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Dendrochronology of *Atriplex portulacoides* and *Artemisia maritima* in Wadden Sea salt marshes

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Abstract The study uses a rather unusual method, dendrochronology, to investigate the growth and survival of *Atriplex portulacoides* L. and *Artemisia maritima* L. on salt marshes at two field sites on the Dutch North Sea barrier islands of Terschelling and Ameland. By providing information on longevity of these typical salt-marsh shrubs, dendrochronology offers an indirect way to investigate the influence of management regime – grazing in this case – on marsh quality and areal extent. Diminishment of salt marshes is a continuing concern in the northern Netherlands. The two shrub species studied here, *A. portulacoides* and *A. maritima*, are common to salt marshes. With their extensive roots and branches, they facilitate sedimentation and stabilize salt marshes. Using dendrochronology, this study found that annual growth rings could be identified to determine shrub age and growth. In *A. portulacoides* these rings took the form of a narrow band of terminal parenchyma. In *A. maritima* they were made up of unlignified marginal parenchyma together with higher vessel density at the beginning of the growing season. Growth rings indicated that intense grazing was clearly detrimental to the survival of *A. portulacoides* at the Terschelling site. However, grazing facilitated survival of *A. maritima* at the Ameland site by reducing light and nutrient competition from grasses. No growth trends could be found, however, as the lifespan for both species is short and many other influences on shrub growth could be identified.

Keywords Salt marsh · Shrubs · Age determination · Sedimentation · Grazing

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Introduction

Salt marshes are a unique ecosystem in the upper intertidal coastal zone of Europe's temperate regions. They are also one of the key habitats protected by the Habitats Directive (1992) and are designated as Natura 2000 sites (Ministerie van Economische Zaken Lanbouw & Innovatie 2011; Ministerie van Volkshuisvesting Ruimtelijke Ordening & Milieu 2007). In 2009, the Wadden Sea was added to the World Heritage List (UNESCO 2009). In addition to forming a valuable habitat for vegetation, the salt marshes along the Dutch Wadden Sea coast are an important feeding and breeding ground for waterfowl and waders. The salt marshes, furthermore, contribute to coastal protection, as they dampen incoming waves (Brampton 1992; Costanza et al. 2008; Gedan et al. 2011; King and Lester 1995; Möller et al. 2001). Appreciation of salt marsh's flood protection function has led to increased interest in marsh conservation and restoration for goals other than nature protection (Deltaprogramma 2010). Although the present salt-marsh area in the Wadden Sea is designated a nature conservation zone, most of it is of anthropic origin. Since the Middle Ages, farmers have actively reclaimed the erstwhile natural salt marshes along the Wadden Sea coast for agricultural uses. Up to the 1970s, salt-marsh formation was stimulated for land reclamation purposes. Since then, nature protection has become the main goal, and Wadden Sea salt-marsh dynamics have been monitored (Dijkema et al. 2011; Dijkema et al. 2007). Conservation goals for salt marshes in the Dutch Wadden Sea region are three:

i. to increase the areal extent of the salt marshes;
ii. to enhance natural morphological and dynamic processes;
iii. to enhance the vegetation structure (Ministerie van Volkshuisvesting Ruimtelijke Ordening & Milieu 2007).

Currently, the Dutch salt marshes have stabilized (Dijkema et al. 2011). However, concerns have been raised about the impacts of rising sea levels. If sediment deposition is insufficient to keep pace with the sea-level rise, the salt-marsh area will likely decline. This effect could be amplified by soil subsidence as result of natural gas extraction (Slim et al. 2011). Near Stryp, located on the southern coast of the Dutch North Sea barrier island of Terschelling, the salt-marsh area has been steadily declining for over half a century (Van Loon-Steensma et al. under review).

Vegetation in the intertidal zone is distinctive in that it can cope with salty or brackish water and regular tidal inundation. Grasses, other perennials and dwarf shrubs are dominant in this dense, salt-tolerant vegetation. Besides their ecological value, these plants prevent erosion by cushioning wave impact, while their root systems retain sediment. Accessible areas of salt marshes are often managed by allowing cattle to graze, as grazing is understood to prevent or delay succession towards a grass-dominated vegetation (Dijkema 1983; Dormann and Bakker 2000; Dormann et al. 2000).

