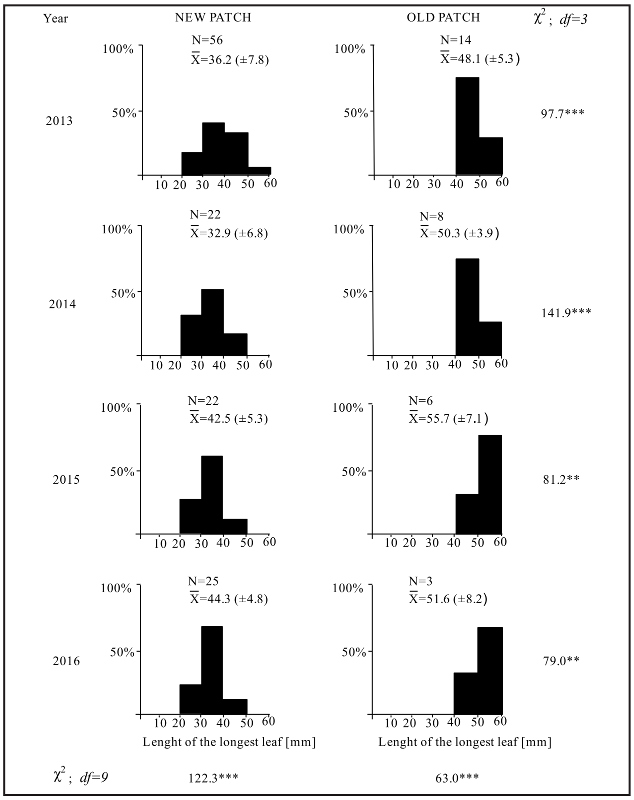

Fig. 3. Length of the longest rosette leaf in the vegetative individuals of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2013–2016. Abbreviations are as in Fig. 2.

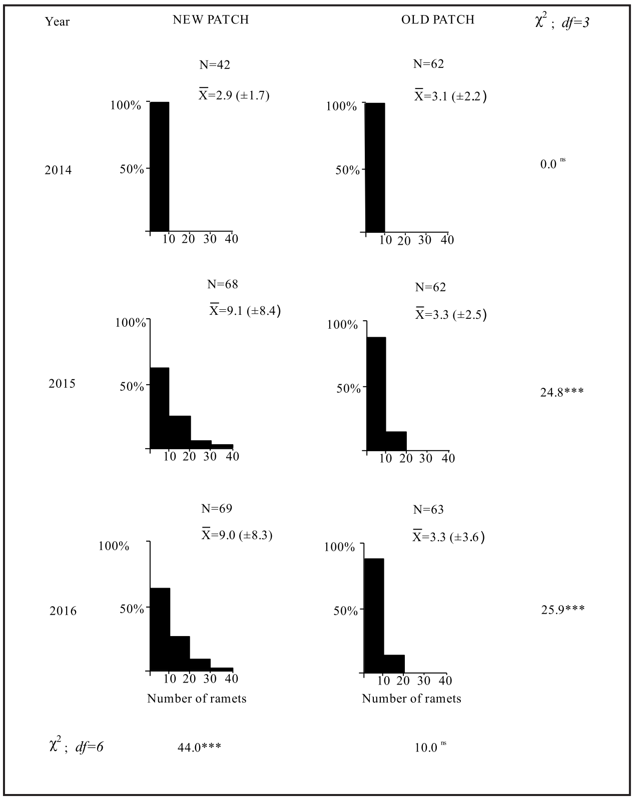

Fig. 4. The number of ramets in the generative ramet clusters of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. Abbreviations are as in Fig. 2.

