OULU 2009
A 529

ACTA
UNIVERSITATIS OULUENSIS

Marika Niemelä

BIOTIC INTERACTIONS AND VEGETATION MANAGEMENT ON COASTAL MEADOWS

FACULTY OF SCIENCE,
DEPARTMENT OF BIOLOGY,
UNIVERSITY OF OULU

ACTA UNIVERSITATIS OULUENSIS
A Scientiae Rerum Naturalium 529

MARIKA NIEMELÄ

BIOTIC INTERACTIONS AND VEGETATION MANAGEMENT ON COASTAL MEADOWS

Academic dissertation to be presented with the assent of the Faculty of Science of the University of Oulu for public defence in Kuusamonsali (Auditorium YB210), Linnanmaa, on 22 May 2009, at 12 noon

OULUN YLIOPISTO, OULU 2009

Acta Univ. Oul. A 529, 2009

Supervised by
Docent Annamari Markkola
Docent Marko Hyvärinen

Reviewed by
Professor Robert L. Jefferies
Doctor Ann Norderhaug

ISBN 978-951-42-9122-7 (Paperback)
ISBN 978-951-42-9123-4 (PDF)
http://herkules.oulu.fi/isbn9789514291234/
ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)
http://herkules.oulu.fi/issn03553191/

Cover design
Raimo Ahonen

OULU UNIVERSITY PRESS
OULU 2009

Niemelä, Marika, Biotic interactions and vegetation management on coastal meadows
Faculty of Science, Department of Biology, University of Oulu, P.O.Box 3000, FI-90014 University of Oulu, Finland
Acta Univ. Oul. A 529, 2009
Oulu, Finland

Abstract

Conservation of rare habitats and species are central elements in the management of semi-natural grasslands of high biodiversity. Understanding the impacts of various abiotic and biotic interactions and management methods on threatened species is fundamental to their conservation. In the present study, effects of competition, plant parasitism, grazing and mowing were studied at the community level in Bothnian Bay coastal meadows and in greenhouse. This was the first time when the impacts of various biotic interactions on the critically endangered creeping alkali grass (*Puccinellia phryganodes*) have been explored in detail in one of its rare occurrences in the boreal vegetation zone in Europe. In addition, questions related to ecological and economical sustainability of cattle grazing on coastal meadows were examined.

Puccinellia phryganodes was found to suffer severely from competition with taller graminoids. Simulated and actual grazing by greylag goose, *Anser anser*, as well as infection by a hemiparasitic plant, *Odontites litoralis*, were found to indirectly benefit *P. phryganodes* by decreasing the competitive advantage of its competitors. In spite of the relatively intensive grazing by greylag goose in the field, *P. phryganodes* experienced a drastic decrease during four years in the grazed experimental quadrats and simultaneously the proportion of the taller graminoids increased substantially. Primary succession of coastal meadow vegetation was found to progress rapidly and continuous formation of suitable open habitats is therefore crucial for the subordinate species. Mowing was found to be an effective management method for some threatened plant species in coastal meadows, but not for *P. phryganodes*, which would probably benefit more, for example, from livestock grazing. Both lightly and rather intensively managed large open meadows could provide optimal habitats for the critically endangered lesser white fronted goose (*Anser erythropus*) as well as for the greylag goose.

The relatively low and variable yield of the coastal meadow vegetation compared to that of cultivated grasslands sets limits how management by cattle grazing can be implemented. Key factors for both the biodiversity management and livestock production in coastal meadows are timing of the grazing season, intensity of grazing and selection of suitable types of animals.

Keywords: cattle, coastal meadow, diet of geese, grazing, management, plant competition, plant parasitism, threatened species, vegetation succession

Acknowledgements

It has been a long way to arrive at the point where I am standing now. The whole process has given me plenty of valuable experience and, importantly, it has enabled me to get to know and collaborate with many great people. First of all, I would like to express my gratitude to my supervisors, Annamari Markkola and Marko Hyvärinen, for promoting and making this journey possible. Annamari has been a friend and a colleague to whom it has always been easy to turn in any matter, and Marko has kindly offered his skills for use whenever needed. I am deeply grateful for all the support that you both have given to me!

The Department of Biology has provided an inspiring environment for doing research. I have had an opportunity to work with excellent colleagues and friends at the university throughout the course of my studies. First, I'd like to thank Juha Markkola for involving me in the life of coastal meadows already during my graduate studies. I am grateful to the following people for their assistance in the field work: Pia Arvola, Sophie Birade, Riku Halmeenpää, Juliana Heikkinen, Riikka Kaartinen, Salla Kaartinen, Anne-Sophie Robin, Paavo Närhi, Emilia Pippola, Anna Tammilehto and Riikka Törmänen. The following co-authors have made important contributions to the published articles in my thesis: Taina Björnström, Aija Degerman, Lauri Erävuori, Pia Mutikainen, Pirjo Rautiainen, Seppo Rytkönen, Pirkko Siikamäki and Juha Tuomi. Special thanks to the following former and present fellow postgraduate students at the Biology Department: Riitta Ahonen, Sami Aikio, Kalle Hellström, Marjut Kreivi, Jarmo Laitinen, Niina Lappalainen, Carolin Nuortila, Henna Pihlajaniemi, Heikki Pöykkö, Annu Ruotsalainen and Piippa Wäli. I am particularly grateful to my roommates Pirjo, Taina and Karita 'Kati' Saravesi, as well as to people the next door, Anu Eskelinen, Sari Piippo and Oili Tarvainen, for all their help and the joyful moments during work and free time. The members of the 'dog-division' of the university have enriched my life outside of work and many of them have also given valuable help to me during my Ph.D. studies; Thank you Katja Anttila, Marja Anttonen, Jari Heikkinen, Helmi Kuittinen, Anne Niittyvuopio and Mari Saarikettu-Känsälä.

Furthermore, the help of many other people in the Biology Department, the Botanical Gardens and the Bothnian Bay Research Station has been indispensable in the implementation of the practical work. Professors Satu Huttunen, Juha Tuomi and Jari Oksanen have kindly helped me to resolve different kinds of questions related to my studies. I want to acknowledge Prof. Robert L. Jefferies and Dr. Ann Norderhaug for reviewing my thesis and for introducing me to new perspectives across many ecological issues. I would also like to express my gratitude to the late Dr. Jouko Siira for his valuable pioneering research on the ecology of the halophytic flora of the Bothnian Bay coastal meadows.

I am grateful for the many collaborators outside the university. MTT Agrifood Research Finland has provided me interesting new research themes and an excellent environment to finish my thesis. Special thanks to Arto Huuskonen, Sari Jaakola and Erkki Joki-Tokola for their invaluable help in guiding me into the LUMOLAIDUN project and for acting as co-authors in the Paper V. I also want to thank all the people in Ruukki for their assistance and nice company. Further, I want to acknowledge the present and former employees from the North Ostrobothnia Regional Environment Centre, Marja Hyvärinen, Tupuna Kovanen, Jorma Pessa, Sami Timonen and Maarit Vainio, as well as Johanna Helkimo in the TE Centre for Northern Ostrobothnia, for all the help in questions related to the conservation and management of coastal meadows.

The study has been financially supported by the Academy of Finland, the Finnish Ministry of Agriculture and Forestry, the Finnish Ministry of Environment, the Maj and Tor Nessling Foundation, NORNET, Olvi-Säätiö, Oskar Öflunds Stiftelse, Oulun yliopiston Apteekin Säätiö, Societas pro Fauna et Flora Fennica and Suomen Riistanhoito-Säätiö. I am grateful for all the support.

Finally, I want to thank my family and friends for sharing the spectrum of life with me. I am especially thankful to my dear friend Minna-Mari Myllykangas for the long journey we have traveled together since we were little girls. Insisting to be mentioned here, are my 'hairy' friends, Ravja and his late mother Peera, which have shared everyday life with me and taken care that I concentrate on essential things. I am deeply grateful to Mirjam Mäenpää-Kirjavainen for these great dogs and for her friendship, as well as to all the numerous new friends, which life around the dogs has brought. Kiitän lämpimästi myös rakasta ystävääni Aino Viitasta kannustuksesta ja monista mukavista hetkistä Lamujoen rannalla.

Suurimmat kiitokseni omistan äidilleni Tuulalle, edesmenneelle isälleni Paavolle, veljelleni Pasille, hänen vaimolleen Jaanalle sekä heidän mainioille pojilleen Pietille ja Niilalle. Myös 'mummolan väellä' on tärkeä sija sydämessäni. Kiitos teille kaikista yhteisistä hetkistä, te olette rakkaimmat ihmiset elämässäni.

Oulu, April 2009 Marika Niemelä

List of original papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Niemelä M, Markkola A & Mutikainen P (2008) Modification of competition between two grass species by a hemiparasitic plant and simulated grazing. Basic and Applied Ecology 9: 117–125.

II Niemelä M, Markkola AM & Hyvärinen M (2009) Impact of goose grazing and primary succession on vegetation and threatened plant species on coastal meadows. Manuscript.

III Rautiainen P, Björnström T, Niemelä M, Arvola P, Degerman A, Erävuori L, Siikamäki P, Markkola A, Tuomi J & Hyvärinen M (2007) Management of three endangered plant species in dynamic Baltic seashore meadows. Applied Vegetation Science 10: 25–32.

IV Markkola J, Niemelä M & Rytkönen S (2003) Diet selection of lesser white-fronted geese *Anser erythropus* at a spring staging area. Ecography 26: 705–714.

V Niemelä M, Huuskonen A, Jaakola S, Joki-Tokola E & Hyvärinen M (2008) Coastal meadows as pastures for beef cattle. Agriculture, Ecosystems & Environment 124: 179–186.

The author's contribution: Marika Niemelä (MN) was responsible for the experimental work in I and II, in III concerning *Puccinellia phryganodes*, and participated in the field work in V. Vegetation sampling in the field, preparation of reference material and microscopic analyses were carried out by MN in IV. Statistical analyses were performed by MN in I and II, by Pirjo Rautiainen and Marko Hyvärinen in III, and by MN together with other authors in IV and V. MN was responsible for writing and interpretation of the results in I, II, V and participated in writing and interpretation in III and IV.

Contents

1 Introduction

1.1 Special features of Bothnian Bay coastal meadows

Coastal meadows of the Bothnian Bay in the northernmost part of the Baltic Sea, one of the largest brackish water basins in the world, represent a globally unique habitat. Low salinity of sea water, isostatic land uplift, lack of tidal fluctuations and a relatively short growing season followed by an ice-covered sea in winter, are special characteristics of this area and substantially affect the nature of the coastal meadows (*e.g.* Tyler 1969b, Dijkema 1990, Kautsky & Kautsky 2000). Flat topography and a large amplitude of irregular water level fluctuations (up to *ca* three metres, Ericson & Wallentinus 1979), together with a high rate of land uplift (*ca* 7 mm year^{-1}, Johansson *et al.* 2004), create extensive meadows along the Finnish coast of the Bothnian Bay. The largest and most uniform coastal meadows of Finland are situated in this area covering in total approximately 2500 ha, which represents *ca* 63% of the country's coastal meadows (Finnish Environment Institute 2008). The relatively young age and isolation of the area together with special features of the Baltic Sea have provided favourable conditions for genetic differentiation of plant populations, thus contributing to the area's evolutionary significance (Dijkema 1990, Johannesson & André 2006). In contrast, isolation may reduce the genetic variation of marginal populations, which may hamper their survival (Johannesson & André 2006, Crawford 2008, Kunin *et al.* 2009).

One characteristic feature of Bothnian Bay coastal meadows is the occurrence of the *Primula sibirica* group of plant species including, *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Arctophila fulva* (Trin.) Andersson and *Primula nutans* Georgi var. *jokelae* L. Mäkinen & Y. Mäkinen (previously *sibirica* Jacq.). The main distribution area of these species is along the shores of the Arctic Ocean, from where they are assumed to have spread to the Baltic Sea via a post-glacial water connection between the White Sea and the Baltic Sea (Ericson & Wallentinus 1979, Kreivi 2009). Due to the isolated location, some of the plant species of the Bothnian Bay have diverged and endemic varieties can be recognised, such as *A. fulva* var. *pendulina* (Laest.) Holmb., or even endemic species, such as *Euphrasia bottnica* Kihlm.

Coastal meadows of the Bothnian Bay also host valuable breeding and migrating avifauna. For example, the wetlands of Hailuoto and Liminganlahti

Bay in Finland belong to the internationally important bird area (IBA) (Heath & Evans 2000) and are part of Natura 2000, a European Union-wide network of protected areas. Approximately 280 breeding or staging bird species have been encountered in the area (Pessa & Anttila 2000).

1.2 Interactions between plants

A characteristic feature of coastal meadows is an elevation gradient from the mean waterline upwards to inland sites. In general, environmental conditions for plant growth ameliorate towards the higher seashore elevations with decreasing abiotic stress (*e.g.* water logging, disturbance caused by wave action) and increasing soil nutrient content (*e.g.* Olff *et al.* 1997, van Wijnen & Bakker 2000, Crain *et al.* 2004). However, the increase in vegetation cover and biomass towards the terrestrial edge of the gradient also multiplies the chances for interactions between the organisms, and thus the probability of biotic stress experienced by an individual. Indeed, the distribution of species in shore habitats has been shown to be controlled by abiotic factors in the more stressful sites, typically near the waterline, and by competitive and other biotic interactions in more favourable physical conditions on the upper shore (*e.g.* Wilson & Keddy 1986, Emery *et al.* 2001, Crain *et al.* 2004).

Subordinate species are usually outcompeted at higher elevations by superior light competitors, which in turn may have a poorer ability to tolerate the harsh conditions on the lower shore (*e.g.* Wilson & Keddy 1986, Bertness 1991, Crain *et al.* 2004; but for exceptions see Pennings & Callaway 1992, Bockelmann & Neuhaus 1999, Ecke & Rydin 2000, Emery *et al.* 2001). Results from experimental studies suggest that zonation of plant species in coastal meadows may be driven by a trade-off between plants' competitive and colonisation ability (*e.g.* Bertness 1991, Brewer *et al.* 1998), or by a trade-off between the competitiveness for below-ground vs. above-ground resources (*e.g.* van der Wal *et al.* 2000a, Emery *et al.* 2001).

