A Native Species with Invasive Behaviour in Coastal Dunes: Evidence for Progressing Decay and Homogenization of Habitat Types

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Abstract A new species has recently invaded coastal dune ecosystems in North West Europe. The native and expansive inland grass, *Deschampsia flexuosa*, progressively dominating inland heaths, has recently invaded coastal dunes in Denmark, occasionally even as a dominant species. A total of 222 coastal locations with 5,000 random sample plots have been investigated. These findings are in contrast to historical records, and *D. flexuosa* has never been considered belonging to coastal dune ecosystems. The occurrence of the typical inland grass in the coastal dunes is a strong indication of increase in nutrient level and that human influences may cause a native species to be invasive in new ecosystems. This could be a radical example of change in species composition due to a long lasting exceedance of critical load of nitrogen. The investigation also showed a general increase in cover of the most dominant species.

Keywords Eutrofication · Habitat types · Dunes, succession · Pinpoint · Critical load

INTRODUCTION

The natural habitats of *Deschampsia flexuosa* are inland heathlands and forest areas on nutrient-poor sandy soils (Gimingham 1972). A high cover of the grass is usually seen after radical interventions, such as fires or clearances, pointing to a strong benefit to the resulting nutrient releases. The grass would dominate for a few years and thereafter steadily decrease in cover, mainly as a result of nutrient depletion and competition from dwarf-scrubs. Probably due to the chronic high deposition of nitrogen from the atmosphere, there has been a change in the former fluctuation of the cover of the grass to a more stable

situation where *D. flexuosa*, and lately also *Molinia caerulea*, are often the dominating species in nutrient-poor inland ecosystems such as wet and dry heath. The same scenario has been observed in a number of western European countries (Bobbink et al. 2003) and (von Oheimb et al. 2010).

Northwest-European dunes ecosystems are changing due to nutrient deposition (Veer and Kooijman 1997; Ketner-Oostra et al. 2006), planting of exotic conifers, changes in grazing pressure, drainage, and climate (Clemmensen et al. 2008). Analysing Danish vegetation data from 2004 and onwards, it became clear that a major and unexpected change has occurred in the coastal dune habitats. *D. flexuosa* is now one of the dominant species in the coastal dunes. The aim of this article is to report on the invasion of *D. flexuosa* into coastal dune ecosystems, since the recording started some hundred years ago and discuss possible reasons.

DESCRIPTION OF COASTAL HABITAT TYPES

The habitat types, to which the dune series belong, follow the EUNIS classification system characterised by a four-number code (EUR 25 European Commission 2003). This manual defines and describes each habitat type on Annex I of the Habitat-directive.

European dune heaths are dynamic coastal ecosystems with breaches and sand drift. The succession from the white dunes via the green and grey dunes to the more stable *Empetrum* dune heath represents a natural succession and also an acidification gradient. The green and grey dunes, normally mentioned as the “fixed” dunes, are covered by perennial grass, herbs, lichens, and mosses, where the more acid grey dune represents a typical lichen habitat.

The dynamics of the grey and green dunes are usually more pronounced than in the decalcified fixed dunes dominated by *Empetrum nigrum*. The former does not have a well-developed top organic layer opposed to the latter. Due to succession and succession reset by sand movement or by local disturbances, large- and small scale mosaics occur.

MATERIALS AND METHODS

A total of 222 Danish coastal dune sites and 5,000 randomised plots were monitored from 2004 to 2008. 10% of the sample plots were revisited every year to follow the dynamics of the vegetation whereas the rest were visited once in the 5-year period. At each site 20 to 60 plots were placed randomly and the coordinates of the plots were transferred to a GPS. In each plot, species abundances were measured by the pin-point method (Kent and Coker 1992) in frames of 50 by 50 cm with 16-grid point.

The average plant cover was estimated under the assumption that the pin-point cover data arose from a zero-inflated generalised binomial distribution (Damgaard 2009). The change in plant cover over time was analysed using a state-space model, where the mean plant cover of the different sites were modelled by latent variables (Bruus et al. 2010; Damgaard et al., in press). The statistical significance of possible trends in the change in cover was assessed from the Bayesian posterior distribution of the annual change, which was simulated using Markov Chain Monte Carlo (Damgaard et al., in press).

RESULTS

In the dry dune ecosystems, including grey-green dunes and the more stabilised dune heathlands, the average cover of *D. flexuosa* are 18 and 20%, respectively, see Table 1.

Most of the natural dominating plant species have had a marked increase in cover (Figs. 1, 2) during the 5-year period from 2004 to 2008 (Bruus et al. 2010). The cover of *Carex arenaria* in the grey and green dune is 20% and with no significant trend (Fig. 1). In the more stabilised dune

heathland (Fig. 2), the cover of *Ammophila arenaria* and *C. arenaria* has a significant increase and more than doubled during the last 5 years to 11 and 25%. Likewise, the cover of *Calluna vulgaris* has increased significantly from 22 to 35% during the 5 years. Oppositely, the cover of bare sand in the grey dunes is relatively low (4%) and in the dune heath less than 0, 5%. Besides the increase in the natural occurring dominants of the dune ecosystems, there

Fig. 1 Cover in % of in the sample plots on grey/green dunes in the period 2004–2008 (avg. and SD for pinpoint data $N = 380$ –510). **a** cover of lichens, **b** mosses, **c** *Deschampsia flexuosa*, **d** *Carex arenaria*, **e** *Calluna vulgaris*, **f** *Empetrum nigrum* and **g** open sand

Table 1 Mean cover of *Deschampsia flexuosa* in % in grey/green dunes and dune heathlands

	Number of stations	Number of sample plots	Mean cover of <i>Deschampsia flexuosa</i> (%)
Grey and green dunes	140	2490	18
Dune heathland	82	2498	20

Fig. 2 The cover is measured in sample plot from dune heath areas in the period 2004–2008 (average and SD for pinpoint data $N = 484$ –648). **a** Cover of *Deschampsia flexuosa*, **b** *Calluna vulgaris*, **c** *Empetrum nigrum*, **d** *Ammophila arenaria*, and **f** open sand

has been room for the newcomer *D. flexuosa* with an average cover around 20% and with no significant change during the period.