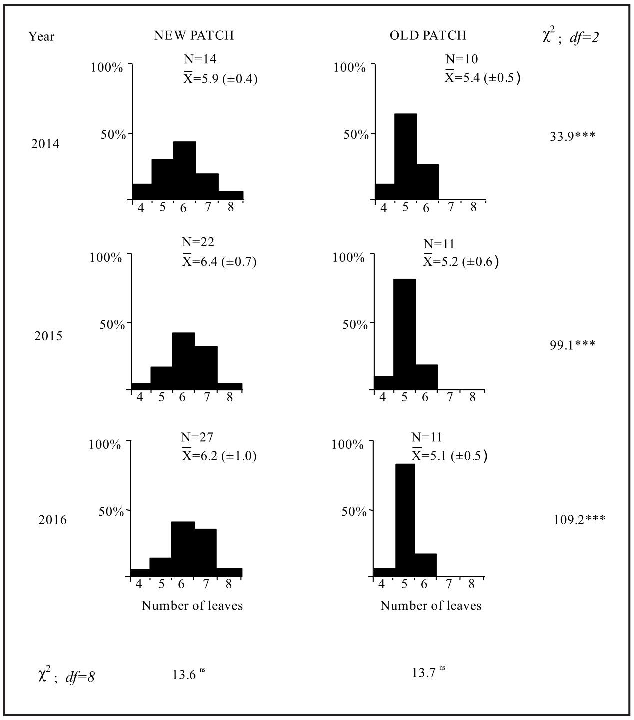

Fig. 5. The number of leaves in rosette in the generative ramet clusters of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. Abbreviations are as in Fig. 2.

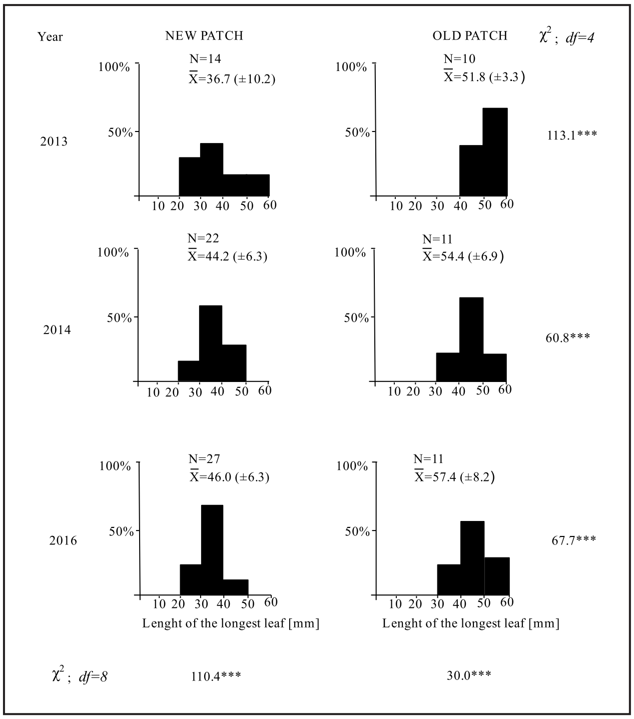

Fig. 6. The length of the longest rosette leaf in the generative ramet clusters of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. Abbreviations are as in Fig. 2.

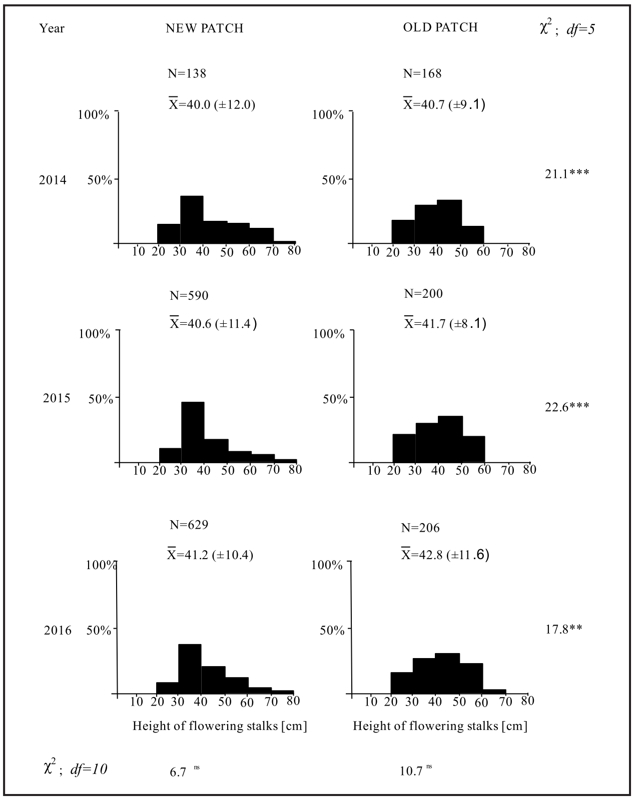

Fig. 7. The height of flowering stems of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. Abbreviations are as in Fig. 2.

