

# Demographics of an endangered coastal plant, *Eryngium maritimum*, near the northeast border of the distribution range in relation to clonal growth



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Gederts Ievinsh\*, Una Andersone-Ozola, Ineta Samsone

Department of Plant Physiology, Faculty of Biology, University of Latvia, Jelgavas 1, Rīga LV-1004, Latvia

\*Corresponding author, E-mail: gederts.ievins@lu.lv

## Abstract

Scientific attention needs to be paid not only to coastal habitat conservation, but also to specific needs of particularly rare or endangered species of protected habitats. The aim of the present study was to obtain additional evidence on the clonal character of growth of *Eryngium maritimum* by demographic analysis of one subpopulation in Latvia during four consecutive seasons. Using the established spatio-temporal criteria for analysis of changes in distribution and number of *E. maritimum* plants, 64 individuals were studied. The individuals showed significant variation in complexity (number of shoots for the particular individual), number of flowers and leaves, as well as developmental phase changes (vegetative to generative and vice versa). In temporal respect, 44 individuals were located within a circle 20 cm in diameter, 15 individuals were located within a circle 30 cm in diameter, and five individuals were located within a circle 40 cm in diameter. For the majority of individuals no offset of shoots could be proposed as they were located within a circle 20 cm in diameter. Only the individuals located within a 30 cm circle potentially could have offset larger than 20 cm, and five individuals located within a circle 40 cm in diameter potentially could have offset larger than 30 cm during four seasons. It was concluded that existing individuals of *E. maritimum* in semi-fixed dune habitats are ramets of a small number of relatively old genets, propagating only by vegetative means. In general, this means that long-term conservation options of the existing populations are rather low.

**Key words:** clonal growth, coastal dunes, demographics, *Eryngium maritimum*.

## Introduction

Dry coastal habitats and their vegetation have received major scientific interest in Europe during the last decade, mainly because of need for a solid knowledge base for implementation of management and conservation actions (Provoost et al. 2011; Ciccarelli et al. 2012; Ciccarelli 2014). In addition to general measures oriented towards conservation of dune habitats, scientific attention needs to be paid also to specific needs of particularly rare or endangered species. One such example is *Eryngium maritimum* L. (Apiaceae), a perennial plant species with a specific distribution only in relatively diverse dry sea coast habitats, from shingle beach to fixed dunes and dry coastal meadow (Andersone et al. 2011). While abundantly distributed all around European coasts about a hundred years ago, the species presently is under risk of extinction, especially, at the northeast border of its distribution range around the Baltic Sea. While it is generally believed that extinction of coastal-specific plant species is primarily related to decrease of area of suitable habitats due to anthropogenic activities or coastal erosion processes (Provoost et al. 2011; Iwasato, Nagamatsu 2017), this is not a suitable explanation for decline of such species

like *E. maritimum* and *Crambe maritima* in the Baltic region, with a large number of potentially suitable sites for these plants in appropriate habitats on coastal areas of Latvia and Estonia. Therefore, conservation efforts for particular vulnerable species need to include biological aspects as well.

Physiological status and problems of natural generative propagation of *E. maritimum* on coasts of the Baltic Sea has been assessed (Andersone et al. 2011; Necajeva, Ievinsh 2013). In particular, it was established that photochemical performance of photosynthesis in *E. maritimum* is extremely sensitive to periods of increased precipitation (Andersone et al. 2011). Also, prolonged periods of precipitation together with low air temperature were devastating for seeds after ripening and, resulting in extremely poor germination rate (Necajeva, Ievinsh 2013). In a functionally-related comparative field study on coastal dunes in Northwest Spain with coexisting *E. maritimum* and three additional species (*Euphorbia paralias*, *Mathiola sinuata*, and *Pancreatium maritimum*), it was established that the species use different physiological strategies to cope in situations of growth-limiting resources (Bermúdez, Retuerto 2014). It was shown that for *E. maritimum*, mainly

photosynthetic capacity but not stomatal diffusion is determining water use efficiency, and consequently, higher drought tolerance of the species.

In spite of recent efforts, there are still gaps in understanding of the biology and ecology of *E. maritimum*, especially for characteristics contributing to establishment and survival of individuals. Clonal growth of *E. maritimum* has been hypothesized, but has never been explored experimentally (Iserman, Rooney 2014). In several studies genetical diversity of *E. maritimum* in the Northern region has been explored (Ievina et al. 2010; Minasiewicz et al. 2011; Ievina et al. 2019). Genetic diversity in both Latvian populations was found to be extremely low, pointing to significant contribution of self-fertilization or clonal propagation in establishment of individuals. However, comparison between isolated populations clearly indicated absence of balance between migration and genetic drift. It was assumed that *E. maritimum* populations at the northeast border of distribution range are in a process of local adaptation following postglacial recolonization of these territories (Ievina et al. 2019). No correlation between genetic diversity and size of population has been found in Poland, which might result from buffering of the genetic effect of fragmentation by both long life span of *E. maritimum* individuals and ability to propagate clonally (Minasiewicz et al. 2011).

The aim of the present study was to obtain additional evidence on the clonal character of growth of *E. maritimum* by demographic analysis of one subpopulation in Latvia during four consecutive seasons. It was hypothesized that individual shoots can shift their location from season to season as a result of regrowth from new root meristems.

## Materials and methods

The study site was located on semi-fixed primary dunes on the coast of the Baltic Sea near Ziemupe, Latvia, where there is a large local population of *E. maritimum* on the South-Eastern Baltic coast (N56°48'4", E21°4'4"). Several



Fig. 1. Part of the study site with *Eryngium maritimum* plants in 2014.

hundreds of *E. maritimum* plants are located in a zone of several kilometers. For the study, a particular site was chosen as having the largest group of individuals, more than one hundred shoots (Fig. 1).

Corners of a plot (6 × 9 m) covering the area with *E. maritimum* plants was marked by permanent wooden poles extending just a couple of centimeters above the soil surface in 2015. Each season in the middle of August, when plants were fully developed and flowering, wooden poles (2 m in height) were temporary installed around the perimeter of the plot at intervals of 1 m. Nylon cord (2 mm, orange color for better visibility) stretched at 0.5 height was used to mark 54 squares (1 m<sup>2</sup> each). Coordinates within each square were registered for each shoot using a metallic angle ruler (0.5 m long) for four consecutive years (2015 to 2108).