Inferior light competitors may also find suitable habitats at higher elevations on the shore. Existing vegetation may be destroyed, for instance, by storm waves, ice scouring, burial by drift or soil material (Cramer & Hytteborn 1987, Bertness 1991, Ewanchuk & Bertness 2003, Funk *et al.* 2004, Rautiainen *et al.* 2007) and by grazing animals (*e.g.* Kauppi 1965, Bakker 1985, Andresen *et al.* 1990, Srivastava & Jefferies 1996). Open patches formed in such a way provide competition-free ground for secondary succession of vegetation. If the disturbed soil is rich in electrolytes, evaporation may enrich salts in the top soil layer resulting in the development of salt patches, which are first colonised by salt-tolerant plant species such as *Salicornia europaea* L., *Spergularia salina* J. Presl & C. Presl and *P. phryganodes* (Siira 1970 and 1985, Bertness 1991). These halophytes may facilitate the establishment of other plant species by gradually ameliorating the soil conditions, for example by reducing salinity and by increasing the oxygen and nutrient content of the soil (Bertness 1991, Ewanchuk & Bertness 2003).

Parasitic plants are frequent components of coastal meadow vegetation (*e.g.* Snogerup 1983, Pennings & Callaway 1996, Marvier 1998) and may have significant effects on plant community composition and dynamics (for a review see Press & Phoenix 2005). Similar to herbivores, they may display host preferences, reduce host biomass, alter host allocation patterns and mediate interactions between host plants and other organisms (Pennings & Callaway 2002). Parasitic plants have been shown to increase species diversity via suppression of dominant species of the plant community (*e.g.* Pennings & Callaway 1996, Davies *et al.* 1997, Grewell 2008) though contrasting results may also emerge if inferior competitors are suppressed (Gibson & Watkinson 1992). Few studies have simultaneously examined the effects of plant parasitism and herbivory on host performance (Goméz 1994, Puustinen & Salonen 1999, Puustinen & Mutikainen 2001). Combined impacts of parasitism and herbivory involve both direct and indirect effects where the consumers may change the performance of host plants as well as the quality and availability of the hosts as a resource for consumers (Price *et al.* 1986, Smith 2000).

1.3 Interactions between coastal meadow vegetation and herbivores

Coastal wetlands may produce abundant plant biomass, although there is considerable variation due to the wide range of environmental conditions within and between sites (Adam 1993). Consequently, these habitats have a potential to host a high variety of herbivores ranging from small invertebrates (*e.g.* Silliman & Bertness 2002) to birds and large mammals (*e.g.* Bakker 1985, Bazely & Jefferies 1986, van der Wal *et al.* 2000c). At the community level increased plant biomass is usually coupled with decreased nutritional quality as plants increasingly allocate resources to structural tissues due to intensified light competition in the course of vegetation succession (*e.g.* Olff *et al.* 1997, Kuijper *et al.* 2004). Similarly, biomass and the nutritional quality of a plant are negatively correlated and a younger stage in plant growth provides higher nutritional quality than an old one (*e.g.* Prop & Deerenberg 1991, Fox *et al.* 1998).

Forage quality significantly affects a herbivore's food preference and foraging intensity, which in turn feed back to vegetation through various direct and indirect effects (Jefferies *et al.* 1994, Mulder 1999, Wardle *et al.* 2004). Grazing may, for example via acceleration of nutrient cycling, improve the compensation growth and nutrient concentration of plants, resulting in a positive gain for the herbivore. However, an increase in grazing intensity to a very high level may initiate a process of vegetation destruction (*e.g.* Srivastava & Jefferies 1996) and lead to a loss of forage for the herbivore (*e.g.* Cooch *et al.* 1991).

Body size and digestive system structure determine much of the nutritional demands and thus dietary choices of vertebrate herbivores (*e.g.* Jefferies *et al.* 1994, Van Soest 1994, Begon *et al.* 1996, Rook *et al.* 2004). Wild geese, which can be classified as intermediate-sized herbivores, have relatively inefficient digestive capacity and thus need to maximise their intake of high quality forage (*e.g.* Prop & Deerenberg 1991, Loonen & Bos 2000, Fox & Kahlert 2003). Due to these constraints grazing by geese is mainly limited to the relatively young stages of succession, which offer nutritionally favourable forage (*e.g.* Olff *et al.* 1997, Fox *et al.* 1998, van der Wal *et al.* 2000b,c).

As a consequence of increased populations of several goose species during recent decades, geese have become important grazers in many coastal areas (*e.g.* Bazely & Jefferies 1986, Fox *et al.* 1998, Van Eerden *et al.* 2005). Grazing by geese and other intermediate-sized herbivores has been shown to hinder vegetation succession by slowing down the colonisation by later successional species (*e.g.* Joenje 1985, Bazely & Jefferies 1986, Rowcliffe *et al.* 1998, Kuijper *et al.* 2004). However, at moderate grazing intensities geese are able to prevent vegetation succession only for a limited period, and when tall less palatable plants begin to dominate, geese clearly avoid these sites as feeding grounds (Bazely & Jefferies 1986, Olff *et al.* 1997, Rowcliffe *et al.* 1998, Loonen & Bos 2000, van der Wal *et al.* 2000b,c). It was suggested by Huisman *et al.* (1999) that this shift from the top-down control of vegetation by herbivores to the bottom-up control of herbivores by tall vegetation entails a change from nutrient to light competition between plants (leading to reduced forage quality) along with increased productivity of the salt-marsh.

Large ruminant herbivores like cattle are able to utilise considerably coarser plant material than smaller herbivores. Large herbivores therefore function more like generalists in their food selection (*e.g.* Van Soest 1994, Begon *et al.* 1996), although showing clear selectivity and dietary shifts during the grazing season as well (Jerling & Andersson 1982, Hessle *et al.* 2008). Correspondingly, cattle are able to graze the older vegetational stages of the successional gradient in a coastal meadow and restore and sustain early vegetational stages more effectively by their foraging than small herbivores (*e.g.* Tyler 1969a, Bakker 1985, Jensen 1985, Olff *et al.* 1997, Kleyer *et al.* 2003). As a consequence, the bottom-up control by tall plant species in productive late-successional vegetation may be reversed to top-down control by large herbivores. The major difference in the impact of grazing between small and large herbivores is the greater extent of trampling disturbance by large herbivores. This is an important mechanism triggering secondary succession in coastal meadows (*e.g.* Tyler 1969a, Siira 1970, Bakker 1985).

Geese have been shown to utilise forage in coastal meadows where potentially tall vegetation is frequently grazed by livestock (Olff *et al.* 1997, Loonen & Bos 2000). Grazing, for example by cattle and sheep, was found to improve the habitat quality for geese by decreasing the amount of tall-growth, unpalatable vegetation and increasing the proportion of low-growth, early successional meadow plants. Similarly, winter grazing by hares on tall-growth, late successional species was shown to facilitate grazing by geese (van der Wal *et al.* 2000c). Due to facilitative effects via modification of the foraging conditions, some herbivore species may thus increase the overall herbivore diversity. Consequently, intensified grazing may further promote the existence of plant and animal species dependent on low-growth vegetation, assuming that grazing does not become too intensive.

1.4 Utilisation and management of coastal meadows

Human impact on coastal meadows has been considerable ever since the beginning of their usage for agricultural purposes. For this reason, they are classified as semi-natural grasslands in Finland (Schulman *et al.* 2008). For centuries coastal meadows have been exploited as an important source of forage for livestock (*e.g.* Tyler 1969a, Siira 1970, Dijkema 1990, Bakker *et al.* 1997, Vainio & Kekäläinen 1997, Markkola & Merilä 1998). Until the beginning of 20th century the most traditional use was to cut hay for winter forage, after which livestock were allowed to graze the meadows. As cultivation in arable fields in northern Europe gradually started to displace forage collection from semi-natural grasslands at the end of 19^{th} century, coastal meadows were increasingly used only as pastures for livestock and many of them were abandoned during the second half of the 20^{th} century (*e.g.* Tyler 1969a, Bakker *et al.* 1997, Vainio *et al.* 2001).

Decreased traditional use and eutrophication have resulted in overgrowth by taller vegetation, especially by the common reed [*Phragmites australis* (Cav.) Trin. ex Steud.], on the shores of Baltic Sea on a large scale (*e.g.* Tyler 1969a, Dijkema 1990, Jutila 2001). Abundance of the tall growing *P. australis* has strongly increased especially along sheltered shores (Vainio *et al.* 2001). In addition, conversion to arable and building land, as well as ditching, have contributed to the loss of coastal meadows. Consequently, the area of low-growth coastal meadows has diminished and many of the species of the early successional stages have become rare or threatened (*e.g.* Ryttäri *et al.* 2001, Schulman *et al.* 2008). Boreal Baltic coastal meadows are listed in the EU Habitats Directive as a priority natural habitat type, the conservation of which is a particular responsibility of the European Community (Council Directive 92/43/EEC). In the recent red listing of habitat types in Finland, coastal meadows were classified as critically endangered (Schulman *et al.* 2008). At present, approximately 4200 ha of coastal meadows are left in Finland, which is less than 10% of the amount in the 1950's (Schulman *et al.* 2008).

As a response to the considerable decrease of semi-natural grasslands and their biodiversity during the last few decades, management of these habitats has become an important target of EU agri-environment support schemes (Salminen & Kekäläinen 2000, Isselstein *et al.* 2005, Kuussaari *et al.* 2008). Human activity in semi-natural grasslands has largely changed from resource acquisition as a livelihood to the management of the landscape and biodiversity. Management actions have brought important supplementary income to farmers (Franzén & Lehtomaa 2005) and the indirect economic benefits may be substantial as well. For example in North Ostrobothnia, large areas of coastal meadows are managed by livestock grazing (Niemelä *et al.* 2006a) potentially constituting a considerable economic benefit for local farmers and indirectly supporting nature tourism via improved landscape and habitat quality (Pessa & Anttila 2000, Mikkola-Roos & Niikkonen 2005).

Frequently encountered problems in the management of semi-natural grasslands in Finland are related to grazing intensity, grazing of semi-natural grasslands in connection to cultivated pastures, use of supplementary forages and the defects of the support system (Salminen & Kekäläinen 2000, Lumijärvi *et al.* 2002, Huuskonen 2006, Pykälä 2007, Kuussaari *et al.* 2008, Kemppainen & Lehtomaa 2009). Appropriate management methods are of critical importance for the conservation of biodiversity of semi-natural grasslands (Alanen & Pykälä 2004, Kuussaari *et al.* 2008). Likewise, suitable management practices are important in order to support the welfare of grazing animals and the economics of management in semi-natural grasslands (*e.g.* Franzén & Lehtomaa 2005, Isselstein *et al.* 2005, Huuskonen 2006).

In the conservation of threatened species, identification of habitat requirements of these species, their population structure and critical life history stages in their population dynamics are essential in planning effective management actions (Ryttäri & Kettunen 1997, Kuussaari *et al.* 2004). According to the results of the genetic analysis of the structure of *A. fulva* populations by Kreivi *et al.* (2005), a metapopulation model might be appropriately applied to this species and other early successional plant species of coastal meadows. The persistence of species inhabiting fragmented landscapes as a metapopulation is dependent on the availability of suitable habitat patches, successful dispersal and colonisation of those sites (Hanski 1999). Hence, long-term persistence of these species could be improved by slowing down the successional process in sites where viable populations exist, by creating new open patches, and by aiding the dispersal and establishment of plant propagules at these sites.

1.5 Aims of the study

Management of threatened habitats and their species requires a full understanding of natural and human-induced processes affecting them. Vegetation of the Bothnian Bay coastal meadows have been studied for at least a century (*e.g.* Leiviskä 1908, Kauppi 1965, Siira 1970, Vartiainen 1980, Autti 1993) with an emphasis on their threatened plant species. For example, threatened plant species of the area include *Primula nutans* (*e.g.* Mäkinen & Mäkinen 1964, Ulvinen 1997, Degerman-Fyrsten 2001, Strengell 2003, Kreivi *et al.* 2006, Kreivi 2009), *Puccinellia phryganodes* (*e.g.* Siira & Haapala 1969, Siira & Merilä 1985, Markkola *et al.* 1989, Siira, unpublished) and *Arctophila fulva* (Siira 1994, Rautiainen *et al.* 2004, Kreivi *et al.* 2005, Rautiainen *et al.* 2007, Kreivi 2009). Research has also been carried out on the avifauna of Bothnian Bay coastal meadows (*e.g.* Rönkä 1996, Ruokonen *et al.* 2004, Pessa *et al.* 2006, Koivula *et al.* 2008).

The present work aims to examine biotic factors affecting the performance of the threatened species, as well as the ecological and economical sustainability of cattle grazing as a management tool to maintain these threatened species and their habitats. First, the impact of various biotic interactions (competition, plant parasitism, herbivory) on the critically endangered *P. phryganodes* was studied in Papers I and II. Habitat requirements and diet selection of the critically endangered lesser white-fronted goose (*Anser erythropus* L.) were investigated in Paper IV. Second, the efficiency of greylag goose (*Anser anser* L.) grazing (Paper II) as well as mowing and other management methods (Paper III) on sustaining populations of the threatened plant species were determined. Finally, the suitability and prerequisites for beef cattle grazing in the management of the coastal meadows was studied in Paper V.

In Paper I, the effects of the annual root hemiparasitic plant, *Odontites litoralis* (Fr.) Fr., on the growth of the two host species, *P. phryganodes* and *Agrostis stolonifera* L., and on the outcome of competition between these two grasses were investigated in a greenhouse experiment. Previous field observations had confirmed that in some years, *O. litoralis* extensively parasitised the largest population of *P. phryganodes* at Isomatala, Hailuoto. The following questions were addressed: (i) Does infection by a parasitic plant and simulated grazing of the host plants modify the competitive interactions between the two host grasses? (ii) Is the performance of the parasitic plant affected by simulated grazing of the host?