The current study focuses on two dwarf shrub species that are typical on salt marshes: *Atriplex portulacoides* L. or "sea purslane" (syn. *Halimione portulacoides* (L.) Aellen, family *Amaranthaceae*) and *Artemisia maritima* L. or "sea wormwood" (syn. *Seriphidium maritimum* (L.) Poljakov, family *Asteraceae*). *A. portulacoides* has a well-branched root system that can a reach length of 50 cm, which is similar or even greater than the length of the above-ground plant components. *A. maritima* also has a well-branched root system, commonly reaching a depth of some 25 cm (own field measurements).

Regarding the wood structure of these species, *A. portulacoides* is characterized by small groups of solitary vessels with a diameter of 30–50 μm and indistinct annual ring boundaries (Schweingruber and Landolt 2010). A transverse section shows cap- or arc-like, unlignified tangential parenchyma (see explanation in the Results section) and is rayless (Butnik 1983; Heklau et al. 2012). Rays are bands of storage cells in the wood which are orientated perpendicularly to the main axis of the stem.

No literature was found specifically on *A. maritima*, but within the same genus, wood features are diverse and annual ring detection is not always straightforward (Schweingruber et al. 2013).

Although literature is available on the wood structure and formation of these two species or genera, as far as we know no dendrochronological studies have been carried out. The current study uses dendrochronology to investigate their growth and survival on salt marshes at two field sites on the Dutch North Sea barrier islands of Terschelling and Ameland. By providing information on the longevity of these typical salt-marsh shrubs, dendrochronology provides an indirect way to investigate the influence of management regime – grazing in this case – on marsh quality and areal extent.

Materials and methods

Study area and sampling

Two salt marshes were selected for this study: a salt marsh east of Stryp Polder on the Isle of Terschelling (53.4000° N, 5.3167° E) and a salt marsh at Neerlands Reid on the Isle of Ameland (53.4480° N, 5.7300° E). Terschelling and Ameland are Dutch North Sea barrier islands (Figs. 1 and 2).

On both sites the predominant dwarf-shrub species was sampled since this is more likely to be influenced by management practices. *A. portulacoides* is abundant on the salt marsh at Stryp. This is typical of Europe's temperate marshes, as extensive stands of *A. portulacoides* are a key feature that distinguishes these marshes from the salt marshes of other

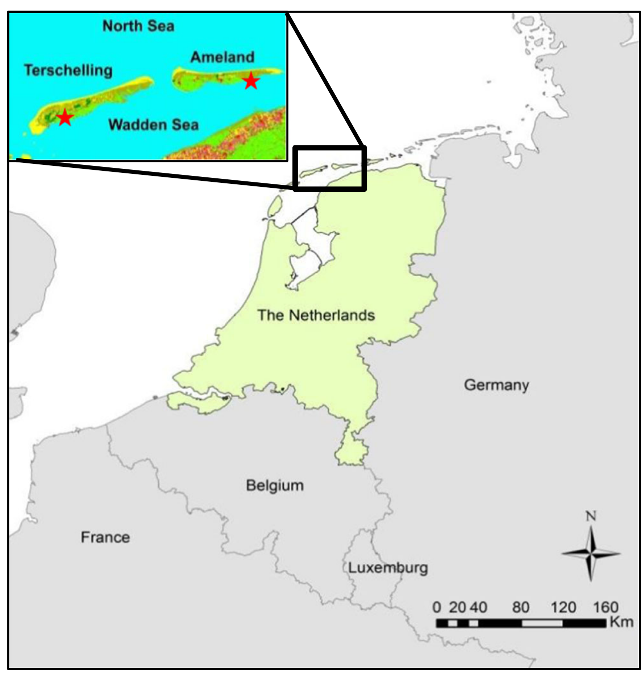

Fig. 1 Location of Stryp on the Isle of Terschelling (53.4000° N, 5.3167° E) and location of Neerlands Reid on the Isle of Ameland (53.4480° N, 5.7300° E), both indicated by red stars. Terschelling and Ameland are both Dutch North Sea barrier islands