Three terms, “shoot”, “ramet” and “individual” were used to describe the spatial and temporal distribution of *E. maritimum* plants. “Ramet” was defined in a spatial context for each particular year. Either a single flower-bearing stem extending from the soil or a number of associated leaves

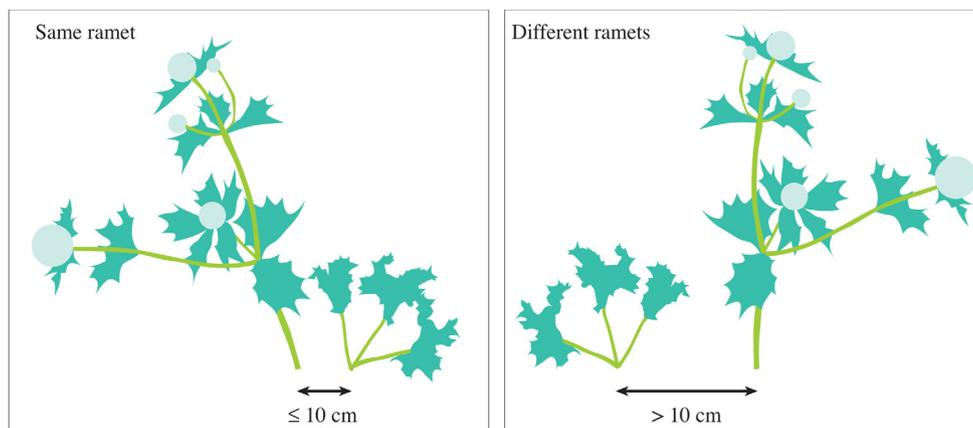


Fig. 2. Schematic view of generative and vegetative shoots of *Eryngium maritimum* showing the principle of discrimination between same and different ramets.

extending from a common point in soil was defined as a “shoot”. A separately located shoot was registered as a “ramet”. Several individual shoots within a circle of 10 cm were registered as belonging to one ramet with the same coordinates, recording location of the centre (Fig. 2). If distance between shoots were larger than 10 cm, they were recorded as separate ramets. The number of flowers and number of leaves was determined for each shoot in each ramet. “Individual” was defined in a temporal context, based on spatial distribution of ramets for each particular year, as a ramet appearing at the same location within a circle 20 cm in diameter during the consecutive years. However, due to either possible “movement” of existing shoots or appearance of new shoots from year to year, circles of larger diameter were also used, as described below.

Possible change of location with time was evaluated according to temporal change of coordinates of a ramet. It was estimated that an average difference in distance of 20 cm could be related either to measurement error due to rather irregular appearance of flowering shoots, with horizontal dimensions usually being 0.3 to 0.5 m in diameter, or small offset. Therefore, temporal changes in location of an individual ramet within a circle 20 cm in diameter were accepted as threshold for the same spatial location. Further, circles with diameter of 30 and 40 cm were assumed to indicate moderate and large spatial offset between years, respectively. Circles of these sizes were also used in all cases where the number of shoots per ramet was larger than one and temporal changes of location did not allow to discriminate the exact location of particular individual ramets. The lack of a particular shoot for one year was not taken into account as proving absence of the particular ramet, as this may have been caused both by natural or anthropogenic impact (damage leading to destruction of a shoot) at any point during the season before the actual survey.

Analysis of clonality of *E. maritimum* plants in field conditions was performed by observation in its natural habitat during 2007 to 2009 in Latvia (Užava, Ventspils region; N57°14'49", E21°25'52") and in 2007 in UK (Newborough, Isle of Anglesey, Wales; N53°7'58", W4°21'40").