In Paper II, the importance of grazing by the greylag goose, *Anser anser*, on the performance of *P. phryganodes* and other coastal meadow plant species was studied in a five-year field experiment. Vegetation changes in naturally grazed open plots and non-grazed exclosures were compared at two successional stages. Goose grazing was hypothesised to slow down succession by depressing the invasion and growth of later successional species. Consequently, conditions in the plots of grazed vegetation were assumed to remain favourable to small forbs and graminoids, such as *P. phryganodes*. Due to a preference for low-growth vegetation by grazers, the impact of goose grazing was hypothesised to be more pronounced in the earlier successional stage of the coastal meadow where the tall later successional species were mainly absent. In addition, the diet of greylag geese foraging in the area was examined in order to estimate potential selectivity of the herbivore and to better interpret the observed changes in vegetation in recent years.

The efficiency of different management methods designed to slow down the decline of the threatened plant species, *P. phryganodes*, *A. fulva* and *P. nutans,* was examined in separate field experiments during four years (Paper III). Removal of surrounding taller vegetation by mowing and bush removal was expected to prevent or slow down habitat deterioration. It was predicted that vegetative reproduction of all the aforementioned three plant species would increase in response to the treatment. Moreover, these management practices were expected to increase sexual reproduction in *P. nutans*.

Diet and habitat selection of the extremely threatened goose species *A. erythropus* were studied during spring staging in Bothnian Bay coastal meadows (Paper IV). The aim was to determine if the species has special requirements in relation to diet and habitat selection. Based on field observations, *A. erythropus* was expected to prefer the largest coastal meadows, providing a long escape distance in the case of interference, during spring staging. An important objective was to find more effective ways to manage habitat quality in goose staging areas.

Finally, beef cattle performance, forage yield and forage quality were examined in a three-year study on four coastal meadows (Paper V). Beef cattle grazing has become a common management practice in coastal meadows in recent years, though a knowledge of the nutritional adequacy of the forage for cattle in these coastal meadows has been scarce so far. This information can be used to evaluate the economical profitability of grazing on coastal meadows and to assess sustainable livestock production and biodiversity management in these habitats. It was predicted that animal and forage production on coastal meadows would be lower than that in cultivated grasslands. In addition, the nutrient balance of coastal meadows was calculated for phosphorus in order to estimate the significance of supplemental feeding of calves as a potential source of eutrophication.

2 Material and methods

2.1 Study species and sites

The focal plant species studied was *Puccinellia phryganodes* (Papers I, II, III), which is one of the first colonisers of salt-marsh shores of the Arctic Ocean (Jefferies 1977, Jefferies *et al.* 1979). It has a discrete occurrence in the northernmost part of the Baltic Sea, along the eastern coast of the Bothnian Bay (Siira & Merilä 1985). This is one of the rare occurrences of *P. phryganodes* in the boreal zone in Europe (Hultén 1962). The populations are of evolutionary interest in terms of their adaptation to changing climatic conditions at this southerly location. *P. phryganodes* is divided into four geographical subspecies mainly based on the leaf epidermal morphology and the observed variation in chromosome number (taxonomy summarised by Elven 2007). According to current knowledge, the species is suspected to be autopolyploid. The Fennoscandian *P. phryganodes* belongs to the subspecies *sibirica*, and its cytotype has been found to vary from triploid (*e.g.* most Norwegian specimens are of this type) to tetra- and even hexaploid (Elven 2007). The ploidy level of *P. phryganodes* in the Bothnian Bay is not known. The observed leaf epidermal characteristics of the species in the Bothnian Bay (spinules, papillose cells; Niemelä 1999) fit well with the 'Siberian type' (subsp. *sibirica*) (Sørensen, 1953).

P. phryganodes is a small perennial clonal graminoid producing easily detaching axillary shoots on prostrate ramets. Flowers are regularly formed, abundantly in some years (Jefferies *et al.* 1979, personal observation), but the species has been reported to be sterile over much of its range (Sørensen 1953). The subspecies *phryganodes* ('Beringian type' according to Sørensen) probably reproduces sexually based on its good floral development and seed set (Elven 2007). Furthermore, due to the observed high genetic variation of *P. phryganodes* in Arctic Canada, Jefferies & Gottlieb (1983) suggest that sexual reproduction may take place as a rare event. Vegetative propagules released, for example by foraging activities of geese, may root in suitable conditions at new sites (Chou *et al.* 1992). In the field, a stand of *P. phryganodes* is approximately five-cm tall and the length of the stolons range from 10 to 20 cm (Siira & Merilä 1997).

Until the 1960's, growing sites of *P. phryganodes* in the Bothnian Bay were mostly on secondary salt patches in coastal meadows grazed by livestock, but cessation of grazing led to overgrowth by tall vegetation and gradual disappearance of these upper open habitats (Siira & Haapala 1969, Siira & Merilä 1985). Nowadays, *P. phryganodes* occurs mainly on open primary saline soils near mean water level. The species has been found in a total of 17 locations in the Bothnian Bay, five populations existed at the beginning of the 21st century (Siira & Merilä 1985, Siira & Merilä 1997, Siira unpublished) but only two of them could be found in 2007 (in Isomatala and in small islets south of it, Markkola 2007). The known distribution area of *P. phryganodes* in the Bothnian Bay was at its largest in the 1960's when the sothernmost growing site was found in Lohtaja (Siira 1985), *ca* 150 km south of Oulu; since then the range of the species has diminished considerably. In 2008, the status of *P. phryganodes* was changed from the IUCN class endangered to the class of a critically endangered species in Finland (Kemppainen & Eeronheimo 2008). *P. phryganodes* is listed in a group of species needing special protection (Finnish Nature Conservation Law LSA 913/2005, EU Habitats Directive 92/42/EEC).

The impact of grazing by greylag geese on *P. phryganodes* and other coastal meadow plant species (Paper II) was studied on the south-east shore of the island of Isomatala in Hailuoto, *ca* 35 km west of Oulu, where the largest population of *P. phryganodes* in the Bothnian Bay exists (Fig. 1). The species has been displaced from the earlier salt patches of the inner island by taller vegetation but has continuously dispersed towards the mean waterline on newly emerged soils along the southern shore and on the youngest islets (Siira & Merilä 1985, Siira & Merilä 1997, Siira, unpublished). The coastal meadows of Isomatala are intensively grazed by greylag geese during their moulting period from early June until mid-July. The number of moulting individuals has increased from *ca* 200 individuals in 1970's to *ca* 3200 in 2008, representing the largest moulting population of greylag geese in the Bothnian Bay (Markkola & Merilä 1998, Juha Markkola, personal communication). Patchy vegetation near the mean waterline is composed of low-growth graminoids and forbs followed later in succession by increasingly closed meadow vegetation with taller graminoids such as *Calamagrostis stricta* (Timm) Koeler and *P. australis* (Fig. 2). Part of the upper meadows of Isomatala has been managed by the implementation of tractor mowing since 1987 (Siira & Merilä 1997), including areas beside the study site. In non-mown upper meadow areas, *P. australis* forms dense and tall-growth stands narrowing the zone of low-growth vegetation to near the mean waterline. In 2008, Isomatala was fenced as part of a larger pasture grazed by beef cattle (Jorma Pessa, North Ostrobothnia Regional Environment Centre, personal communication).

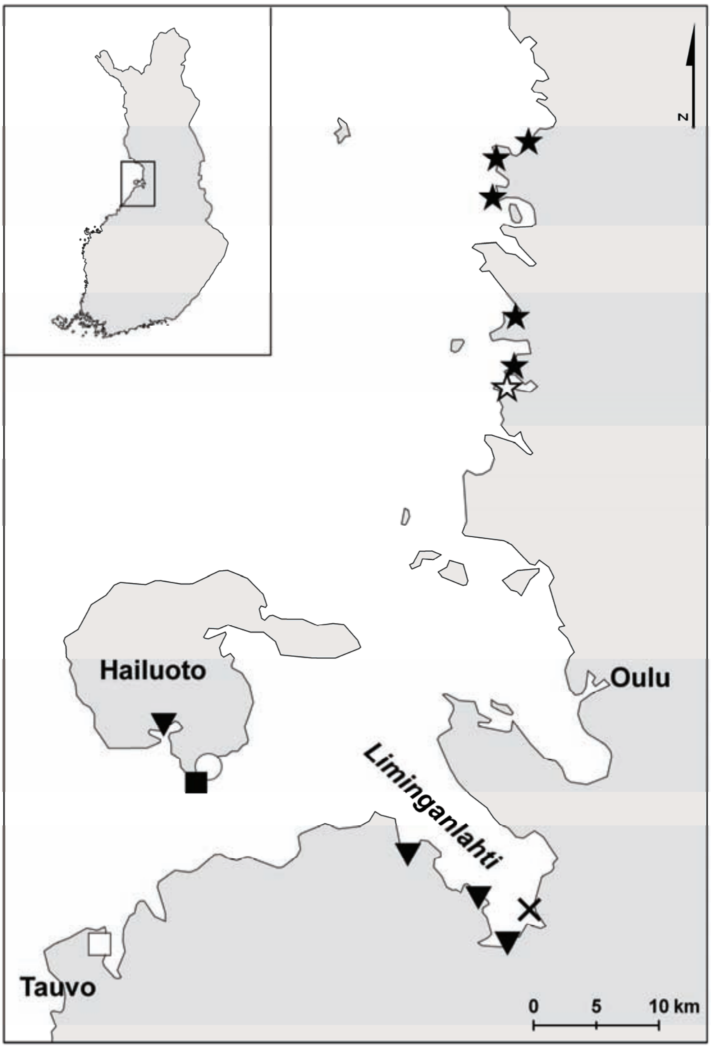

Fig. 1. Study sites of *P. phryganodes* (filled square = goose grazing, open square = mowing experiment), *A. fulva* (cross), *P. nutans* (filled stars = mowing experiment, open star = shrub removal), *A. erythropus* (open circle) and cattle grazing (filled triangles). Map: Marja Anttonen.

Fig. 2. Habitat of *Puccinellia phryganodes* in Isomatala, Hailuoto. Upper: low-elevation coastal meadow with an exclosure preventing grazing by greylag goose. Lower: taller vegetation at higher elevation (*P. phryganodes* as low-growth yellowish patches).

The effect of mowing in the management of *P. phryganodes* (Paper III) was studied in Tauvo, *ca* 50 km SW from Oulu (Fig. 1), the first known location of the species in the Bothnian Bay (a sample collected in 1926 by B. Lemberg, *sensu* Lindberg 1929). All the known patches of *P. phryganodes* in this area were and are small and scattered. There might have been periods when the species was absent (Siira & Merilä 1997, Siira, unpublished). The sandy soil of Tauvo is almost neutral and contains little organic matter associated with a very low nutrient content, compared to the finer-grained soil of Isomatala, which is more acidic and contains considerably higher amounts of organic matter, nutrients and electrolytes (Siira 1985, Siira, unpublished).

During the first years of the study (2000–2001) *ca* 120 *P. phryganodes* patches, on average 58 cm in maximum diameter and with 1.5 dm^2 of ground cover, were found mainly within 100–450 m inland from the mean water level in Tauvo. Vegetation was relatively sparse and dominated by low-growth species, although in many places *P. australis* had started to invade the area from nearby moister sites. Since 2002, part of the Tauvo meadow has been managed by the use of tractor mowing to prevent the spread of *P. australis* and shrubs (Jorma Pessa, North Ostrobothnia Regional Environmental Centre, personal communication).

The management experiments for the critically endangered, *A. fulva* (Rassi *et al.* 2001), were conducted on the eastern shore of Liminganlahti Bay (III), *ca* 20 km south of Oulu (Fig. 1). The area holds the largest population of this relatively tall perennial clonal grass in the Baltic Sea (Siira 1994, Rautiainen *et al.* 2007). The population has been declining during recent decades (Siira 1994) and the latest decline in the population size, since the beginning of the 21st century, has been alarmingly rapid (Rautiainen *et al.* 2007). *A. fulva* grows here mainly in shallow water and small patches of the species situated on the upper shore are easily displaced by other vegetation (Rautiainen *et al.* 2004, 2007).

Response of *P. nutans* to different management methods (Paper III) was studied in six locations ranging 25–50 km north of Oulu (Fig. 1). *P. nutans* is a small perennial rosette-forming forb species capable of dispersing by both sexual and clonal means (Mäkinen & Mäkinen 1964). The distribution of the species in the Bothnian Bay ranges from Kokkola in Finland to Luulaja in Sweden (Ulvinen 1997). The abundance of *P. nutans* has strongly decreased during the past decades and at present it is classified as endangered in Finland (Rassi *et al.* 2001, Ryttäri *et al.* 2001).

The lesser white-fronted goose, *A. erythropus* (Paper IV), is an extremely threatened species breeding in the tundra zone from Fennoscandian Lapland to eastern Siberia (Lorentsen *et al.* 1999). Hunting and habitat destruction on the migratory staging grounds and wintering areas have caused a drastic decline of *A. erythropus* populations and it is globally one of the most threatened bird species, ranked as vulnerable in the IUCN red list and as critically endangered in Fennoscandia (Lorentsen *et al.* 1999, BirdLife International 2008a). It is also included in Annex I of the EU Birds Directive (79/409/EEC). The Fennoscandian population has decreased from *ca* 10 000 individuals to only 20–30 breeding pairs during the past century (Tolvanen *et al.* 2004, Markkola *et al.* 2004). Bothnian Bay coastal meadows, which used to be an important spring and autumn staging area for the species, have been visited during the past two decades merely in spring by fewer and fewer individuals (Markkola *et al.* 2004).