DISCUSSION

The current presence of *D. flexuosa* is in striking contrast to historical records of the coastal dunes. One hundred years ago, E. Warming did not observe *D. flexuosa* in the coastal dunes (Warming 1909), and likewise two other comprehensive studies (Böcher 1937) and (Pedersen 1974) did not report the presence of *D. flexuosa* in the coastal dunes. The latter reference was a national mapping of distribution of grasses. Thus, the establishment and spreading of the new species has occurred during the last few decades

The cover of *C. arenaria* in the grey and green dune is 20%, and the cover shows no trend over the past 50 years. The relatively high cover of *C. arenaria* may be due to an increased level of nutrients in the soil (Ketner-Oostra and Sykora 2004). Overall, the dominating and natural occurring species in the coastal dune heathlands have increased in most parts of North Western Europe at the expense of “the white dunes”, and most probably also at the expense of lichens and mosses. The general increase in cover and decrease in “the white dunes” (Fig. 3) and the related increase in biomass may have accelerated soil development (Jones et al. 2004), and thereby probably both speed and direction of the succession.

Traditionally, the coastal dune ecosystems North Western parts of Denmark have been considered nutrient poor, both due to the repeatedly disturbed soil conditions characterised by aeolian well-sorted sand of mainly quartz and to the relatively low nutrient input from the air opposed to inland ecosystems. A major soil characteristic of coastal heath opposed to inland heath is the very low content of carbon in the soil horizons (Nielsen et al. 2000).

The main vegetation characteristic of the coastal dunes is the open structure, which is caused by sand drift together with processes of dune stabilisation and the episodic transgressive dune formation, which constantly resets the

Fig. 3 Aerial photos are showing the same part of the coastline with dune ecosystems. Left photo is from 1954 and right from 2008

succession process. However, aerial photos from 1954 and 2008 from the west coast of Denmark clearly show that the “white dunes” has diminished due to expansion of the vegetation during the past 50 years (Fig. 3).

The Netherlands have also experienced a dramatic loss of open- and species-rich vegetation in the dune ecosystems during the past decades, and a widespread invasion by tall grasses and bushes (Veer and Kooijman 1997) has been observed. Here, comprehensive damage to lichens due to nitrogen deposition has been observed as well as a growth of mosses at the expense of lichens (DeSmidt and van Ree 1991; Greven 1992).

The critical load for nitrogen for dune heath is 10–20 kg N ha⁻¹ year⁻¹ (Bobbink et al. 2003). In many western European countries, the atmospheric deposition of nitrogen is close to the lower level of the critical load for coastal dune heaths, which indicates that changes are expected in the long term. On the Danish island Læsø (Laesø), which has a deposition of nitrogen less than 10 kg N ha⁻¹ year⁻¹, repeated surveys of botanical sample plots showed practically no changes in the composition of the vegetation over a 45-year period (Christensen 1989). Oppositely (Remke et al. 2009) found at a deposition interval from 3–8 kg N ha⁻¹ year⁻¹, a shift from lichen-rich short grass vegetation towards species-poor vegetation dominated by the tall graminoid like *C. arenaria*. Therefore, she propose an update of the critical load for acidic, dry coastal dunes to be in the range of 4–6 kg N ha⁻¹ year⁻¹ wet deposition. This suggestion is supported by our data showing marked changes in the vegetation during a 5-year period and with a deposition level in dune heath 8–13 kg N ha⁻¹ year⁻¹ (Ellermann et al. 2010).

It is a common suggestion that chronic and extensive pressure, such as eutrophication of soil and vegetation, reduces the nitrogen stress which earlier was the norm in most semi-natural ecosystems. The release of this constraint often creates simplified ecosystems with a lower diversity due to changes in the competitive conditions imposed by nutrients. This development parallels the development in the grass *Molinia caerulea* some 30 years ago in Holland, where the grass invaded dry inland heaths. Homogenisation of terrestrial ecosystems as acid grasslands (Stevens et al. 2004), heathlands (Bobbink et al. 1998), ombrotrophic bogs (Tomassen et al. 2004), and dunes manifests itself through increased cover of tall graminoids and a decrease in small herbs and lichens (Remke et al. 2009). The changes of the vegetation in heathlands and bogs in the Netherlands in the late 1970s/early 1980s (Heil and Diemont 1983; Aerts and Berendse 1988) did not manifest itself in Denmark till one or two decades later. A similar delay now seem to exist for the changes in the coastal areas compared to changes in the inland ecosystems, with the result that the coastal areas

seemingly undergo similar changes in directions of higher, more and denser biomass and a parallel introduction of native and expansive grass species with invasive traits in coastal dune ecosystems. The invasion and expansion of *D. flexuosa* in coastal dunes is a critical new step in deterioration of semi-natural ecosystems and a further step in homogenization of nutrient-poor ecosystems tending to alter the structure and function of nutrient-poor habitat types in the direction of unfavourable conservation status.

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