## Results

### Demographic analysis

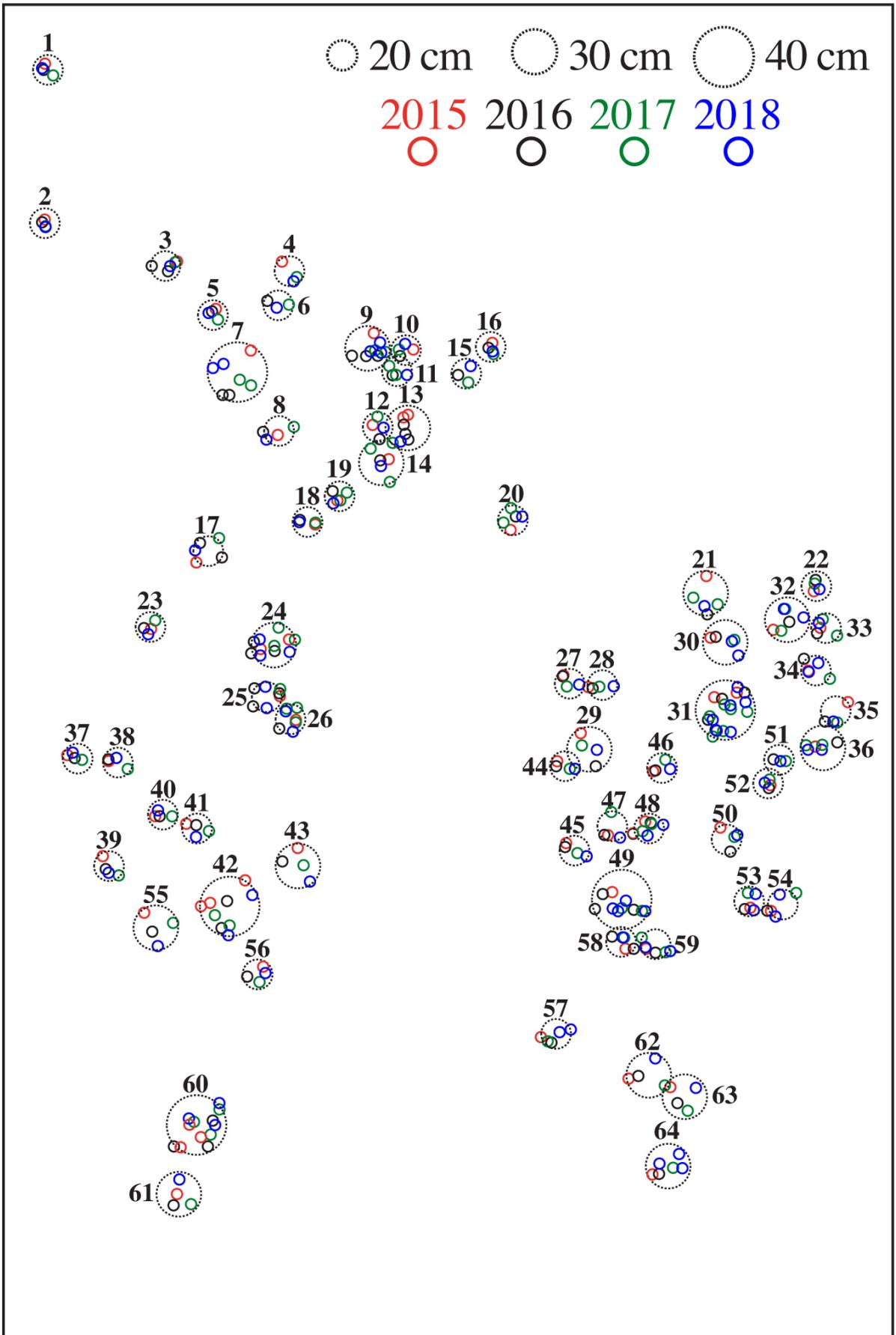
Using the established spatio-temporal criteria for analysis of changes in distribution and number of *E. maritimum* plants, 64 individuals were studied (Fig. 3). The number of ramets changed relatively little between years with a tendency to increase over time (Table 1). A strikingly lower number of ramets in 2015 in comparison to other years was caused by subjective factors resulting in differences in interpretation of criteria for determination of “ramet” in the particular year, which was done in field conditions, leading to some underestimation of their number. Total number of shoots showed some temporal variation, but only within a 15% range (Table 1). Ratio between generative and vegetative shoots was relatively stable during 2015 to 2017 (70 to 77% for generative shoots and 23 to 30% for vegetative shoots), but this proportion significantly shifted in 2018, reaching 57% for generative shoots and 43% for vegetative shoots (Fig. 4, Table 1). In 2018, this was associated with a decrease of total numbers of flowers and leaves, and also average number of flowers per shoot (Table 1). Concomitantly, the average number of generative shoots per individual as well as average number of flowers per individual decreased (Fig. 5A). In contrast, the average number of vegetative shoots per individual and average number of leaves per individual showed a somehow negative correlation (Fig. 5B).

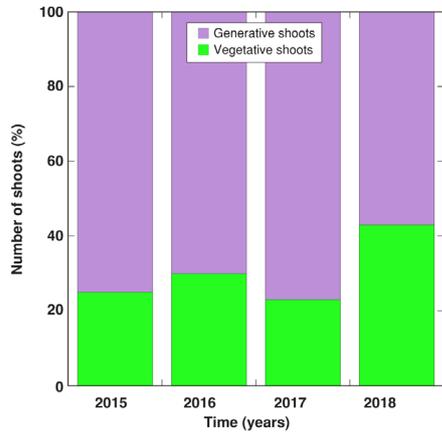
In temporal aspect, 44 individuals were located within a circle 20 cm in diameter, 15 individuals were located within a circle 30 cm in diameter, and five individuals were located within a circle 40 cm in diameter (Fig. 3). Data on temporal changes of numerical morphological values for individuals of *E. maritimum* and changes in location of separate shoots are presented graphically according to the established criteria for 20-, 30- and 40-cm circles separately. In addition, for 20 and 30 cm groups, two subgroups are shown for each of them, depending on whether there were changes in number of ramets for a particular individual or not.

Individuals registered within a circle 20 cm in diameter and showing no changes in number of ramets (only one) over a period of four years were the largest group with 29 cases in total (Fig. 6). However, these individuals showed

**Table 1.** Summary of changes in number of shoots, flowers and leaves in different years of *Eryngium maritimum* plants at the study site

Year	Total number of ramets	Total number of shoots	Generative shoots			Vegetative shoots		
			Number of shoots	Number of flowers	Average number of flowers per shoot	Number of shoots	Number of leaves	Average number of leaves per shoot
2015	68	151	113	1115	9.9	38	210	5.5
2016	84	171	119	1112	9.4	52	204	3.9
2017	87	157	121	1116	9.2	36	151	4.2
2018	92	146	83	716	8.6	63	298	4.7





**Fig. 4.** Proportion of generative and vegetative shoots of *Eryngium maritimum* in different years.

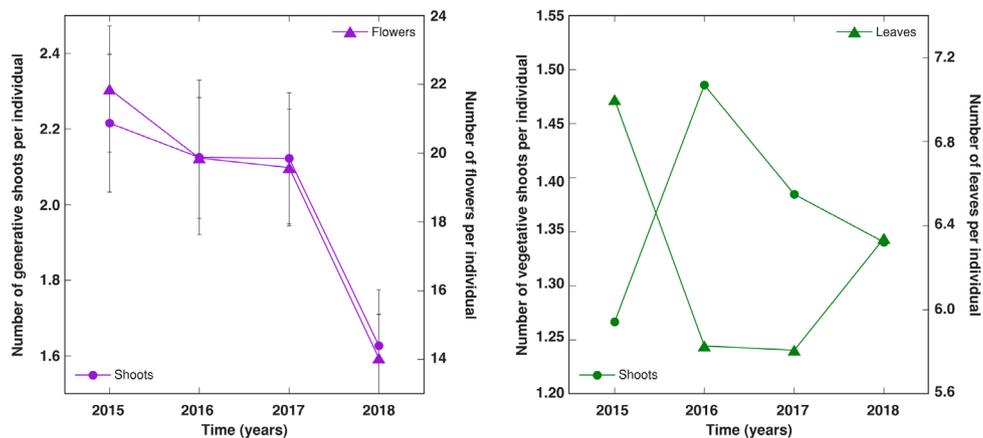
significant variation in complexity (number of shoots for the particular individual), number of flowers and leaves, as well as developmental phase changes (vegetative to generative and vice versa). A number of individuals had only one shoot for the whole time span (Nos. 51, 8, 15, 47, 38), but always changes in developmental phase were involved at some point. Seven individuals had one permanent shoot, with a second shoot appearing for one year, either vegetative or generative (Nos. 39, 44, 45, 10, 16, 52, 35). For some individuals, there were changes in developmental phase. For several individuals, two shoots were present for two separate years (Nos. 50, 12, 22, 27, 23) or longer (Nos. 18, 41, 6, 37). Three and more shoots appeared for the rest of individuals (Nos. 28, 40, 46, 4, 5, 1, 2, 56), but there were large fluctuations both in respect to number of shoots as well as number of flowers over time. The most typical example of a climacteric developmental sequence was individual No. 56, with increase of number of