Diet selection of *A. erythropus* (Paper IV) was studied on an approximately 1 km^2-large coastal meadow of Tömppä in the southern part of Hailuoto (Fig. 1). The area is characterised by relatively low-growth coastal meadows. *P. nutans* is present as scattered patches in the upper meadow and a small stand of *P. phryganodes* also occurs in the SW perimeter of the meadow (observed still in 2001, Niemelä, personal observation) (Markkola & Merilä 1998, Niemelä 1999). During 1986–2002, the area was managed by the use of mowing and from 2004 onwards it has been grazed by beef cattle (Markkola & Merilä 1998, Johanna Helkimo in TE Centre for Northern Ostrobothnia, personal communication).

Finally, vegetation quality and yield, and the growth of beef cattle (Paper V) were studied in three coastal meadows on the southern and western coasts of Liminganlahti Bay and in one location in Hailuoto (Fig. 1). These meadows were commonly mown and grazed up to the first half of the 20^{th} century, after which grazing continued in some of the meadows until the 1970–80’s (Vainio & Kekäläinen 1997, Hägg *et al.* 2006). During the break in the management practice, *P. australis* had become an abundant species in many of the meadows. Since grazing was re-started with beef cattle in mid-1990’s, the amount of *P. australis* has considerably decreased and the proportion of the low-growth graminoids has increased (Hägg *et al.* 2006). The cattle from the study farms were composed of suckler cows, which were mainly crossbred beef cattle with some past influence of dairy breeds. The breed of the calves was determined according to their sires, which were pure-bred bulls of the *Simmental*, *Limousin* and *Charolais* breeds.

The nomenclature of plant species follows Hämet-Ahti *et al.* (1998) and that of bird species follows BirdLife International (2008b).

2.2 Experimental designs

A general overview of the experimental designs is described here. More detailed descriptions are given in each paper. The impact of interspecific competition, infection by the hemiparasitic plant (*Odontites litoralis*) and simulated grazing on *P. phryganodes* and *A. stolonifera*, as well as the performance of the hemiparasite were studied for a complete life cycle of the hemiparasite during April–June in 2002 in a greenhouse experiment (Paper I). The spatial and temporal occurrence of the annual *O. litorali*s is unpredictable, especially in the early successional stage, where the high water level in early-/mid-summer caused by southern winds may destroy almost all seedlings of the species in some years. For example, in 2002 the hemiparasite was largely missing from the early successional meadows of Isomatala (personal observation). For this reason, and in order to control the number of the host species, the experiment was conducted in a greenhouse. Rooted shoots of the two grass species (*P. phryganodes* and *A. stolonifera*) and seedlings of *O. litoralis* (plant material was collected from Isomatala in autumn 2001), were planted in pots in the following combinations: (i) each grass species alone, (ii) grass species together, (iii) *O. litoralis* with one or both of the grass species and (iv) *O. litoralis* alone. Only one individual of each species was present in each replicate of these treatments, *i.e.* intraspecific competition was not included, whereas the occurrence of interspecific competition varied. In the middle of the experiment, when the hemiparasite started to flower, the grasses in half of the pots (15 replicates in each treatment) were clipped roughly simulating the selective grazing by greylag geese.

To study the impact of grazing by greylag geese on *P. phryganodes* and other coastal meadow vegetation during 1999–2003, experimental quadrats of 0.5 x 0.5 m were established as pairs in different locations at the site where the main population of *P. phryganodes* grew in Isomatala (II). Quadrat placement was based on the following characteristics: The canopy of the vegetation was closed, *P. phryganodes* was present and either early or late succesional stage vegetation was represented. A quadrat was considered to represent an earlier successional stage if the ground cover of *P. australis* and *C. stricta* were together less than 5%. The quadrats in each pair were assigned randomly as two treatments (grazed, non-grazed). Grazing was prevented using 1 x 1 m exclosures (Fig. 2). The number of replicates was eight in each combination of successional stage and grazing treatment. The diet of greylag goose was studied in 2002 from faecal samples collected from the grazed experimental quadrats at both successional stages at the end of May and June.

The management experiments of *P. phryganodes* and *A. fulva* were carried out in 2000–2003 and those of *P. nutans* in 1999–2002 (Paper III). Twenty-four patches of *P. phryganodes* were selected in Tauvo, and twelve of them were randomly subjected to simulated mowing (cutting with scissors in a quadrat of 1 × 1 m). Another twelve quadrats served as controls. Total cover of *P. phryganodes* was 1.1 % on average at the beginning of the experiment. The response of *A. fulva* to one of the three treatments (control, mowing, combined mowing and soil turning) was studied in fourteen randomly selected patches (10–435 m^2) in Liminganlahti Bay. Three experimental quadrats (1.5 x 1.5 m) were established at the edge of each *A. fulva* patch and allocated randomly to the treatments. The effect of mowing on the management of *P. nutans* was studied in five populations and the impact of shrub removal was studied on one population. All populations were located in Haukipudas and Ii. In each of the six populations of *P. nutans*, ten 0.4 x 0.4 m quadrats were established and half of them were randomly allocated to the management treatment, the other half served as controls.

For each of the three species, mowing was done yearly in late summer by cutting the vegetation with shears or a scythe in the experimental quadrats and the area in close proximity (Paper III). The cut vegetation was subsequently removed. As low-stature species, *P. phryganodes* and *P. nutans* were mainly left intact, although the ripened flower stalks of *P. nutans* were usually cut. Most of the *A. fulva* shoots were partly cut along with the other vegetation. The soil turning applied in the study of *A. fulva* was conducted in the first two years to imitate the impact of ice scouring. Shrubs were cut in August every year at the site where the population of *P. nutans* grew.

Habitat selection of *A. erythropus* (Paper IV) was studied by comparing the sizes (width of the geolittoral and hydrolittoral zones) of 9 meadows used by *A. erythropus* in the Bothnian Bay during the past 10 years. Twenty randomly selected meadows were chosen between Kalajoki, 64°15 'N and Kuivaniemi 65°30' N. In order to identify the diet of the *Anser* geese, reference material of available plant species was first collected from the Tömppä meadow and some other parts of Hailuoto (Paper IV). Epidermal tissues of *ca* 50 vascular plants were prepared and photographed. A random sample of *ca* 200 droppings, potentially belonging to 31 *A. erythropus* individuals, was collected from the meadow of Tömppä in May 1993 (Paper IV). The availability of potential dietary plant species for *A. erythropus* was assessed by estimating the percent cover of all vascular plant species in 169 randomly sampled 1 m^2 quadrats in Tömppä. Faecal samples of *A. anser* were collected in 2002, just before the moult of the geese at the end of May, and in the middle of the moult period at the end of June (Paper II). The droppings were collected from 15 grazed experimental quadrats inside an area of 2.0 m in diameter.

The research on forage properties and the growth of beef cattle was conducted as a farm study in four coastal meadow pastures of Liminganlahti Bay and Hailuoto during 2003–2005 (Paper V). In each pasture, one exclosure (*ca* 10 x 20 m) was erected yearly in a different location. Eight 25 x 50 cm samples of aboveground live vegetation were cut from each exclosure at one-week intervals in June and once at the end of July. The measured variables from the samples are presented in Chapter 2.4. These first-cut samples represented vegetation grazed during the previous years but not grazed during the year of sampling. In addition, subsequent growth from sample quadrats mown at the end of June was sampled one month later. Growth of cattle was monitored by weighing all calves at the beginning and the end of each grazing season. Supplemental forage was offered to the calves (only calves had an access to the supplement) on two farms during July–August in 2004–2005, while the calves on the other two farms served as controls. Oats or a commercial concentrate was used as a supplement. Beef calf data of A-Farmers Ltd, representing the general performance of beef calves reared in variable environments (mainly in cultivated grasslands) in northern Finland, were used for comparison. The significance of supplemental feeding of beef calves as a potential source of eutrophication was estimated by calculating a nutrient budget for phosphorus (P) for the coastal meadows in 2004–2005.

2.3 Plant performance measurements

In the greenhouse experiment, plants were harvested three months after planting, when capsules of *O. litoralis* were fully ripened (I). Shoots and roots of *P. phryganodes*, *A. stolonifera* and the hemiparasite were dried and weighed and the capsules of the hemiparasite were counted. The number of haustoria of *O. litoralis* per unit length of host roots (a sample of 20 root pieces, 3–4 cm in length, from each grass individual) was counted under a dissection microscope.

In the field study of the effects of goose grazing, yearly measurements of plant parameters were done in August–September (II). The cover of vascular plant species was estimated using the point quadrat method (Stampfli 1991) and species diversity was expressed as the Shannon-Wiener Index (H'). Thickness of the litter layer, maximum shoot heights and the number of flowering shoots of abundant competitors (taller graminoids) of *P. phryganodes* were measured. Dry biomass of the aboveground live and dead vegetation was estimated at the end of the experiment in 2003.

In management experiments of the threatened plant species (Paper III), the number of *P. phryganodes* and *A. fulva* shoots and *P. nutans* rosettes, seedlings and flowering individuals, as well as the cover of *P. phryganodes* were used as response variables. In addition, the cover of other vascular plants was estimated visually in each experiment prior the management treatments.

2.4 Forage and herbivore performance measurements

Intensity of goose grazing was estimated by collecting droppings of *A. anser* from the experimental quadrats in the earlier and later successional stages of coastal meadow development in Isomatala at the end of May and June 2002 to obtain the dry weight. Diet composition of the forage eaten by *Anser* geese was determined by identifying the plant epidermal fragments in droppings with the help of the photographed reference samples. The total number of analysed droppings was 100 for *A. erythropus* (Paper IV) and 30 for *A. anser* (Paper II). Using a point quadrat method (Owen 1975, Bhadresa 1986), plant fragments in droppings, spread under a cover glass, were identified under a light microscope. In all, 20 observations per each *A. erythropus* dropping and 50 identifications per *A. anser* dropping were made. In order to determine the diet preferences of *A. erythropus* (IV), a Chesson's electivity index (ε) was calculated for each plant taxon determined from the faecal samples (Chesson 1983). The index relates the proportion of each dietary type in the diet to the proportion available in the meadow, and ranges between −1 and +1. Negative values indicate avoidance and positive values preference for a plant taxon selected by the geese.

Vegetation samples from the four coastal meadow pastures used by beef cattle (Paper V) were weighed for their dry matter (DM) and analysed for digestible organic matter (DOM), neutral detergent fibre (NDF) and crude protein (CP)(methods described in Huuskonen *et al.* 2007). In addition, mineral concentrations (N, P, K, Ca, Mg, S, Na, Fe, Zn, Cu and Mn) of the vegetation samples were determined in 2003 following the methods of Luh Huang and Schulte (1985). The dominant plant species in the exclosures were identified in 2005. The vegetation height was measured yearly in June and July on the same dates when the vegetation samples were collected. Height measurements were made at 50–100 points in each pasture in the areas which had been grazed longest (since mid-1990's).

Daily live weight gain (g day^{-1}) of each beef calf was calculated by dividing the change in live weight by the number of days that the calves spent on the coastal meadow pasture (Paper V). Live weights (LW) of the calves on coastal meadows at the end of the grazing season were compared with weaning weights of beef calves from the data provided by A-Farmers Ltd using corresponding breeds (*Simmental* and *Limousin*), age classes and breeding seasons. Adequate data on age and breed of calves were obtained only from two coastal meadows and the calves of the other two farms (and therefore the *Charolais* breed) could not be used for the comparison.

In the calculation of the phosphorus (P) budget (Paper V), yearly inputs and outputs of P were averaged over the farms, years and the two types of supplements used in the supplemental feeding of the calves. Data of the parameters were mainly obtained from the literature and from environmental authorities (described in detail in Paper V). Briefly, the input sources included deposition from air (precipitation), the supplemental forage and additional minerals offered to animals according to the feeding plan, and the output comprised the nutrients that left the system by leaching and via animal growth.

2.5 Data analysis

Host performance in the different treatments (competition, parasitism and simulated grazing) was examined separately for *P. phryganodes* and *A. stolonifera* (Paper I). The importance of host presence, competition between the two grass hosts, as well as clipping of the hosts, were analysed for hemiparasite performance. The frequency of the hemiparasite haustoria on roots of the two host species was compared and their response to competition and simulated grazing was analysed for both host species. All the analyses were done using ANOVA in the SPSS (version 13.1; SPSS Inc., Chicago, IL, USA) statistical package.

Changes in the cover of the plant species, diversity (Shannon-Wiener H-Index), thickness of litter layer and the maximum shoot heights during the years in the grazed and non-grazed plant communities of the two successional stages (Paper II) were analysed with repeated measures ANOVA because of the interdependence of observations between years. The analysis of *P. phryganodes* cover values was performed separately for the two successional stages (due to unequal variances), and the cover of *C. stricta* and *P. australis* was analysed only for the later successional stage because the determination of the two successional stages was based on the occurrence of these two species, which were largely missing from the earlier stage. Pairwise comparisons between the treatments within the two successional stages were done using t-tests. Biomass of aboveground vegetation at the end of the experiment in the two treatments and successional stages was analysed by two-way ANOVA. Biomass of greylag goose droppings was analysed separately for May and June 2002 by one-way ANOVA. All tests were performed using the mixed procedure of SAS Enterprise Guide version 4.1 (SAS Institute Inc., Cary, NC, USA).

The influence of the management treatments on the threatened plant species (Paper III) was analysed with R statistical software (Ihaka & Gentleman 1996). The number of *P. phryganodes* and *A. fulva* shoots and *P. nutans* rosettes, seedlings and flowering individuals was analysed using a generalised linear model with a log-link, as customary with variables following a negative binomial distribution. The impact of each treatment was evaluated by the change in the model deviance that follows a Chi-square distribution. The change in the cover of *P. phryganodes* following a treatment was analysed by the use of a one-way ANOVA.

The width of the geolittoral and hydrolittoral zones of staging places of *A. erythropus* and the reference meadows were compared using a t-test (Paper IV). In determining the dietary preferences of *A. erythropus*, the reliability of the electivity indices (ε) was tested using the bootstrap method (Dixon 1993, Efron & Tibshirani 1993). The original ε-values of each plant taxon were re-sampled without replacement 1000 times, and an empirical *p*-value was achieved by counting the proportion of p-values that were on the other side of the boundary of neutral selection (ε=0) in relation to the original ε-value.