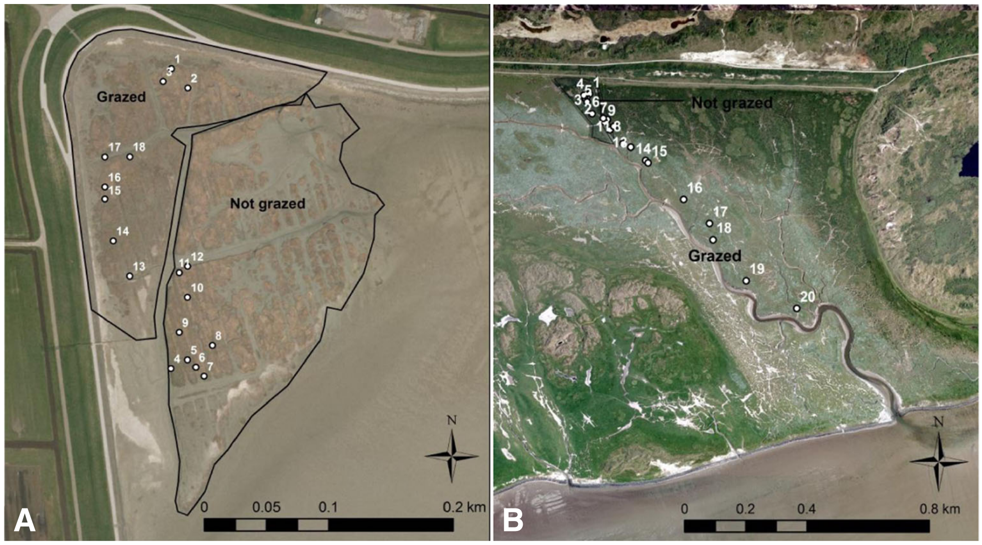

Fig. 2 Sampling location of **a** *Atriplex portulacoides* L. on the salt marsh near Stryp Polder and **b** *Artemisia maritima* L. on the salt marsh at Neerlands Reid. Grey shading **b** indicates areas with high dominance of this grey-coloured species. Aerial photographs: Netherlands Land Registry Office (Kadaster), 2010 and 2009, respectively

temperate regions (Adam 1990). The dwarf shrub *A. portulacoides* is prominent in salt-marsh vegetation from Denmark southwards (Adam 1990). There is no *A. maritima* at Stryp, due to the marsh's low elevation, which is near sea level. *A. maritima* grows mainly on salt marshes at higher elevations (field observations; Schaminée et al. 1998).

Plant sampling was carried out at the end of the growing season in December 2012 and before the start of the new growing season in March 2013. The Stryp study site can be divided in two zones. One zone is intensively grazed by sheep, while the other is not influenced by grazers or browsers (Fig. 2a). The grazing period is from June/July until the end of October, with a density of 11 animals/ha (personal communication). In both the grazed and non-grazed areas, nine samples of *A. portulacoides* were randomly selected (Fig. 2a).

Due to the higher elevation of the salt marsh at Neerlands Reid, there is a dominance of *A. maritima*, as well as a presence of *A. portulacoides*. Like Stryp, this marsh can be divided into two zones: one grazed and the other non-grazed. Here, cattle and hares are the grazers, and there is a predominance of *Elytrigia atherica* in the non-grazed area (Fig. 2b). The grazing period of the cattle is from June until the end of November, with a density of 0.42 animals/ha (personal communication). The marsh at Neerlands Reid is larger than that at Stryp. To ensure inclusion of plants from both less and frequently inundated areas, sampling was done along a transect defined perpendicular to the coast. Ten sample locations were chosen along this transect in the grazed and non-grazed sections. Because *A. maritima* appears in clusters (i.e., multiple plants were found at each sampling location), a final sample size of 22 plants in the grazed part and of 15 plants in the non-grazed part was obtained (Fig. 2b). Whole plants (incl. roots) were sampled, to ensure that individual plants were selected, and not branches that had rooted due to burial by silt sediment under the influence of frequent tidal inundation.

Sample preparation and measurements

For both species, samples were taken at ground level and at 5 cm below and above ground level. In cases where the stem was considered particularly large and thick below ground, an additional sample was taken at approximately −10 cm. Sampling at these different heights served two purposes: (i) it enabled the researchers to accurately identify annual ring boundaries (i.e., growth rings in the wood structure indicating the end of one growing season and the start of the next) in cases where the stem base had been buried by sediment; and (ii) it provided a way to validate annual ring boundary detection by crosschecking the annual growth curves (i.e., similar growth patterns should be obtained in the different stem sections of the same individual).