flowering shoots from 3 to 4, followed by decrease to 2, with a shift to a single vegetative shoot.

For 15 individuals with shoots also located within a circle 20 cm in diameter, number of ramets was larger than one and their number changed with time (Fig. 7). One simple case involved an individual (No. 11) with a single generative shoot appearing in 2016, splitting in two vegetative shoots located more than 10 cm apart in 2017, followed by development of one generative shoot a year later (No. 11). In the other cases, larger but fluctuating numbers of shoots were involved, with two or even three ramets, together with apparent full or partial developmental phase changes. In one case (No. 59), a single vegetative shoot with one leaf in 2015 gave a generative shoot with 14 flowers in 2016, and developed two ramets with three shoots in 2017, further developing four shoots with 24 flowers and six leaves, showing a characteristic increasing developmental sequence.

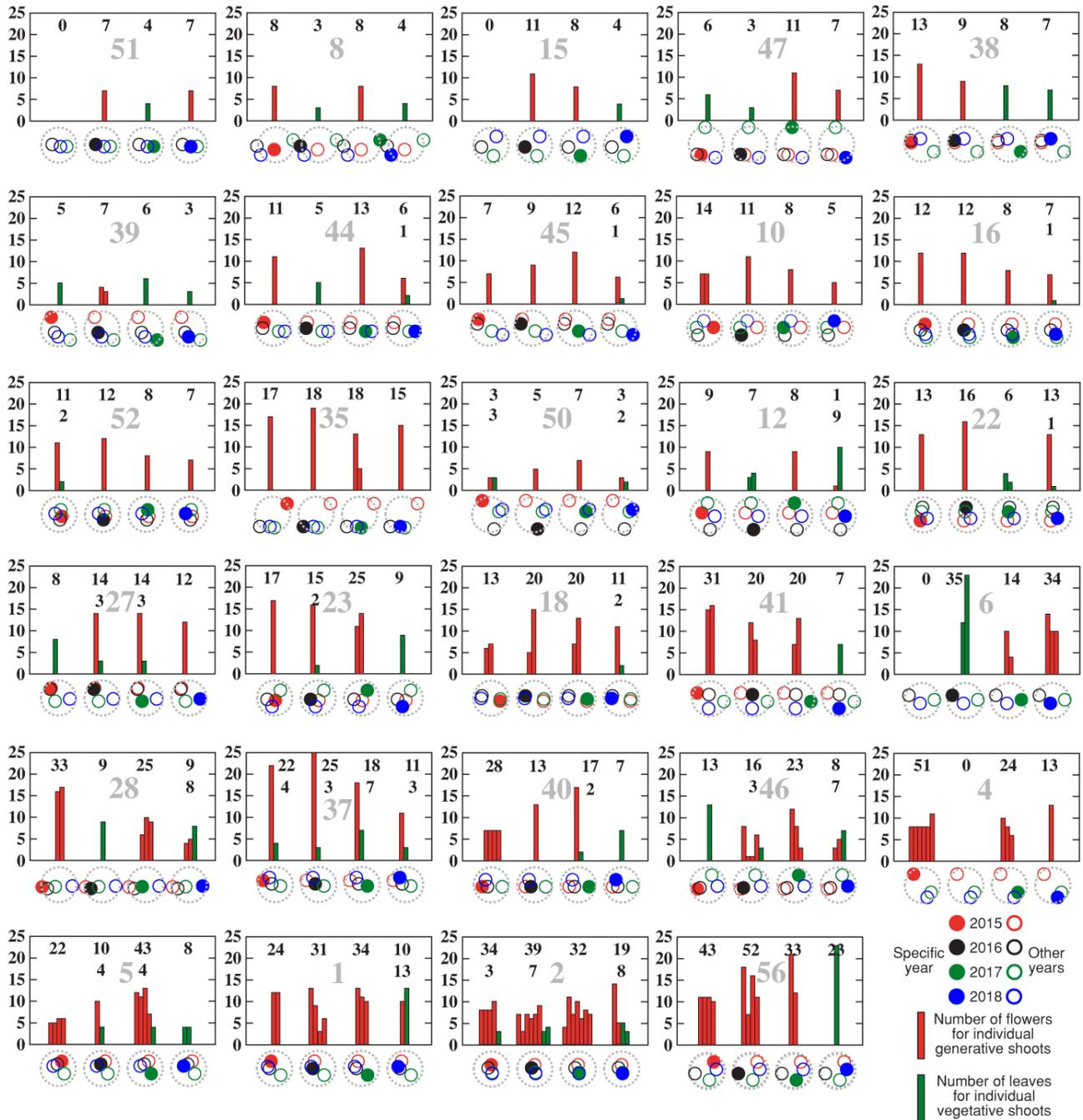
In total, 15 individuals were located within a circle 30 cm in diameter, and six showed no changes in a number of ramets (Fig. 8) and nine were characterized by a change in number of ramets (Fig. 9). Relatively large variation between individuals of the first group was evident, ranging from an individual with one persistent shoot (No. 29) to an individual with six shoots from 2015 to 2017, decreasing to only three shoots in 2018 (No. 55). In the second group, there were individuals producing two ramets only for one season (Nos. 21, 14) or two seasons (Nos. 30, 36, 32), but some individuals temporarily had a larger number of ramets (Nos. 13, 9, 24). For several individuals, location of shoots changed between years.