The calf live weight in the coastal meadows and in the data of A-Farmers Ltd, with respect to breed, age, sex and farm, were compared using ANCOVA using the lm function (Paper V). The daily weight gain of the calves in the studied coastal meadows was examined using ANOVA. Because of the many uncontrollable background variables and low number of replicates, the vegetation variables and the effect of supplemental feeding on the daily gain were not tested statistically. All the analyses were done using the R statistical package (Ihaka & Gentleman 1996). More detailed information about statistical analyses (*e.g.* transformations made to correct deviations from the assumptions of ANOVA) are given in each of the Papers (I–V).

3 Results

3.1 Plant performance affected by biotic interactions and management

3.1.1 Competition, parasitism and simulated grazing

Competition, infection by a hemiparasitic plant and simulated grazing reduced the aboveground biomass of both *P. phryganodes* and *A. stolonifera* (Paper I). However, the negative impact of interspecific competition on the aboveground biomass of *P. phryganodes* was nearly two-fold compared to that of *A. stolonifera* (52% and 29%, respectively). Also, parasitism reduced the biomass of *P. phryganodes* slightly more (by 59% vs. 45% in *A. stolonifera*). In contrast, simulated grazing decreased the aboveground biomass of *A. stolonifera* relatively more (by 73%) compared with that of *P. phryganodes* (by 53%) when compared to non-clipped treatments.

In the case of the growth of *P. phryganodes* there was a significant interaction between competition and parasitism. Competition with *A. stolonifera* decreased the aboveground biomass of non-parasitised *P. phryganodes* by 56% and that of parasitised plants by 36%. While the total aboveground grass biomass per pot was reduced, the relative proportion of *P. phryganodes* was increased by both simulated herbivory and by parasitism in cases where both host species were present. Parasitism decreased root biomass by 64% in *P. phryganodes* and 36% in *A. stolonifera* compared to the non-parasitised treatments. In contrast, simulated herbivory did not affect the root biomass of *P. phryganodes* but decreased that of *A. stolonifera* by 40%.

Hemiparasitic *O. litoralis* benefited considerably from the presence of the host species, whereas the identity and number of hosts did not have a significant effect. The number of capsules was significantly lower when the hemiparasite was grown without a host than when grown with either host species (*P. phryganodes* or *A. stolonifera*) or with both of them. The frequency of *O. litoralis* haustoria on host roots was higher in *P. phryganodes* (0.54 ± 0.05 haustoria cm^{-1}, mean ± 1 SE) than in *A. stolonifera* (0.20 ± 0.03 haustoria cm^{-1}). When *A. stolonifera* was present as another host with *P. phryganodes*, the frequency of hemiparasite haustoria on the roots of *P. phryganodes* decreased by 42%. In the case of *A. stolonifera*, the presence of *P. phryganodes* did not result in a significant reduction in haustoria frequency. Simulated grazing of the host had no effect on the number of capsules of the hemiparasite or the haustoria frequency on host roots.

3.1.2 Grazing by Anser anser

The ground cover of several plant species changed significantly during the five-year experiment (Paper II). At the beginning of the experiment in 1999, *P. phryganodes* was one of the dominant species: the estimated mean cover was 86% and 54% in the earlier and later successional stages, respectively. The cover of *P. phryganodes* decreased to close to zero in both successional stages during the experiment. Treatment (grazed, non-grazed) did not have a significant main effect. However, the impact of treatment was dependent on time. In the last year of the experiment, *P. phryganodes* was significantly more abundant in grazed quadrats of the earlier successional stage. In the later successional stage, its reduction was slightly but significantly slower in grazed quadrats indicated by a significant treatment x year interaction. The cover of small forbs was higher in grazed quadrats than in exclosures in the later successional stage. In the case of *Potentilla anserina*, the benefits of grazing were emphasised in the earlier successional stage where its cover was significantly greater in the grazed quadrats during the three last years of the experiment. The peak in the cover of small forbs (*Potentilla anserina* L., *Plantago maritima* L., *Glaux maritima* L., *O. litoralis, Galium palustre* L., *S. salina, Atriplex* sp.) in 2001 in the grazed earlier successional stage was mainly due to the peak of the annual hemiparasite, *O. litoralis*, which was exceptionally abundant in that year.

In contrast to *P. phryganodes*, many other graminoids, such as *Juncus gerardii* Loisel., *C. stricta* and *P. australis*, increased their cover during the experiment. *J. gerardii* increased more at the earlier successional stage compared to the later stage and more in non-grazed than in grazed quadrats. In turn, *A. stolonifera* increased at the earlier successional stage and decreased at the later stage. Cover of *C. stricta* tended to be lower in grazed quadrats at the end of the experiment. Species diversity (Shannon-Wiener H-index) was significantly higher in the later successional stage and tended to be slightly higher in grazed vegetation but the difference was not significant.

Shoots of *J. gerardii*, *A. stolonifera* and *P. australis* were taller in non-grazed quadrats and a steady increase in maximum shoot height was observed in all combinations of treatments and successional stages towards the end of the experiment. However, in *A. stolonifera* the maximum height started to decrease in the non-grazed later successional stage, so that in the last year no difference was found between grazed and non-grazed quadrats. The number of flowering shoots of *A. stolonifera* increased during the first years of the experiment and then started to decline. The cessation of grazing resulted in a considerably higher number of flowering shoots of *A. stolonifera* in non-grazed quadrats only during the first two years of the study. *J. gerardii* benefited from non-grazed conditions especially in the earlier successional stage where the number of flowering shoots continued to increase in the exclosures throughout the study period.

At the end of the experiment (Paper II), total aboveground biomass of vegetation was significantly lower in the earlier than in the later successional stage (estimated means 170 g m^{-2} vs. 290 g m^{-2} in the two successional stages, respectively). Cessation of grazing resulted in significantly greater biomass but only in the exclosures of the earlier successional stage (estimated means: 111 g m^{-2} vs. 229 g m^{-2} in the earlier and later stage, respectively). Similarly, the litter layer was significantly deeper in the later successional stage and in non-grazed quadrats.

3.1.3 Management of threatened plant species

Mowing of surrounding vegetation did not improve the status of *P. phryganodes* (Paper III). The cover and the number of shoots of *P. phryganodes* declined in both mowed and control quadrats during the experiment and there was no statistically significant difference between the treatments. The total cover of vascular plants was relatively low in both control and mowing treatments increasing from *ca* 24% to *ca* 30% during the experiment, mainly due to the expansion of *J. gerardii*.

In contrast, both *A. fulva* and *P. nutans* benefited from the removal of surrounding vegetation (Paper III). Mowing and combined mowing and soil turning increased the number of *A. fulva* shoots. Management treatments positively affected the number of shoots in the first year after the start of the experiment and this trend was further enhanced during subsequent years. The analysis revealed that the control and the treated quadrats differed during all study years. Combined cutting and soil turning scored a higher median number of shoots in all years than cutting alone.

Mowing markedly increased the number of *P. nutans* individuals in all demographic stages (Paper III). The number of sterile rosettes and flowering individuals in mown quadrats significantly exceeded that of controls during the last two years. Seedlings were separated from the sterile rosettes only in the last year of study and were then significantly more abundant in the mown quadrats. Also in the shrub removal experiment, the management treatment increased the number of sterile rosettes, seedlings and flowering plants of *P. nutans* compared to corresponding values in control quadrats.

3.2 Foraging by geese

A. erythropus preferred large coastal meadows as their spring staging area (Paper IV). The average width of the geolittoral favoured by *A. erythropus* was 960 m compared to 176 m among the reference meadows. The hydrolittoral zone showed the same pattern. The diet of *A. erythropus* during the spring staging in Tömppä consisted of 99.9% of monocotyledonous plants, of which 87.1% were grasses (Paper IV). The most frequently encountered species were *Festuca rubra* L. (43.1%), *P. australis* (30.2%), *C. stricta* (13.4%) and *J. gerardii* (8.4%). *P. phryganodes* was not found in the diet of *A. erythropus*. The results from the study of single droppings, which provide information on diet selection over short intervals, suggested that *A. erythropus* fed especially on *F. rubra* and *P. australis*. According to electivity indices (ε) *A. erythropus* preferred in descending order *P. australis* (ε = 0.73), *Triglochin palustris* L.(ε = 0.7) and *F. rubra* (ε = 0.52). Other species gained negative ε-values as they were avoided by the geese. P-values of the electivity indices were significant for all taxa but not for *T. palustris*, the cover of which was relatively low both on the meadow and in the diet of the geese. *P. australis* and *Eleocharis* spp. were discovered as novel forage plants for *A. erythropus*.

The diet of *A. anser* in Isomatala was composed of 99% graminoids both at the end of May and at the end of June (Paper II). However, the proportion of different species changed considerably during the moulting period. Early in the season, tall graminoids, *C. stricta* and *P. australis,* together formed more than half of the diet. At the end of June, the diet was composed of a more variable set of taxa, *J. gerardii* being the most abundant component. The proportion of *C. stricta* decreased considerably and *P. australis* had almost disappeared from the diet by that time. Instead, the proportion of *P. phryganodes* and *Carex* spp. increased considerably as the growing season progressed. Total biomass of greylag goose droppings on the experimental quadrats in Isomatala did not differ between the earlier and later successional stage at the end of May, whereas at the end of June it was slightly higher at the earlier successional stage.

3.3 Grazing by cattle

The maximum dry matter (DM) yield on the coastal meadows was 1704 ± 608 kg ha^{-1} (mean ± SD) in June over the years (Paper V). At the end of July, the mean yield was 2586 ± 1019 kg DM ha^{-1}. The yield of the subsequent re-growth in the mown quadrats was only 578 ± 228 kg DM ha^{-1}. The average height of the vegetation in the areas with the longest grazing history ranged from 9.2 ± 6.9 cm to 19.6 ± 21.9 cm between the farms at the end of July.

The nutritional quality of the forage weakened during the summer as would be expected. Both the concentrations of digestible organic matter (DOM) and crude protein (CP) were highest in June and decreased considerably by the end of July. Likewise, the most favourable (lowest) neutral detergent fibre (NDF) concentrations were measured in June. The lowest (364 g kg^{-1} DM) NDF concentration was in the beginning of June 2005 in vegetation dominated by *A. stolonifera* and *J. gerardii*. In contrast, the highest concentration of DOM (772 g kg^{-1} DM) was found in vegetation dominated by *C. stricta*, and the highest concentration of CP (192 g kg^{-1} DM) in vegetation dominated by *Carex* spp., *C. stricta* and *P. australis*. The mineral concentration of the forage varied greatly between the four pastures and on different occasions during the summer. In particular, the P, S, Na, Fe and Cu concentrations decreased from June to July. The quality of the subsequent re-growth at the end of July was not much higher compared to that of the first-cut yield at the same time.

The daily weight gain of the calves differed significantly between the four coastal meadow pastures. The average growth rate of males was higher (1.022 kg day^{-1}) than that of females (0.981 kg day^{-1}). Also the year affected the daily growth rate of the calves. A significant interaction between farm and year indicated that the superiority of the farms, with respect to the calf growth rates, differed between years. The calf live weight (LW) at the end of the grazing season was significantly affected by age and sex, as expected. In addition, year, farm and breed had a significant effect on the LW, whereas the pasture type did not. Thus, calves grown on the two coastal meadows had equal LWs compared with beef calves in northern Finland, which are mainly reared in cultivated pastures. Interaction between breed and pasture type just fell short of being significant (P =

0.060) suggesting that the *Simmental* breed was capable of slightly better utilisation of coastal meadows than cattle of the *Limousin* breed.

The P load entering the coastal meadows with supplemental feeding of the calves averaged 0.046 kg ha^{-1} $year^{-1}$, which is 4.4% of the total yearly P load (1.034 kg ha^{-1} $year^{-1}$). Compared with this, the additional minerals and deposition accounted for a considerably higher proportion of the total P load, 86.1% and 9.5%, respectively. The amount of P leaving the pasture through the growth of the calves was threefold (0.142 kg ha^{-1} $year^{-1}$) compared with the amount entering with supplemental feeding. According to the calculations, the net P balance was slightly positive (+ 0.848 kg ha^{-1} $year^{-1}$), mainly due to the additional minerals offered to the animals.

4 Discussion

Various biological interactions and management practices were shown to have a considerable impact on the performance of coastal meadow plant species. Interspecific competition strongly suppressed the performance of the focal plant species, *P. phryganodes*. Herbivory and plant parasitism had positive effects on the species via reduced competition. However, grazing by geese and mowing were not able to improve the performance of *P. phryganodes* to the extent expected (Table 1).

Table 1. Impact of biotic and management actions on *Puccinellia phryganodes* in Bothnian Bay coastal meadows concluded from the results of the present study. Zero (0) denotes for neutral, + and − for positive and negative net responses, respectively. Number of marks refers to the intensity of the impact, and a minor impact is presented in parenthesis.

Action	Predicted	Observed
Biotic interactions		
competition (I, II)	−−	−−
plant parasitism (I)	+/−	+
grazing by geese (I, II)		
early successional meadow	++	+
late successional meadow	+	(+)
Management		
mowing (III)	+	0

Availability of coastal meadows with low interference and high forage quality were the most important determinants of habitat quality for the studied *Anser* geese, whereas forage quantity is likely to be the greatest limiting factor for cattle. The importance of different factors and their interactions are discussed in detail at species and habitat level in the following three sections, and are integrated under the last two sections considering the management and future prospects of coastal meadows and their species.