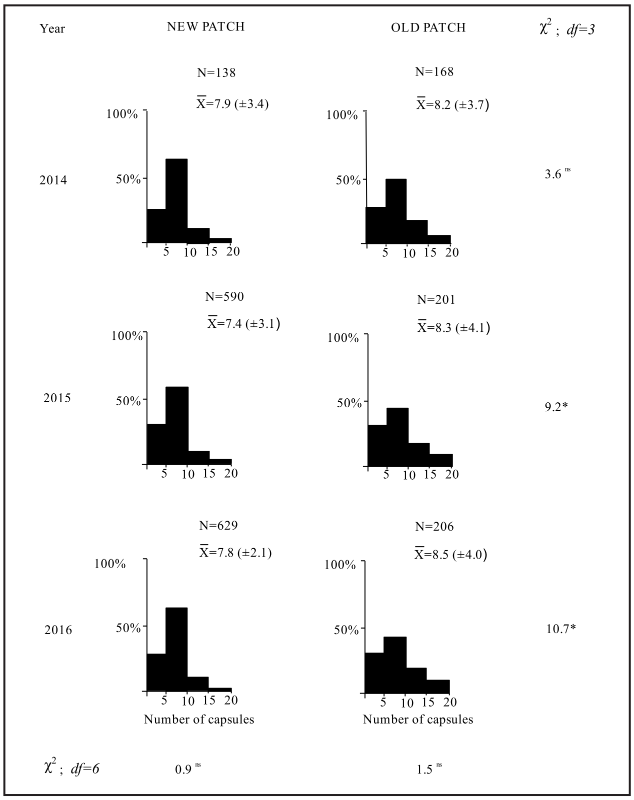

Fig. 8. The number of capsules per flowering stem of *Dianthus carthusianorum* in plots with removed plant canopy (NEW PATCH) and with untouched plant cover (OLD PATCH) recorded in September 2014–2016. Abbreviations are as in Fig. 2.

calcareous grasslands (Maalouf & al. 2012). According to Jentsch & Beyschlag (2003 and literature cited therein), a lack of ground colloids in sandy soils results in low water storage capacity, whereas during succession the humus content increases, improving water-holding ability. Artificial disturbance and subsequent land colonisation by low-stature taxa contributed to considerable light availability at the ground surface in the NEW PATCH. A similar phenomenon has been observed by many authors (see Jacquemyn & al. 2003, Derner & Wu 2004). Gross & al. (2007) also showed a much greater light interception by standing vegetation in the undisturbed grasslands than in the managed ones. Moreover, the performed observations confirm the findings of Gilhaus & al. (2015), who noted lower soil pH values in the overgrown sand grasslands than in the restored ones. These authors argued that, during succession, pH in the upper soil decreased through leaching of the base cations and litter accumulation. On the contrary, Schnoor and Olsson (2010) and Olsson & Ödman (2014) provided evidence that soil perturbation does not affect the values of soil pH in the sand grasslands.

Abundance and age structure of individuals/ramet clusters of *D. carthusianorum*

Observations showing substantial recruitment of *D. carthusianorum* seedlings in the NEW PATCH correspond to the earlier investigations of this species (Kladivová & Münzbergová 2016) and its congeners (Schnoor & Olsson 2010, Kostrakiewicz-Gierałt 2014a, b). The successful post-disturbance growth and development of *D. carthusianorum* individuals were in accord with the observations of transplanted genets of *Dianthus morisanus* in the sand dunes (Cogoni & al. 2013). The low level of recruitment of seedlings in the OLD PATCH, observed solely at the beginning of the study period, has contributed to a slight increase in the abundance of population of the target taxon. The long-term cessation of offspring emergence may augment in the future the risk of population extinction, already observed in small populations of *Dianthus guliae* Janka (Gargano & al. 2015).