At each sample height, a transverse section was prepared (ca. 25 μm) using a sliding microtome (G.S.L.-1 microtome, WSL, Birmensdorf, Switzerland). All cross-sections were stained with a safranin/astrablue solution for five minutes. Safranin stains lignified tissue red; astrablue stains non-lignified cells blue. Following dehydration in a graded ethanol series (50 %, 95 % and 100 %), the samples were rinsed with Roticlear©, mounted in Rotimount© and dried for three consecutive days under weights. Annual growth boundaries were then identified under a microscope (DM2500, Leica, Cambridge, UK) using Leica imaging software (version 3.6.0). Annual stem growth increments were measured and dated using WinTSAP© software (Rinntech, see www.rinntech.de).

To test the difference between grazed and non-grazed zones the non-parametric Spearman correlation test was used. Statistical analyses were carried out using SPSS 21 statistical software.

Vessel diameter was measured on a random selection of two samples per species using the Image J software (Rasband 2014).

Results

Despite the fact that *A. portulacoides* forms indistinct annual boundaries, it was possible to correctly detect annual rings for most plants by comparing the growth curves at the different sampling heights.

Ring boundaries were visible as narrow bands of terminal parenchyma (i.e., a small band of parenchyma cells indicating the annual growth ring boundary, Fig. 3a), though sometimes they were partially obscured by the cap- or arc-like, unlignified tangential parenchyma or interxylary phloem (Fig. 3b and c). Vessel diameter ranged from ~10-40 μm, with an average of ~30 μm. Two samples from Stryp could not be dated with confidence and were therefore left out. One of these was from the grazed zone and the other from the non-grazed zone. For the Stryp field site, the final sample size for analysis was therefore eight plants from each zone. Browsing marks on branches could be clearly distinguished in the grazed zone, sometimes resulting in a 'bonsai' shaped growth form. However browsing scars within the wood could not be detected.

Annual ring detection was more straightforward in *A. maritima*. The density of the vessels was greater at the beginning of the growing season, and a band of unlignified marginal parenchyma was clearly visible with the astrablue coloring (Fig. 4a and b). Vessel diameter was similar throughout the growing season and therefore the species can be characterized as diffuse porous. Vessel diameter ranged from ~2-20 μm, with an average of ~10 μm.

For *A. portulacoides*, age distribution was between 3 and 15 years, with the older shrubs found in the non-grazed zone (Fig. 5). All of the shrubs sampled from the grazed zone were young (3–7 years), while all plants in the non-grazed zone were 6 years or older. There was a significant difference in age of *A. portulacoides* between the grazed and non-grazed zone (R^2=0.5960, P=0.0148).

For *A. maritima*, no significant difference was found in age between the grazed and non-grazed areas (R^2=0.2290, P= 0.271). The maximum plant age was 8 years.

Despite accurate annual ring boundary detection, no growth chronology could be established across individuals of the same species. This meant that climatic and tidal effects could not be analysed. Annual ring increments ranged from 0.06 mm to 1.64 mm for *A. portulacoides* and from 0.07 to 1.96 mm for *A. maritima*.

Discussion

Dendrochronology proved a useful technique for age determination of the sample plants, especially in areas where silt was frequently deposited. A description found in the literature of the wood structure of *A. portulacoides* indicated the presence of annual ring boundaries (Schweingruber and Landolt 2010). Vessel diameters were in accordance to the findings of Schweingruber and Landolt (2010). The current study not only confirmed that ring detection is possible in *A. maritima*, but also that dendrochronology is a useful tool to determine when these species became established. *A. maritima* had clearer ring boundaries, exhibiting wood features very similar to *Artemisia caucasica* Willd. (Schweingruber et al. 2013). Yet it is different from *A. caucasica* in that it has smaller, partially lignified rays. Another difference is *A. maritima*'s more densely grouped vessels early in the growing season along the unlignified marginal parenchyma (see Fig. 4a and b). Vessel diameters are clearly smaller than those of *A. portulacoides*.

Our samples of both species were young in age, relative to the timeframe of the effects of climate change. Furthermore, they displayed influences of their specific local growing conditions, such as wave impact, competition by grasses and allocation of reserves to side branches. For these reasons, it was not possible to obtain a clear master chronology of growing trends (i.e., similar growth curves between all individuals) and thus to assess the impact of climatic factors.