4.1 Significance of biotic interactions for *Puccinellia phryganodes*

Performance of *P. phryganodes* in the Bothnian Bay has been poor throughout the recorded history of the species (Siira & Merilä 1985, Siira & Merilä 1997, Siira unpublished, Markkola 2007). This may be partly explained by the isolated location of the species in the boreal zone outside its main distribution along the arctic/subarctic seashores. In general, small and fragmented plant populations at range margins may face genetic impoverishment, which may adversely affect the ability of a population to adapt to biotic and abiotic stresses, and changing environmental conditions (*e.g.* Bridle & Vines 2006, Kreivi 2009, Kunin *et al.* 2009). For example, recent findings of low genetic variability of the North European populations of *P. nutans*, indicate that the species has undergone several genetic bottlenecks during its post-glacial dispersal westwards from the probable eastern refugia (Kreivi 2009). Moreover, *P. phryganodes* is known to be polyploid in Fennoscandia (reviewed by Elven 2007), a property, which may increase the fitness of species in harsh arctic conditions, for example, by masking harmful alleles and resulting in favourable changes in plant morphology and physiology (*e.g.* Futuyama 1998, Brochmann *et al.* 2004, Crawford 2008). However, in a more benign climate different properties are likely to be needed, and infertility, a frequent consequence of polyploidy, reduces a population's ability to adapt to new conditions.

Interspecific competition is considered as one of the main determinants of plant species distribution at a local scale (Crawley 1997), but may also affect species range at larger geographical scales (Bridle & Vines 2006). Competitive exclusion after cessation of grazing and hay making has been suggested to be the main reason for the decrease of *P. phryganodes* and many other threatened plant species of the coastal meadows in the Bothnian Bay (*e.g.* Siira & Merilä 1985, Ryttäri & Kettunen 1997). Indeed, the results of the present study show that *P. phryganodes* suffered greatly from competition with other graminoids both in the greenhouse and in the field. The negative impact of interspecific competition on the aboveground biomass was more detrimental to *P. phryganodes* than to *A. stolonifera* indicating that *P. phryganodes* is clearly the weaker competitor of these two species (Paper I). In the field study of the largest population of *P. phryganodes* in Isomatala, *P. phryganodes* was replaced in a few years by taller graminoids in the experimental quadrats (Paper II). A similar decreasing trend in the abundance of *P. phryganodes* was also observed in Tauvo, although the decline was not as drastic, probably because the total cover of vegetation remained at a relatively low level (Paper III, see also Arvola 2003). However, four years after our experiment, stands of *P. australis* and *J. gerardii* had partially covered the growing sites of *P. phryganodes* in Tauvo, despite mowing, and none of the previously known occurrences in Tauvo was found in the inventory in 2007 (Markkola 2007).

The present study was the first to describe the role of plant parasitism as a biotic agent affecting the performance *P. phryganodes* (Paper I). The results indicated that together with goose grazing, infection by a hemiparasitic plant, *O. litoralis*, has the potential to increase the performance of inferior competitors in the coastal meadow community. Such a role has also been suggested for many other plant parasites in natural and semi-natural grasslands (*e.g.* Pennings & Callaway 1996, Davies *et al.* 1997, Callaway & Pennings 1998, Pywell *et al.* 2004, Bardgett *et al.* 2006, Grewell 2008). Plant parasites are able to create small-scale 'disturbance' by suppressing infected plants and creating gaps in closed meadow vegetation. When dominant plants of the community are infected, recruitment of inferior competitors may benefit from the increased open space (Pennings & Callaway 1996, Callaway & Pennings 1998). In the present study, infection by the root hemiparasite *O. litoralis* led to the withering of surrounding vegetation (including *P. phryganodes*) within a radius of *ca* 10 cm around the hemiparasite in Isomatala (personal observation), thus potentially creating open space for plant colonisation.

In the greenhouse experiment (Paper I), the higher frequency of haustoria attached to roots of *P. phryganodes* suggested that it is the preferred host of the hemiparasite. *P. phryganodes* also suffered a relatively higher biomass loss due to the hemiparasite infection compared to *A. stolonifera*. However, despite the more negative direct impact of the hemiparasite infection on *P. phryganodes* than on *A. stolonifera,* parasitism indirectly benefited *P. phryganodes* by decreasing the relative competitive advantage of *A. stolonifera* (Paper I). The results may be largely explained by the effects of simulated grazing, which caused considerably higher biomass loss in *A. stolonifera* than in *P. phryganodes*, and seemed to be the main driver influencing the competitive relationship between these two graminoids. The negative impact of the hemiparasite on *A. stolonifera* and the corresponding positive effect on the relative competitive status of *P. phryganodes,* were particularly discernible in the simulated grazing treatment. These results relate to field conditions at the higher elevations of the low-growth meadow, where the two grass species grow 'interwoven' together so that the geese are likely to graze vegetation non-selectively (*i.e. P. phryganodes* is not selected for, contrary to what might be expected based on its higher nitrogen content, see Chapter 4.3). Therefore, vegetation would be grazed at an even height, resulting in a disproportionately higher biomass removal of the taller species, *A. stolonifera*. This, together with the hemiparasite infection, could result in relative improvement of the competitive status of the subordinate *P. phryganodes*. In contrast, at lower elevations, where the two grass species grow in a more patchy pattern, possibly more selective grazing and parasitism against *P. phryganodes* may enhance its competitive exclusion. At lower elevations, however, seedlings of *O. litoralis* are more often destroyed by sea water in early/mid-summer.

The field experiment in Isomatala (Paper II) confirmed that grazing by greylag goose had several positive indirect effects on the subordinate species of the plant community. Biomass and height of vegetation, as well as the ground cover and number of flowering shoots of some common graminoids, were kept at a lower level by grazing compared to non-grazed swards. Faecal analyses showed that most of the dominant graminoids were abundant in the diet of the greylag goose. The negative impact of geese on the tall graminoids *P. australis* and *C. stricta* is strongest during the early season when they were the main dietary components of the geese. Kuijper *et al.* (2004) reported a similar pattern influencing the invasion of a late successional grass species, *Elymus athericus* (Link) Kerguélen, in North Sea salt marshes, which was suppressed by geese and hares at the seedling stage. The positive impact of grazing on subordinate species could be seen as a slightly, but statistically significantly, better performance of *P. phryganodes* and small forbs in the grazed quadrats.

The impact of greylag goose was most evident at the earlier successional stage, as was expected (Paper II). For example, geese reduced the biomass of vegetation significantly only at that stage. Therefore, vegetation was more under top-down control by geese at the earlier successional stage, whereas at the later stage, the situation more closely resembled bottom-up control by taller vegetation rather than control by herbivores. However, in spite of the indirect positive effects of grazing, *P. phryganodes* experienced a drastic decrease in cover in grazed quadrats and the proportion of the taller graminoids had increased substantially by the end of the experiment. Obviously, since the vegetation canopy has been closed, *i.e.* bare soil is no longer available, which was the case in the first year of the study, *P. phryganodes* is rapidly displaced by later successional species even in intensively grazed areas.

A high grazing intensity by waterfowl, however, may delay succession by several years and thus prolong the life span of *P. phryganodes* swards (Bazely & Jefferies 1986, Hik *et al.* 1992) and other early successional salt marsh halophytes (Joenje 1985). In contrast, Handa *et al.* (2002) found that very high densities of geese had destructive effects even on swards of *P. phryganodes* in the salt marshes of the Hudson Bay. Overgrazing may become a threat also in the coastal meadows preferred by the greylag goose in the Bothnian Bay, if the availability of suitable foraging sites in the moulting area does not increase with the growing goose population. Overgrazing by flocks of moulting geese has already been considered to be one possible reason for the disappearance of *P. phryganodes* from some localities in the Bothnian Bay (Markkola 2007). Large scale grubbing of below-ground plant parts, which has been found to have an considerable impact on tidal marsh vegetation in the autumn feeding grounds of *A. anser* in the Netherlands (Esselink *et al.* 1997), has not been observed in the Bothnian Bay (personal observation). In the case that the population of *A. anser* continues to increase in the area, grubbing may become a greater risk in the future.

4.2 Vegetation succession

The results of the present study in Isomatala (Paper II) show that the composition of vegetation in coastal meadows may undergo a substantial change within four years. Ground cover of vegetation remained at *ca* 100% throughout the experiment but the composition of vegetation changed towards that characteristic of the later successional stage (Paper II). Similarly, Ericson (1980) found that lower sea-shore meadow communities were replaced by upper ones within a decade on the west coast of the Gulf of Bothnia. The vegetation changes in Isomatala are in accordance with the earlier descriptions of the successional changes in vegetation in the Bothnian Bay (*e.g.* Ericson 1980, Vartiainen 1980, Siira 1984), and indicate that primary succession is ultimately driven by isostatic uplift.

In the study of *A. fulva* (Paper III), only slight changes in species composition were observed in the non-disturbed control quadrats as the vegetation canopy was already relatively closed at the beginning of the experiment. After soil turning, re-growth of vegetation (*e.g. Carex aquatilis*) was rapid. In a separate study on patch dynamics of *A. fulva*, succession rapidly progressed around those *A. fulva* patches which were surrounded by relatively open vegetation early in the experiment, resulting in canopy closure within a few years (Rautiainen *et al.* 2007).

The rate of primary succession on a sea-shore depends on, for example, the colonisation abilities of the species at a site (Ericson 1980 and 1981, Vartiainen 1980). Furthermore, short-term variations in water level and the occurrence of various disturbances may enhance or retard vegetation succession compared to that assumed based on the rate of isostatic uplift (Ericson 1981, Cramer & Hytteborn 1987). Also, the status of soil fertility and moisture may affect the rate of succession (Prach *et al.* 1993). In the case of *P. phryganodes* and the surrounding vegetation, the rate of change seemed to be highest in the closed vegetation in Isomatala (Paper II) and lowest in the relatively sparse vegetation of Tauvo (Paper III). This finding may be explained by the poorer nutritional and drier conditions of Tauvo (Siira 1985, Siira, unpublished). For example, growth of individual *P. phryganodes* patches differed greatly between the two areas in 2003: patch diameter changed during the growing season on average by −0.36 cm in Tauvo (SD 1.3 cm, n=26) and by +4.91 cm (SD 3.6 cm, n=7) on the small islets south of Isomatala (Niemelä, unpublished data). Eutrophication of the Baltic Sea, especially of coastal waters (Kauppila & Bäck 2002, Lundberg 2005) may have accelerated the rate of vegetation succession along the sea-shores.

4.3 Coastal meadows as a forage source for herbivores

A survey of the diet of the two *Anser* species on three occasions showed some similarity in their dietary choices, although considerable changes in the composition of the diet were found as the growing season progressed (Papers II, IV). The diet of the critically endangered *A. erythropus* was found to be composed mainly of common plant species in the coastal meadows of the Bothnian Bay. Overall, the diet of both *A. erythropus* and *A. anser* was composed almost exclusively of graminoids (99%). Variation in plant tissue susceptibility against damage during digestion, however, may have affected to some extent the observed relative abundances of the species in the diet. For example, a proportion of species with readily digestible tissues (*e.g.* forbs; Duru 1997) may have been underestimated in the diet to some degree. The two goose species had many forage species in common, although they were grazed in different proportions. This most probably reflects the differences in the availability and quality of forage plants during May and June in the two coastal meadows, as well as the nutritional demands of the geese in the given phases of the season. In early May, when *A. erythropus* staged in Tömppä, the diet likely was composed of plants, which were available in the scanty vegetation at that time and provided sufficient energy in an easily digestible form (Paper IV). Prop & Deerenberg (1991) suggest that the geese efficiently gather “metabolisable energy” and that this is the main determinant of dietary choice when the quality of forage plants is high (*i.e.* early in the growing season, Paper V).

High protein and low cell wall concentration have been found to be common characteristics of plant species selected by geese (*e.g.* Thomas & Prevett 1980, Sedinger & Raveling 1984, Fox *et al.* 1998, Fox & Kahlert 2003) and changes in these properties during the growing season could partly explain the observed dietary shift of *A. anser* (Paper II). *P. phryganodes* is a high quality forage plant (Ngai & Jefferies 2004) having a *ca* 1.5 times higher concentration of nitrogen in shoots than *A. stolonifera* (Niemelä & Markkola, unpublished results). For example, *P. phryganodes* is preferred by the lesser snow geese (*Chen caerulescens caerulescens*) in the salt marshes of Canada (*e.g.* Jefferies *et al.* 1979, Cargill & Jefferies 1984, Ngai & Jefferies 2004) and by *A. erythropus* in Norwegian feeding grounds (Aarvak *et al.* 1996). A related species *P. maritima* is highly preferred by moulting *A. anser* in Denmark and its high protein concentration is thought to be the main reason for this choice (Fox *et al.* 1998). Lack of *P. phryganodes* in the diet of *A. erythropus* (Paper IV) and its relatively low occurrence in the diet of *A. anser* (Paper II) may be explained by its unavailability as it is rare, especially in Tömppä. The requirement of a safe habitat (*i.e.* large open meadows with low risk of predation and human disturbance) is a decisive determinant in feeding ground selection for both moulting *A. anser* (Kahlert *et al.* 1996) and staging *A. erythropus* (Markkola *et al.* 1998), thus determining the availability of different forage plants. In this study, *A. erythropus* was clearly shown to prefer the largest coastal meadows in the area (Paper IV).

The study of forage and cattle production in the coastal meadows of Liminganlahti Bay and Hailuoto (Paper V) produced data needed in the management of the coastal meadows subject to modern grazing practices. Forage yield of the coastal meadows was approximately one fourth that of cultivated pastures in Finland (data of Valio Ltd). Furthermore, low precipitation during the growing season may considerably reduce the plant biomass of coastal meadows (de Leeuw *et al.* 1990), which may partly explain the observed yearly variation in yield in the present study. Forage quality of the coastal meadows in terms of DOM, CP and NDF was approximately at the same level as that in cultivated fields (data of Valio Ltd). However, concentration of some nutrients was at a lower level (K, P) while other elements were present in excess in the vegetation (Na, Fe, Mn) compared to the amounts in cultivated grasses (MTT 2006). While the forage quality clearly decreased during the summer in non-grazed vegetation in the present study, no significant decrease was found in the quality of grazed vegetation in an Estonian coastal meadow reflecting the renewing effect of grazing via re-growth of vegetation (Köster *et al.* 2005).