Studies showing the positive effect of mechanical removal of plant cover and topsoil on the emergence and development of individuals of Carthusian Pink support the findings showing spontaneous post-disturbance establishment of *Koeleria glauca* (Olsson & Ödman 2014), as well as *Aira caryophyllea* L., *Ornithopus perpusillus* L. and *Jasione montana* L. (Gilhaus & al. 2015). Moreover, Gilhaus & al. (2015) argued that topsoil removal, self-greening via recruitment from the propagule bank, and subsequent grazing might be particularly successful approaches for restoration of the endangered sand grasslands. On the other hand, studies by Rico & Wagner (2016) proved that grazing has a negative effect on the vitality of *D. carthusianorum* populations, contributing to reduction of their spatial genetic structure.

Traits of vegetative and generative individuals/ ramet clusters of *D. carthusianorum*

A greater production of rosette leaves by vegetative individuals growing in the NEW PATCH, stable in consecutive years, may have been caused by sufficient light availability, which was not limited by any neighbours growing in close vicinity. Reduction of rosette leaf numbers in immature individuals of *Arabidopsis thaliana* (L.) Heynh. as an effect of considerable shading was observed by Cookson and Granier (2006). On the other hand, they argued that shading induces diminishing of the dimensions of leaves. This finding is in opposition to our observations showing a remarkable increase in the length of leaves in consecutive years at both study sites and significantly longer leaves in the individuals of *D. carthusianorum* growing in the OLD PATCH. In regard to the large body of literature (see Kim & al. 2005), it can be pointed out that lamina length was highly responsive to herbaceous shade, and increases in this value enable optimisation of the plant's photosynthetic efficiency.

A significantly greater number of the above-ground units of *D. carthusianorum* and their increase in consecutive years, noticed exclusively in the NEW PATCH, may be the result of the free space suitable for production of new ramets. This scenario seems to be concordant with models predicting that in frequently disturbed habitats and in changing environment clonal growth is advantageous (Fahrig & al. 1994, Fukui & Araki 2014). A substantial vegetative multiplication of ramets in competitor-free sites and suppression of clonal growth in crowded environments has been found in other root-splitters (Colling & al. 2002), as well as in species creating horizontal above-ground (van Kleunen & al. 2001, Winkler & Stöcklin 2002) or hypogeogenous (Koutecká & Lepš 2011) stems in grasslands and meadows.

Variability of the traits of leaf rosettes in the generative ramet clusters of *D. carthusianorum* resembles that in the vegetative genets and, similarly, may depend on light availability conditioned by the character of surrounding plants. This outcome corresponds to the observations conducted on *Dianthus superbus* L. populations (Kostrakiewicz-Gierałt 2013b), where the length of leaves varied over the course of secondary succession.

The constant height of flowering stems over time, as well as the number of capsules and seeds achieving lower values in the NEW PATCH may be due to occurrence of low-stature plants in the immediate vicinity and lack of any necessity to overtop them. Creation of higher generative stems in the OLD PATCH may improve the visibility of flowers and enhance pollinator service, as well as increase the chances for successful dispersal in possibly more favourable sites. Occurrence of high generative stems in the vicinity of plants achieving considerable dimensions was also observed in *Dianthus superbus* (Kostrakiewicz-Gierałt 2013b), while the increased production of fruits as a result of substantial population density was noted in *Dianthus gratianopolitanus* Vill. (Putz & al. 2015).

Conclusions

Observations showed that habitat conditions in gaps originating from artificial removal of phytomass and topsoil in abandoned sand grassland enable the successful regeneration of *D. carthusianorum* populations. Low-statured neighbours scattered within a post-disturbed site enable the substantial vegetative growth of ramet clusters of the target species, creation of numerous small rosette leaves, and production of short generative stems with a moderate number of capsules and seeds. These traits may prolong the persistence of the target species in a newly-colonised site. On the other hand, the adjacent plants abundantly distributed in patches with untouched vegetation mechanically hampered the clonal growth of ramet clusters of *D. carthusianorum*, while domination of the tall-growing taxa triggered out the creation of few, long rosette leaves, as well as high generative stems bearing a substantial number of fruits and propagules, which might increase the chances of a successful escape from an overcrowded site.

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