Individuals with temporal distribution within a circle 40 cm in diameter were most difficult to interpret (Fig. 10). These included ones with possibly largest offset of shoots between seasons and significant changes in number of



**Fig. 5.** Changes of average number of generative shoots and flowers per individual (A) and average number of vegetative shoots and leaves per individual (B). Data are means  $\pm$  SE for A. For a sake of clarity, SE not shown in B.

**Fig. 3.** General schematic distribution of *Eryngium maritimum* individuals (encircled by dotted line and numbered consecutively) on the study site within 20-, 30- or 40-cm circles with location of ramets (small open circles) in each particular year.



**Fig. 6.** Temporal changes of numerical values for individuals within a circle 20 cm in diameter with no changes in location or number of ramets. Each individual is represented by a separate graph with a column(s) for each consecutive year from left to right. Numbers in grey indicate the number of particular individual according to Fig. 3. Number of flowers for generative shoots are indicated by red columns, and number of leaves for vegetative shoots are indicated by green columns. Upper row of numbers at the top of each graph indicate total number of flowers per ramet, and lower row numbers indicate total number of leaves per ramet. Positions of ramets in the particular year is indicated by closed circles of the respective colour, and open circles of respective colour indicate its position in other years. Individuals are presented in an order of increasing number of shoots per ramet.

ramets. The most pronounced case of offset, up to 35 cm, was seen for individual No. 7 with a relatively low number of flowers and leaves. The most pronounced change in number of ramets was for individual No. 31, with two ramets (four shoots) in 2015 developing in four ramets

(nine shoots) in 2016, further splitting to six ramets (eight shoots but mostly small vegetative) in 2017 and remaining so in 2018 with nine shoots, mostly generative.

No presence of seedlings at any stage of development throughout the study period was noted for the study site.

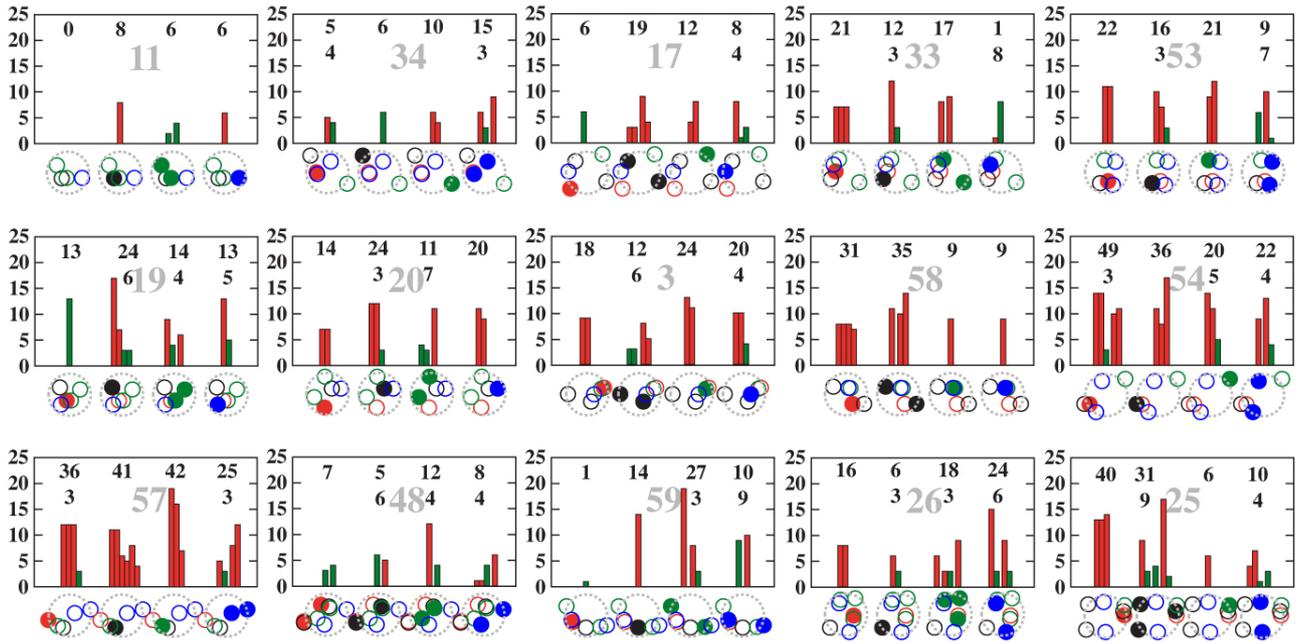


Fig. 7. Temporal changes of numerical values for individuals within a circle 20 cm in diameter with no changes in location but with changes in number of ramets. For information, see legend and description to the Fig. 6.

*Analysis of clonality in field conditions*

Observations on the clonal character of *E. maritimum* were performed in semi-fixed primary sand dune habitat with active dune erosion during autumn-winter storms (Fig. 11). At the beginning of the vegetation season, in early May, on parts of eroded dune many bare root fragments were visible still connected with soil. Development of shoot and root initials were observed on vertical roots 30 to 40 cm below

the previous level of dune surface (Fig. 11A). Formation of shoots were observed also on numerous horizontally oriented often mechanically damaged roots (Fig. 11B, C, D). Later these initials were partly covered with sand and formed relatively large generative shoots that eventually developed flowers (Fig. 11E, F, G). Later in the season, regrowth of numerous vegetative shoots was sometimes observed, evidently associated with deeper buried roots