The daily live weight gain of the crossbred beef calves averaged 1 kg day^{-1} during the grazing season in the four studied coastal meadows of the Bothnian

Bay (Paper V). Considerably higher growth rates (*ca* 1.3–1.5 kg day^{-1}) have been measured for several types of crossbred beef calves in feeding experiments in cultivated grasslands (Manninen & Huhta 2001, Manninen *et al.* 2005). However, comparison of the animals in the present study to the beef calves in northern Finland, in general, showed no significant difference in live weight gain per day. Similarly, Virkajärvi (1999) found no differences in the performance of nursing beef calves reared in an extensive forest-meadow pasture compared to calves reared in an intensively managed pasture. Comparison of the live weight of the calves indicated that the *Simmental* breed might be better adapted to the coastal meadows than the *Limousin* breed. Smaller-sized beef breeds such as *Hereford* or *Aberdeen angus* might be better adapted to less productive grasslands, as they are more effective in use of forage compared with larger breeds (Estermann *et al.* 2002). For the same reasons, various landrace breeds may be better suited to manage semi-natural grasslands as supported by recent studies (Rook *et al.* 2004, Sæther *et al.* 2006, Hessle *et al.* 2008).

4.4 Adjusting various goals and methods in management

Conservation of rare or threatened habitat types and their species, as well as maintenance of valuable cultural landscapes, is the rationale for the present management of semi-natural grasslands (Salminen & Kekäläinen 2000, Alanen & Pykälä 2004, Isselstein *et al.* 2005). The precise objectives vary depending on local features, for example, presence of species requiring special protection. Habitat demands of a single species and species groups may differ greatly, which has to be taken into account in planning management practices. In general, plant species richness requires more intensive management than maintaining the species richness of insects (*e.g.* Andresen *et al.* 1990, Pöyry *et al.* 2006). For example, Bakker (1985) found that many halophytic plant species were more abundant in grazed than in mown (less disturbed) coastal meadows because grazing creates bare soil allowing the establishment of species.

While mowing was shown to be an effective management method for *A. fulva* and *P. nutans* (III), grazing by livestock may be more suitable for the habitat management for *P. phryganodes*, especially as former occurrences of the species were known to be concentrated in exposed salty sediments created by livestock grazing (Siira & Haapala 1969, Siira & Merilä 1985). In addition, mowing was found to be ineffective in preventing a decrease of *P. phryganodes* at Tauvo (Paper III). Moreover, mowing of upper shore meadows with closed canopies by using a high cutting height and leaving cut vegetation on the meadow, did not create open habitats suitable for the species in either Isomatala or in Tömppä (personal observation). Furthermore, tractor mowing has been ineffective in preventing the spread of taller vegetation in relatively open vegetation of Tauvo (Markkola 2007).

Many waterfowl species, such as geese, and waders prefer intensively grazed coastal meadows, which provide suitable feeding and breeding sites (Mikkola-Roos 1995, Vulink 2001, Pessa *et al.* 2006). For example, *A. erythropus* was found to increasingly stage on coastal meadows grazed by cattle instead of utilising the Tömppä meadow, which was managed by mowing (Markkola 2001). This change in the preference of staging grounds coincided with the establishment of many new coastal meadow pastures in the 1990's. However, later successional species, *P. australis*, was a preferred forage plant for both *A. erythropus* and *A. anser* in spring. Therefore, maintenance of lightly managed meadows with sparse and low-growth *P. australis,* in addition to more intensively managed meadows, could be the optimal habitat management practice for the geese.

In the management of the overall biodiversity of grasslands, a moderate density of grazing animals has usually been found to be the best choice, as suggested by the intermediate disturbance hypothesis (Connell 1978), because it results in a mosaic of vegetation with varying grazing intensity, providing suitable habitats for a variety of species (*e.g.* Zeevalking & Fresco 1977, Andresen *et al.* 1990, Kleyer *et al.* 2003). However, a variety of management practices should be performed, varying in space and time, especially when there is a need to fulfil specialised habitat requirements of some threatened species or species groups (Jutila 1999, Salminen & Kekäläinen 2000, Alanen & Pykälä 2004, Pöyry *et al.* 2006).

Previous management practices and their distribution at various spatial and time scales may have a considerable impact on the observed plant species diversity and its response to current management (Gustavsson *et al.* 2007). The ecological conditions created by current methods may differ considerably from those sustained by traditional practices, and therefore support a different kind of species assemblage (Gustavsson 2007). If the amount of suitable habitats has decreased to a low level, as the situation often is with semi-natural grasslands, use of appropriate methods in target areas is not always enough. Additional measures, such as management of surrounding areas and adding dispersal propagules from a regional species pool, may be required in order to maintain desired plant species diversity (*e.g.* Norderhaug *et al.* 2000, Hellström *et al.* 2006).

Results of Paper V allow some conclusions concerning the present grazing practices in coastal meadows. First, in meadows where tall-growth species, especially *P. australis*, were already largely suppressed, grazing pressure as low as 0.4 adults of beef cattle ha^{-1} was found to result in the desired low height of vegetation. Hence, the recommendation of 0.5–1.0 suckler cows ha^{-1} for coastal meadows (Decree 14.11.2000/106 of the Finnish Ministry of Agriculture and Forestry) may be too high in some cases. In contrast, in the restoration phase higher cattle densities may be required to reduce the dominance of tall-growth species (*e.g.* Kleyer *et al.* 2003, Niemelä *et al.* 2006b). To ensure the welfare of cattle, mean height of vegetation should not decline much below 10 cm, otherwise growth of cattle may suffer considerably (Spörndly *et al.* 2000, Vehkaoja *et al.* 2005).

Second, delaying the start of the grazing season from early June until mid-June on the coastal pastures of the Bothnian Bay would probably improve both the breeding success of many bird species (Pessa *et al.* 2006) as well as the performance of cattle because of better availability of forage (Paper V). However, in order to ensure the availability of sufficient high quality of forage, a later start of the grazing season is not recommended, and in areas dominated by *P. australis* grazing should be started early in June (Niemelä *et al.* 2006b).

The third conclusion from Paper V is that supplemental feeding, which has been shown to improve the pre-weaning weight gain of nursing beef calves (*e.g.* Jensen *et al.* 1999, Gelvin *et al.* 2004), does not create a significant eutrophication risk for coastal meadows according to a calculated nutrient budget. Additional minerals, which are allowed to be given to grazing animals on semi-natural grasslands, were shown to create a much higher risk of eutrophication. Authorisation of supplemental feeding of beef calves is requested by farmers especially during the late grazing season when the quality and availability of forage of coastal meadows are considered to be too low to fulfil the demands of the grazing animals (Lumijärvi *et al.* 2002). However, the implementation of supplemental feeding was found to be problematic on the large coastal meadows. For example, the availability of supplement may be difficult to control because the calves may follow cows far away from the feeder. The actual economic benefits of the realisation of supplemental feeding require further research.

4.5 Future prospects

In the future, global climate change is predicted to cause many problems in the functioning of ecosystems. One of the main risks regarding the coastal habitats, is the rise of sea water level, which is expected to partially counteract the effect of land uplift (Johansson *et al.* 2004). This may reduce the relative rate of the emergence of virgin soil and thus narrow successional zones creating a serious threat for low-growth plant species dependent on competition-free space. In addition, extreme weather events, such as storms, are predicted to become more common in the Baltic Sea under changing climate conditions (Haanpää *et al.* 2006). Increased flooding may reduce soil salinity on the coast of the low-saline Bothnian Bay leading to poorer conditions for halophytic plant species such as *P. phryganodes*. More glycophilous species with a good ability to tolerate flooding, for example *P. australis* (Gries *et al.* 1990) and *A. stolonifera* (Lenssen *et al.* 2004), may in turn benefit from moister and less saline conditions at the expense of subordinate species. Higher levels of disturbance may encourage establishment of low-growth plant species by increasing gaps in existing vegetation, but it may also have a negative impact as local small populations of rare plant species may experience a higher risk of extinction. Thus, the severe decline of the populations of *P. phryganodes* and *A. fulva* in the beginning of 21st century (Markkola 2007, Rautiainen *et al.* 2007) reflects both the ongoing deterioration of the habitats as well as the susceptibility of these rare species to disturbances.

Sufficient intensive management of the upper part of the shore is likely to be increasingly important in the future in order to maintain the diversity of low-growth coastal meadows vegetation. For example, cattle grazing may create suitable open patches for early successional plant species in extant vegetation (*e.g.* Tyler 1969a, Siira 1970, Bakker 1985), thus extending their living space. Fortunately, management of coastal meadows in the Bothnian Bay has considerably increased with the aid of EU agri-environmental subsidies (Paper V). However, there is still a scarcity of information about the impacts of modern grazing practices on semi-natural grasslands. For example, more knowledge is needed regarding the effects of beef cattle grazing on coastal meadows (Schulman *et al.* 2008).

Results of the management of the coastal meadows by cattle grazing in the Bothnian Bay have been promising for the conservation of both vegetation (Hägg *et al.* 2006) and avifauna (Pessa *et al.* 2006). For example, the occurrence of *P. nutans* has increased in some coastal meadows and it has also appeared in some new areas managed by grazing (Hägg *et al.* 2006). Nevertheless, additional conservation measures are needed especially for *P. phryganodes* and *A. fulva*, which have relatively weak dispersal ability due to lack of seed production. In addition to the efficient habitat management of the extant populations, availability of suitable habitat especially in close vicinity of the present and recently disappeared occurrences of the species should be inventoried and their area increased when necessary. Transfer of plant propagules to favourable growing sites could significantly aid the survival of these species in the flora of the Bothnian Bay. Even though earlier populations of *P. phryganodes* originating from transplanted individuals evidently have not survived until today (Siira & Merilä 1997, Siira, unpublished, Markkola 2007), the trials have produced encouraging and valuable information stressing the importance of continuous management of the habitats.

5 Conclusions

Coastal meadows and many species found there have become threatened after the traditional use of semi-natural meadows decreased during the past century. In the Bothnian Bay, a combination of many special features brings additional value to coastal meadows making them unique worldwide. Consequently, management of these habitats is important for maintaining biodiversity and landscape. In order to effectively manage coastal meadows a thorough understanding of natural and human-induced processes affecting this habitat type is needed.

In the present study, the impact of various biotic interactions on the critically endangered plant *Puccinellia phryganodes* was expored in detail for the first time in one of its rare occurrences in the boreal vegetation zone in Europe. The effect of plant parasitism on the species has not been studied earlier. *P. phryganodes* was found to suffer severely from competition with other graminoids. Simulated and actual grazing by greylag goose, *Anser anser*, as well as infection by a hemiparasitic plant *Odontites litoralis* were found to indirectly benefit *P. phryganodes* by decreasing the competitive advantage of neighbouring plants. Grazing by geese also improved the performance of small forbs and tended to increase plant species diversity.

In spite of the relatively intensive grazing by greylag goose in the field, *P. phryganodes* experienced a drastic decrease over four years in grazed experimental quadrats and the proportion of taller graminoids increased substantially. The coastal meadow ecosystem progressively shifted from top-down control by herbivores to bottom-up control by taller vegetation along the succession gradient. The present findings emphasise the importance of conducting field experiments at various successional stages when exploring the impacts of various biotic interactions. The results indicate that primary succession of vegetation may progress very rapidly on shores with low topography, such as in the Bothnian Bay. Therefore, the continuous formation of suitable open habitat for subordinate species is critical. All processes increasing the openness of vegetation, including herbivory and plant parasitism, may play a significant role in the maintenance of plant species diversity in these coastal meadows.

Management of semi-natural grasslands should be based on well-defined objectives that are achieved using economically and ecologically sound and feasible methods. Depending on the area, precise targets may vary at the landscape, habitat and species levels. In the Bothnian Bay, conservation of rare habitats and species are central items to be considered in management of coastal meadows. The studied plant species benefited to some extent from different of management practices. For example, while mowing was shown to be an effective management method for the threatened plant species *Arctophila fulva* and *Primula nutans*, *P. phryganodes* was predicted to benefit more from livestock grazing, which more effectively creates the open space required by this small graminoid.

The critically endangered lesser white-fronted goose, *Anser erythropus*, prefers large coastal meadows where the risk of predation and human disturbance is low. Avoidance of disturbance is important in habitat selection for both *A. erythropus* as well as moulting *A. anser*. Therefore, all management practices that create open low-growth meadows improve habitat quality. The present study provides new information about the diet selection of *A. erythropus*. To promote the availability of preferred dietary plants, maintenance of both lightly and rather intensively managed meadows would be optimal habitat management for the geese. Considering the different habitat requirements of the many valuable species of Bothnian Bay coastal meadows, differing management practices are needed, varying in space and time.

It is important to ensure the economic sustainability of management for the farmers, who in practice carry out most of the management work in the coastal meadows. Relatively low and variable yields of coastal meadow vegetation sets limits on how different management practices using cattle grazing can be implemented without risking the welfare of the grazing animals. Key factors for both biodiversity management and livestock performance in coastal meadows are timing of the grazing season, density of grazing animals and selection of suitable types of hebivores.

In the future, relative sea level rise induced by climate change is likely to narrow the natural early successional vegetation zone in coastal meadows. Consequently, maintenance of the valuable low-growth vegetation may be increasingly dependent on effective management that includes the upper part of the shore. For example, cattle grazing may create suitable open patches for inferior light competitors in the middle of extant vegetation. Fortunately, management of coastal meadows has considerably increased due to the aid of EU agri-environmental subsidies. Additionally, the outcome of coastal meadow management using cattle has been promising. However, there is still a scarcity of information concerning the impacts of modern grazing practices on the nature of semi-natural grasslands. Furthermore, survival of the critically endangered *P. phryganodes* and *A. fulva*, as members of the flora of the Bothnian Bay, require intensified management of the existing populations by enhancing the availability of suitable habitats and possibly aiding their dispersal by transplantation to favourable growing sites.