The intensive grazing at Stryp was clearly detrimental to *A. portulacoides*. Mostly young shrubs (3–4 years) with

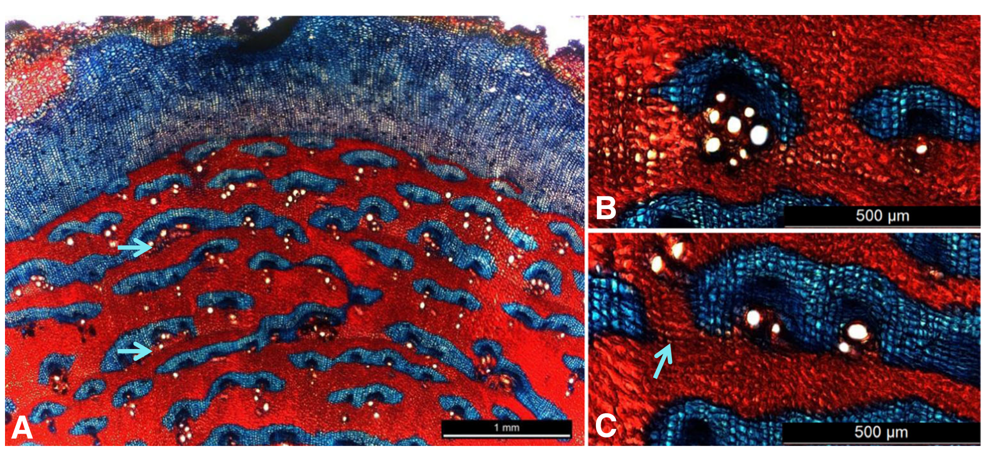

Fig. 3 **a** Transverse section of *Atriplex portulacoides* L. Annual ring boundaries are defined by a narrow band of terminal parenchyma (indicated by blue arrows). **b** Clouds of branch with capand arc-like, unlignified tangential parenchyma or interxylary phloem. **c** Partially obscured annual ring boundary by the cap- and arc-like, unlignified tangential parenchyma

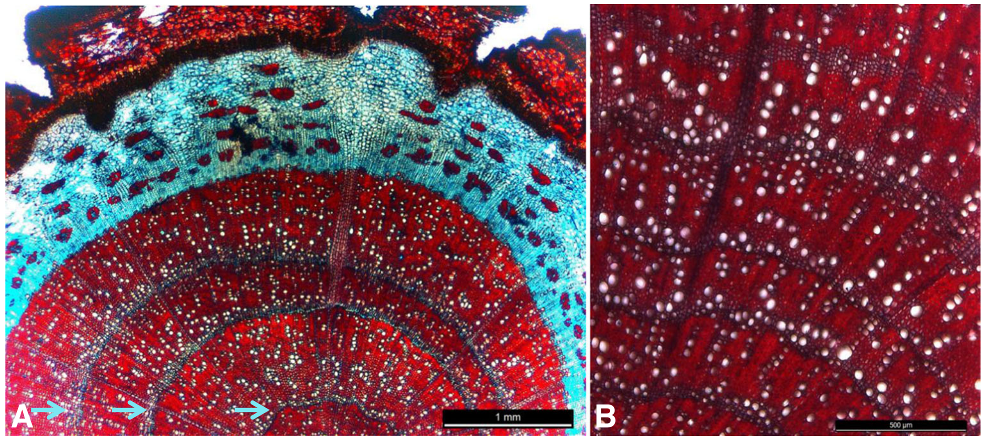

Fig. 4 **a** Transverse section of *Artemisia maritima* L. Annual ring boundaries are clearly defined by a narrow band of terminal parenchyma (indicated by blue arrows) and larger vessel density at the beginning of the growing season. Vessels are diffuse-porous, meaning that they are evenly distributed throughout the growth ring. **b** A detailed section of Figure 4a

browsing marks on the branches were found (those that had not yet succumbed to grazing), with some slightly older individuals (6–7 years) remaining in less accessible places (e.g., along fences and creeks; specifically samples 1–3, 13, 17 and 18; see Fig. 2a). No other wood anatomical characteristics related to browsing, such as browsing scars, were found. This study did not look at past browsing events, but follow up studies could look at the presence of a lipoid layer, an indication for browsing (Heklau and Von Wehrden 2011). Absence of older individuals in the grazed part indicates mortality caused by grazing, which was also found in other studies (Dormann and Bakker 2000; Dormann et al. 2000). Within the non-grazed zone, most *A. portulacoides* was found near the drains (field observations), where there was less competition from the dominant grass (*Spartina anglica*). This does not necessarily mean that new establishment of *A. portulacoides* is hampered since selective sampling of older individuals was preferred to maximise the dendrochronological time series.