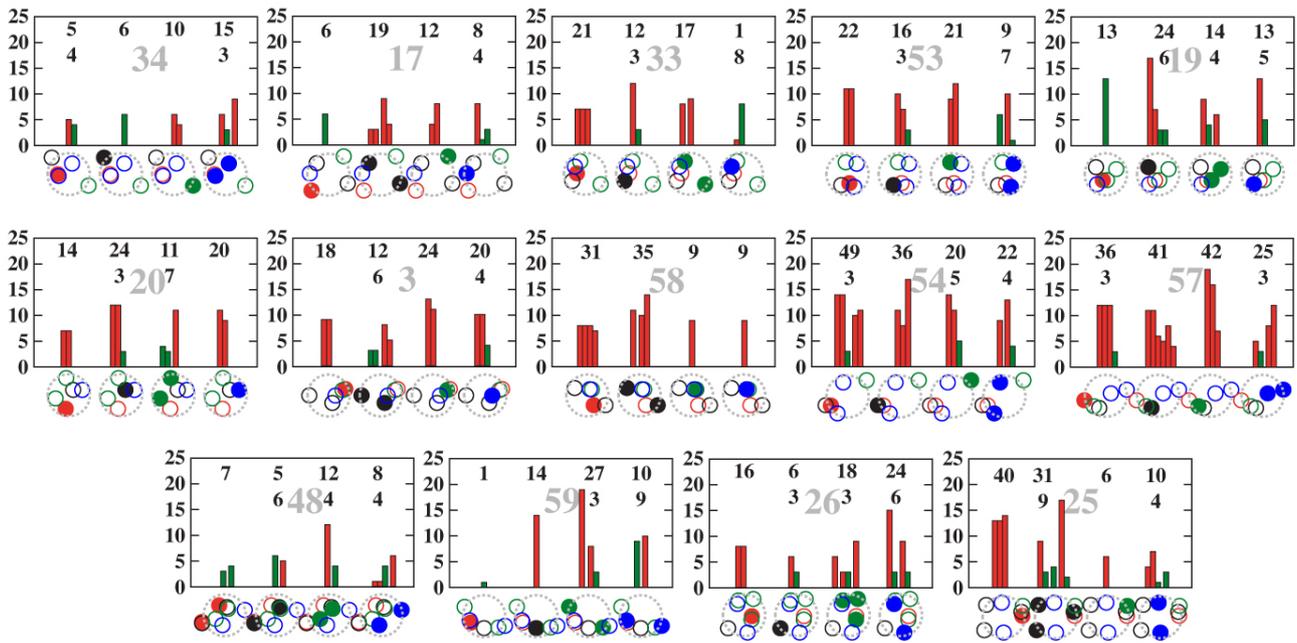
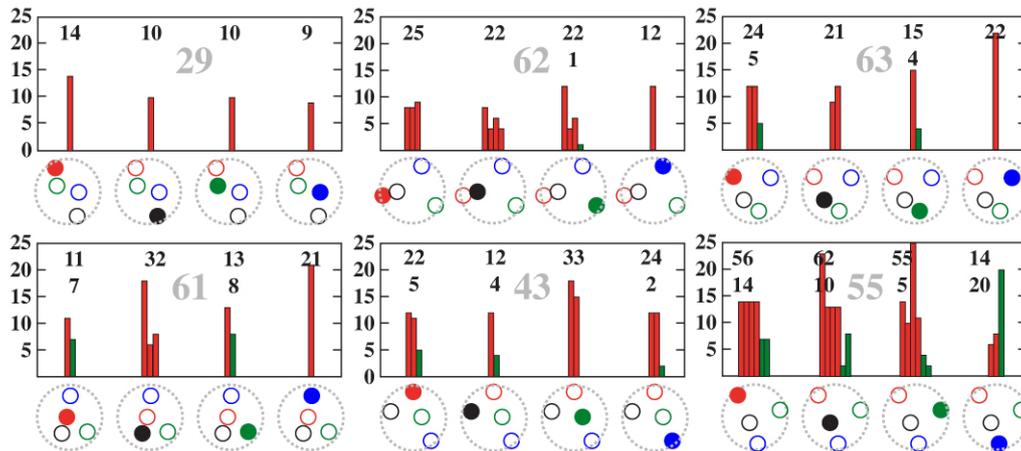


Fig. 8. Temporal changes of numerical values for individuals within a circle 30 cm in diameter with possible change in location but no changes in number of ramets. For information, see legend and description to the Fig. 6.



**Fig. 9.** Temporal changes of numerical values for individuals within a circle 30 cm in diameter with possible change in location and changes in number of ramets. For information, see legend and description to the Fig. 6.

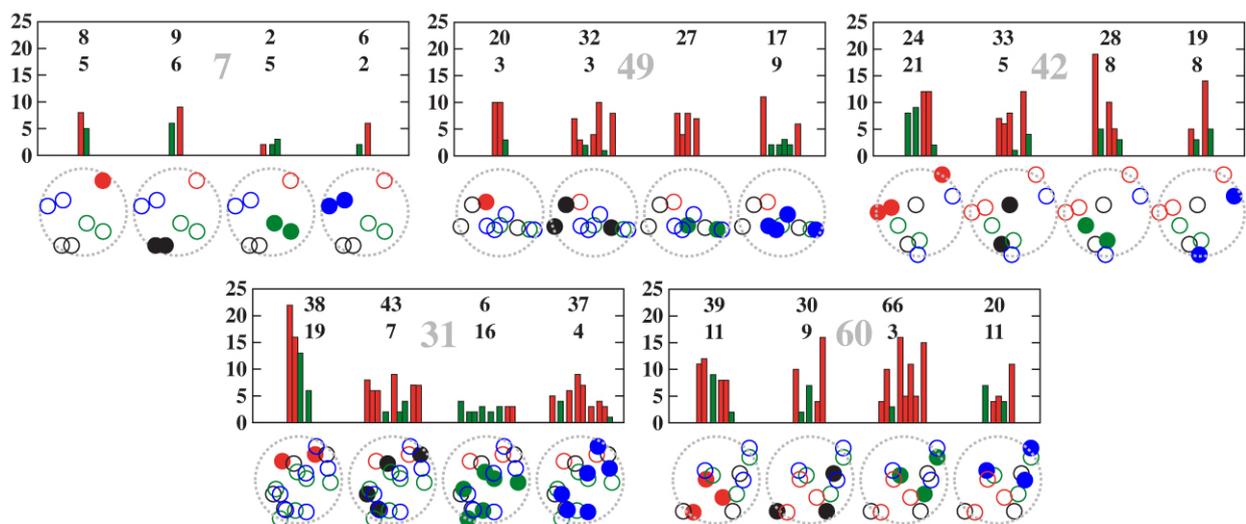
at the base of eroded dune (Fig. 11H). Larger generative shoots developed further from the eroded dune to the beach side, developing from roots damaged in previous seasons (Fig. 11I).

A clonal network of horizontally-oriented roots of *E. maritimum* was observed on an eroded dune ridge in a shallow dune system of the Abermenai dune complex at the end of a branch of Menai Strait in Isle of Anglesey, Wales, UK (Fig. 12). Individual shoots were numerous, relatively small, and clearly interconnected by a network of shallow roots at the depth of 15 to 40 cm from soil surface.

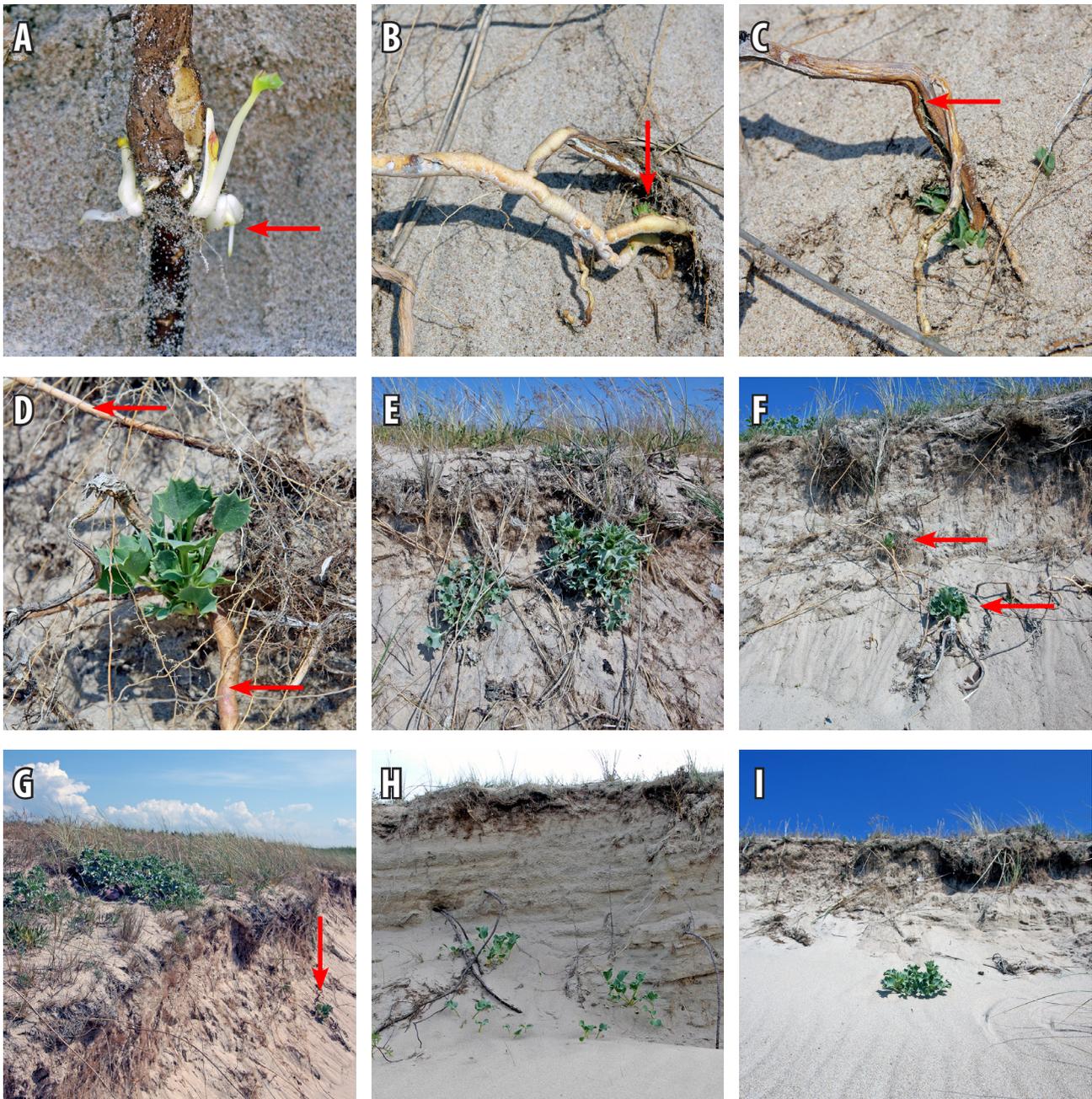
## Discussion

There is a general scientific and popular belief that populations and the distribution range of *E. maritimum* in Northern Europe are declining (see Iserman, Rooney 2014 for a review). However, there is no common view

on causes of the decline, whether it results from natural or anthropogenic factors, or both. Historical records of distribution in Northern part of the distribution range of *E. maritimum* have been analyzed in Norway (Curle et al. 2007), Poland (Żółkoś et al. 2007) and Lithuania (Aviziene et al. 2008; Olšauskas, Urbonienė 2008). It was suggested that in Norway, the population of *E. maritimum* has been relatively stable and fluctuating due to natural factors, but data on decrease in size in certain localities mostly indicate local human disturbance (Curle et al. 2007). In Poland, population size and distribution has decreased in Gdańsk region, mostly due to anthropogenic effects (transformation of coastal habitats and increasing recreational pressure; Żółkoś et al. 2007). However, problems with generative reproduction have been suggested as the main reason of reduced distribution and decreased number of individuals of *E. maritimum* during the second half of the previous century in Lithuania (Aviziene et al. 2008). In Lithuania,



**Fig. 10.** Temporal changes of numerical values for individuals within a circle 40 cm in diameter with possible change in location and changes in number of ramets. For information, see legend and description to the Fig. 6.