On the salt marsh at Neerlands Reid, grazing had the opposite effect on establishment of *A. maritima*. In the grazed zone *A. maritima* was much more abundant (field observations and aerial photographs; Fig. 2b). This indicates that survival and establishment of these plants is facilitated by grazers, which contradicts the findings of Dormann et al. (2000). The grazers avoid *A. maritima* in favour of dominant grasses, which reduces competition for light and nutrients by these grasses (i.e., *Puccinellia maritima*, *Festuca rubra*, *Agrostis stolonifera*) and *Juncus gerardii*. At Neerlands Reid, therefore, grazing delayed vegetation succession on the salt marsh (Dijkema 1983; Dormann and Bakker 2000; Dormann et al. 2000). The animals pass over *A. maritima* because of its strong scent and toxic santonin content (Van Genderen et al. 1996). This accounts for the similar age distribution of the plants in the grazed and non-grazed areas.

Conclusions

This study found that both *A. maritima* and *A. portulacoides* are suitable subjects for dendrochronological study, particularly when the year of plant establishment is important. Unfortunately, both species appear to have a limited life expectancy, which restricts their usefulness for detecting climate-growth relations over time and the impact of tidal flooding in the case of Neerlands Reid. Furthermore, limited conclusions can be drawn from the growth chronology of these species, due to the high influence of site-specific factors, including wave impact and competition from other species, and the

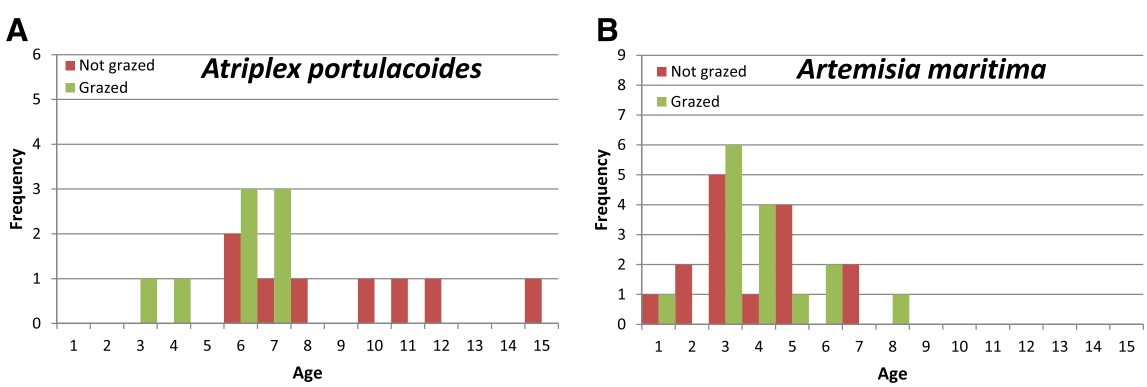

Fig. 5 **a** Absence of older specimens of *A. portulacoides* L. in the grazed zone of the salt marsh at Stryp, while in the non-grazed zone shrubs up to age 15 were found. **b** No effect of grazing found on establishment of *A. maritima* L. on the salt marsh at Neerlands Reid. Sample specimens were age 8 at maximum

horizontal development (rather than vertical growth) of the main stem.

Nonetheless, this study found that determination of the year of establishment is possible, which can provide an important starting point for more elaborate studies that relate the year of establishment to environmental factors or management practices at that time. These could provide baseline information for policymaking to preserve these species.

A. portulacoides is intolerant to intensive grazing by sheep, but hardy in areas where grasses are less dominant. Reducing grazing pressure on the salt marshes as on Stryp could therefore prevent further diminishment of *A. portulacoides*. Grazing was advantageous to *A. maritima*, as cattle kept dominant grasses in check, therefore delaying succession towards a grass-dominated area. Ages of plants sampled were similar in the grazed and in the non-grazed areas, confirming that the shrub is passed over by grazers.

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