**Fig. 11.** Clonal character of *Eryngium maritimum*, allowing regrowth of shoots after dune erosion. A, development of shoot and root (indicated by arrow) initials at node of vertical root at the beginning of May. B, bare root fragments with shoot development (indicated by arrow) in June. C, bare roots (indicated by arrow) with signs of shoot development at the lower end in June. D, bare roots of different thickness (indicated by arrows) with developing generative shoot in the center in June. E, larger generative shoots developed on root parts in July. F, small generative shoot developed on root parts in July. G, the same shoot as in F (indicated by arrow), shown from above. H, development of vegetative shoots on sand-buried root parts in August. I, generative shoot developed on beach side of dune from root fragments after erosion in August.

the number of individuals of *E. maritimum* decreased from 5828 plants in 1975 to 3511 in 1981, and 1894 in 2006, resulting in decrease of abundance of *E. maritimum* 3.3 times during the period from 1975 to 2006 (Olšauskas, Urbonienė 2008). As a result of analysis of past and present habitats of *E. maritimum* in Poland, it was concluded that both natural (abrasion by storms) and anthropogenic

(dune forestation and recreation) factors are associated with decrease in number and area of suitable habitats for the species (Łabuz 2007).

The majority of the studies on distribution of *E. maritimum* are based on the assumption that vegetative shoots represent young independent individuals and that they nearly irreversibly switch to the generative phase at



**Fig. 12.** Clonal network of horizontally-oriented roots (indicated by arrows) of *Eryngium maritimum* on an eroded dune ridge in a shallow dune system at the end of a branch of Menai Strait in Isle of Anglesey, Wales, UK.

older age (Curle et al. 2007). Seed germination and seedling establishment is an integral part of this model (Aviziene et al. 2008). Thus, in a study performed in Norway with a population of *E. maritimum* containing 105 to 145 individuals, it was postulated that each individual belongs to one of three groups, i.e., small vegetative (indicated as sterile), large vegetative, and generative (indicated as fertile; Curle et al. 2007). Vegetative individuals with three or less leaves were regarded as unestablished plants, and those with more leaves as established. The studied population was dominated by small vegetative individuals, and it was concluded that survival probability of small vegetative individuals was low (26 to 37%), compared to survival probability of large vegetative (70 to 100%) and generative (71 to 76%) plants.

During a previous study in 40 *E. maritimum* microsites in Latvia, without mapping of exact location of each shoot but rather by counting the number of shoots per particular microsite during five consecutive years, it was established that a highly fluctuating trend in number of both vegetative and flowering shoots was characteristic for about 80% of the microsites (Andersone et al. 2011). Only about 10% of microsites showed a distinctive increasing trend, but for the remaining 10% the trend was decreasing. This pattern was repeatedly confirmed also in the present study. In addition, it was clearly shown that individuals can rather unpredictably switch from generative to vegetative phase and back, although mostly persisting in the generative phase.

So far, clonal character of *E. maritimum* has not been assessed experimentally, but has been suggested often (Turnel 1947; Curle et al. 2007; Żółkoś et al. 2007). There is a strong reason to suggest that *E. maritimum* has an ability to propagate vegetatively from underground buds located at

taproots. This type of clonal growth, root sprouters, appears to be relatively rare or simply underexplored due to the not-so-obvious nature of the clonality by a random observer. The concept of clonality of *E. maritimum* can forecast (i) that location of single shoots can change with time, and (ii) that number and size of shoots at particular location can change with time. The results of four-year observation and mapping of accurate locations of each shoot clearly showed that for the majority of individuals no offset of shoots could be proposed, as they were located within a circle 20 cm in diameter (Figs. 6, 7). Only 15 individuals located within a 30-cm circle potentially could have offset larger than 20 cm (Figs. 8, 9), but five individuals located within a circle 40 cm in diameter potentially could have offset larger than 30 cm (Fig. 10) during four seasons. In addition, while 36 individuals showed no changes in the number of ramets, but with possible changes in number of shoots (located less than 10 cm apart), 28 individuals showed either disappearance of existing ramets or appearance of new ones (located within the respective circle, but at a distance larger than 10 cm), or both, during a four year period.

For root sprouters, two important functional roles of vegetative propagation have been recognized: to act (i) as an aid of vegetative regeneration after disturbance and (ii) as a mechanism of root foraging in a heterogeneous environment (Klimešová, Martínková 2004). Typical clonal root sprouting plants are characterized by spreading horizontal roots, in general similar to the ones in photograph of *E. maritimum* plants found on an eroded dune ridge in Wales, UK (Fig. 12). It seems, however, that the second aspect of clonality of root sprouters is not of much relevance for *E. maritimum*, at least, in conditions of a thick layer of sand in semi-fixed primary dunes, as in the conditions of Ziemupe and Uzava (Fig. 1). As root and

shoot initials were found on storm-damaged vertical roots (Fig. 11A), it is more likely that formation of adventitious buds on vertical roots were mainly responsible for the characteristic low-dynamic system of shoot demographics, found in the present study.

All cases of “new appearance” were related to regrowth of the same shoot at some distance from a previous point or due to clonal multiplication from root adventitious buds on the same previously existing roots. Larger offset for a single ramet in different years (as in the case of individuals Nos. 43, 55, 62 and 63, Fig. 3) could mean that the bud-producing meristem is located relatively deeper in soil and that the emerging shoot does not follow the same path through soil each year. It was established that in a sand dune substrate, shoots of *E. maritimum* can emerge from a depth of at least 16 cm (Andersone et al. 2011).

In conclusion, it can be assumed that seed germination with successful establishment of seedlings is a rare event in the north-eastern range of distribution of *E. maritimum*, as suggested by several studies (Minasiewicz et al. 2011; Necajeva, Ievinsh 2013) and our long-term field observations. Existing individuals of *E. maritimum* in semi-fixed dune habitats are ramets of a small number of relatively old genets, propagating only by vegetative means. In general it means that long-term conservation options of the existing populations are rather low. However, it is not clear what set of environmental circumstances resulted in successful establishment of existing populations of *E. maritimum* and if ongoing global climate change might result in more successful natural recovery of populations around the Baltic Sea.

### Acknowledgements

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