References

Aarvak T, Øien IJ & Nagy S (1996) The lesser white-fronted goose monitoring programme. Annual Report 1996. Norwegian Ornithological Society. Klæbu. NOF Repportserie. Report No. 7–1996.

Adam P (1993) Salt marsh ecology. Cambridge University Press, Cambridge.

Alanen A & Pykälä J (2004) Perinnebiotooppien hoito. In Tiainen J, Kuussaari M, Laurila IP & Toivonen T (eds) Elämää pellossa – Suomen maatalousympäristön monimuotoisuus. Edita Publishing Oy, Helsinki: 276–289.

Andresen H, Bakker JP, Brongers M, Heydemann B, Irmler U (1990) Long-term changes of salt marsh communities by cattle grazing. Vegetatio 89: 137–148.

Arvola P (2003) Hoidon merkitys uhanalaisille merenrantaniittykasveille Perämeren rannikolla. MSc. thesis, Univ Oulu, Dept Biology.

Autti M (1993) Perämeren niittyrantojen kasvillisuuden luokittelu ja luonnonsuojeluarvojen määrittäminen. MSc. thesis, Univ Oulu, Dept Biology.

Bakker JP (1985) The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. Vegetatio 62: 391–398.

Bakker JP, Esselink P, van der Wal R & Dijkema KS (1997) Options for restoration and management of coastal salt marshes in Europe. In Urbanska KM, Webb NR & Edwards PJ (eds) Restoration ecology and sustainable development. Cambridge University Press, Cambridge: 286–322.

Bardgett RD, Smith RS, Shiel RS, Peacock S, Simkin JM, Quirk H & Hobbs PJ (2006) Parasitic plants indirectly regulate belowground properties in grassland ecosystems. Nature 439: 969–972.

Bazely DR & Jefferies RL (1986) Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. J Ecol 74: 693–706.

Begon M, Harper JL & Townsend CR (1996) Ecology. Blacwell Science Ltd, Oxford.

Bertness MD (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72: 125–137.

Bhadresa R (1986) Faecal analysis and exclosure studies. In Moore PD & Chapman SB (eds) Methods of plant ecology. Blackwell Science, Oxford: 61–71.

BirdLife International (2008a) Species factsheet: *Anser erythropus*. URI: http://www.birdlife.org. Cited 2008/07/06.

BirdLife International (2008b) The BirdLife checklist of the birds of the world, with conservation status and taxonomic sources. Version 1. URI: http://www.birdlife.org/datazone/species/downloads/BirdLife_Checklist_Version_1.zip.

Bockelmann A-C & Neuhaus R (1999) Competitive exclusion of *Elymus athericus* from a high-stress habitat in a European salt marsh. J Ecol 87: 503–513.

Brewer JS, Rand T, Levine JM & Bertness MD (1998) Biomass allocation, clonal dispersal, and competitive success in three salt marsh plants. Oikos 82: 347–353.

Bridle JR & Vines RH (2006) Limits to evolution at range margins: when and why does adaptation fail? TREE 22: 140–147.

Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen A-C & Elven R (2004) Polyploidy in arctic plants. Biol J Lin Soc 82: 521–536.

Callaway RM & Pennings SC (1998) Impact of parasitic plant on the zonation of two salt marsh perennials. Oecologia 114: 100–105.

Cargill SM & Jefferies RL (1984) The effect of grazing by lesser snow-geese on the vegetation of a sub-arctic salt marsh. J Appl Ecol 21: 669–686.

Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297–1304.

Chou R, Vardy C & Jefferies RL (1992) Establishment from leaves and other plant fragments produced by the foraging activities of geese. Funct Ecol 6: 297–301.

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cooch EG, Lank DB, Rockwell RF & Cooke F (1991) Long-term decline in body size in a snow goose population: evidence of environmental degradation? J Anim Ecol 60: 483–496.

Crain CM, Silliman BR, Bertness SL & Bertness MD (2004) Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85: 2539–2549.

Cramer W & Hytteborn H (1987) The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore. Vegetatio 69: 157–167.

Crawford RMM (2008) Plants at the margin. Ecological limits and climate change. Cambridge University Press, Cambridge.

Crawley MJ (1997) The structure of plant communities. In Crawley MJ (ed) Plant Ecology, Wiley-Blackwell: 475–531.

Davies DM, Graves JD, Elias CO, & Williams PJ (1997) The impact of *Rhinanthus* spp. on sward productivity and composition: implications for the restoration of species-rich grasslands. Biol Conserv 82: 87–93.

de Leeuw J, Olff H & Bakker JP (1990) Year-to-year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and inundation frequency. Aq Bot 36: 139–151.

Degerman-Fyrsten A (2001) Uhanalaisen heterostylisen ruijanesikon (*Primula nutans* var. *jokelae*) lisääntymisbiologia. MSc thesis. Univ Oulu, Dept Biology.

Dijkema KS (1990) Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: their development and management. Biol Conserv 51: 191–209.

Dixon PM (1993) The bootstrap and the jackknife: describing the precision of ecological indices. In Scheiner SM & Gurevitch J (eds) Design and analysis of ecological experiments. Chapman & Hall, New York: 290–318.

Duru M (1997) Leaf and stem in vitro digestibility for grasses and dicotyledons of meadow plant communities in spring. J Sci Foog Agric 74: 175–185.

Ecke F & Rydin H (2000) Succession on a land uplift coast in relation to plant strategy theory. Ann Bot Fennici 37: 163–171.

Efron B & Tibshirani RJ (1993) An introduction to the bootstrap. Monographs on statistics and applied probability 57. Chapman & Hall, New York.

Elven R (ed) (2007) Checklist of the Panarctic Flora (PAF) Vascular Plants. Version May 2007, URI: http://www.binran.ru/infsys/paflist/index.htm.

Emery NC, Ewanchuk PJ & Bertness MD (2001) Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. Ecology 82: 2471–2485.

Ericson L (1980) The downward migration of plants on a rising Bothnian sea-shore. Acta Phytogeogr Suec 68: 61–72.

Ericson L (1981) Aspects of the shore vegetation of the Gulf of Bothnia. Wahlenbergia 7: 45–60.

Ericson L & Wallentinus H-C (1979) Sea-shore vegetation around the Gulf of Bothnia. Guide for the International Society of Vegetation Science, July-August 1977. Wahlenbergia 5: 1–142.

Esselink P, Helder GJF, Aerts BA & Gerdes K (1997) The impact of grubbing by Greylag Goose (*Anser anser*) on the vegetation dynamics of a tidal marsh. Aquatic Botany 55: 261–279.

Estermann BL, Sutter F, Schlegel PO, Erdin D, Wettstein H-R & Kreuzer M (2002) Effect of calf age and dam breed on intake, energy expenditure, and excretion of nitrogen, phosphorus, and methane of beef cows with calves. J Anim Sci 80: 1124–1134.

Ewanchuk PJ & Bertness MD (2003) Recovery of a northern New England salt marsh plant community from winter icing. Oecologia 136: 616–626.

Finnish Environment Institute (2008) Table of distribution and area estimates of coastal meadows in Finland. Background data for the assessment of threatened habitat types in Finland (compiled by the expert group of traditional rural biotopes). Unpublished.

Fox AD & Kahlert J (2003) Repeated grazing of a salt marsh grass by moulting graylag geese *Anser anser* – does sequential harvesting optimize biomass or protein gain? J Avian Biol 34: 89–96.

Fox AD, Kahlert J & Ettrup H (1998) Diet and habitat use of moulting Greylag Geese *Anser anser* on the Danish island of Saltholm. Ibis 140: 676–683.

Franzén J & Lehtomaa L (2005) Luonnon monimuotoisuuden säilyttäminen ja hoito – näkökulmia yrittäjyyteen. Lounais-Suomen ympäristökeskuksen moniste 11/2005. Lounais-Suomen ympäristökeskus, Turku.

Funk DW, Noel LE & Freedman AH (2004) Environmental gradients, plant distribution, and species richness in arctic salt marsh near Prudhoe Bay, Alaska. Wetlands Ecol Manage 12: 215–233.

Futuyama DJ (1998) Evolutionary biology. Sinauer Associates, Inc., Massachusetts.

Gelvin AA, Lardy GP, Soto-Navarro SA, Landblom DG & Caton JS (2004) Effect of field pea-based creep feed on intake, digestibility, ruminal fermentation, and performance by nursing calves grazing native range in western North Dakota. J Anim Sci 82: 3589–3599.

Gibson CC & Watkinson AR (1992) The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. Oecologia 89: 62–68.

Goméz JM (1994) Importance of direct and indirect effects in the interaction between a parasitic angiosperm (*Cuscuta epithymium*) and its host plant (*Hormatophylla spinosa*). Oikos 71: 97–106.

Grewell BJ (2008) Parasite facilitates plant species coexistence in a coastal wetland. Ecology 89: 1481–1488.
Gries C, Kappen L & Lösch R (1990) Mechanism of flood tolerance in reed, *Phragmites australis* (Cav.) Trin. ex Steudel. New Phytol 114: 589–593.
Gustavsson E (2007) Grassland plant diversity in relation to historical and current land use. Ph.D. thesis, Swedish Univ Agr Sci, Dept Ecology, Uppsala.
Gustavsson E, Lennartson T & Emanuelsson M (2007) Land-use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. Biol Conserv 138: 47–59.
Haanpää S, Lehtonen S, Peltonen L & Talockaite E (2006) Impacts of winter storm Gudrun of 7th – 9th January 2005 and measures taken in Baltic Sea Region. URI: http://www.astra*Äject.org/sites/download/ASTRA_WSS_report_final.pdf. Cited 2008/12/17.
Handa IT, Harmsen R & Jefferies RL (2002) Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. J Ecol 90: 86–99.
Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford.
Heath MF & Evans MI (2000) Important Bird Areas in Europe. Priority sites for conservation. Birdlife Conservation Series No. 8. Birdlife International, Cambridge.
Hellström K, Huhta A-P, Rautio P & Tuomi J (2006) Search for optimal mowing regime – slow community change in a restoration trial in northern Finland. Ann Bot Fennici 43: 338–348.
Hessle A, Rutter M & Wallin K (2008) Effect of breed, season and pasture moisture gradient on foraging behaviour in cattle on semi-natural grasslands. Appl Anim Behav Sci 111: 108–119.
Hik DS, Jefferies RL & Sinclair ARE (1992) Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. Journal of Ecology 80: 395–406.
Huisman J, Grover JP, van der Wal R & van Andel J (1999) Competition for light, plant-species replacement and herbivore abundance along productivity gradient. In Olff H, Brown VK & Drent RH (eds) Herbivores: Between Plants and Predators. Oxford, Blackwell Science: 239–269.
Hultén E (1962) The circumpolar plants I. Vascular cryptogams, conifers, monocotyledons. Kungliga Svenska Vetenskapsakademiska Handlingar (4. ser.) 8: 1–340.
Huuskonen A (ed) (2006) LUMOLAIDUN Maisemalaiduntaminen luonnon monimuotoisuuden lisääjänä – tasapaino monimuotoisuuden ja tuottavuuden välillä, Maa- ja elintarviketalous 79, Maa- ja elintarviketalouden tutkimuskeskus, Jokioinen.
Huuskonen A, Khalili H & Joki-Tokola E (2007) Effects of three different concentrate proportions and rapeseed meal supplement to grass silage on animal performance of dairy-breed bulls with TMR feeding. Livest Sci 110: 154–165.

Hägg M, Degerman A, Pessa J & Kovanen T (2006) Erilaisten hoitomenetelmien ja -käytäntöjen vaikutus Perämeren rantaniittyjen kasvillisuuteen ja maisemaan. In Huuskonen A (ed) LUMOLAIDUN Maisemalaiduntaminen luonnon monimuotoisuuden lisääjänä – tasapaino monimuotoisuuden ja tuottavuuden välillä, Maa- ja elintarviketalous 79, MTT Agrifood Research Finland, Jokioinen: 17–65.

Hämet-Ahti L, Suominen J, Ulvinen T & Uotila P (eds) (1998) Retkeilykasvio. Yliopistopaino, Helsinki.

Ihaka R & Gentleman R (1996) R: A language for data analysis and graphics. J Comp Graph Stat 5: 299–314.

Isselstein J, Jeangros B & Pavlu V (2005) Agronomic aspects of biodiversity targeted management of temperate grassland in Europe – a review. Agron Res 3: 139–151.

Jefferies RL (1977) The vegetation of salt marshes at some coastal sites in arctic North America. J Ecol 65: 661–672.

Jefferies RL & Gottlieb LD (1983) Genetic variation within and between populations of the asexual plant *Puccinellia* x *phryganodes*. Can J Bot 61: 774–779.

Jefferies RL, Jensen A & Abraham KF (1979) Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. Can J Bot 57: 1439–1450.

Jefferies RL, Klein DR & Shaver GR (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71: 193–206.

Jensen A (1985) The effects of cattle and sheep grazing on salt-marsh vegetation a Skallingen, Denmark. Vegetatio 60: 37–48.

Jensen DO, Okine E, Goonewardene LA, Erichsen-Arychuk C & Milligan D (1999) Growth response of pastured Simmental calves to a high by-pass protein creep supplement. Can J Anim Sci. 79: 557–560.

Jerling L & Andersson M (1982) Effects of selective grazing by cattle on the reproduction of *Plantago maritima*. Holarctic Ecol 5: 405–411.

Joenje W (1985) The significance of waterfowl grazing in the primary vegetation succession on embanked sandflats. Vegetatio 62: 399–406.

Johannesson K & André C (2006) Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, Baltic Sea. Mol Ecol 15: 2013–2029.

Johansson MM, Kahma KK, Boman H & Launiainen J (2004) Scenarios for the sea level on the Finnish coast. Boreal Env Res 9: 153–166.

Jutila H (1999) Vegetation and seed bank of grazed and ungrazed Baltic coastal meadows in SW Finland. Ph.D. thesis, Univ Turku, Dept Biology.

Jutila H (2001) How does grazing by cattle modify the vegetation of coastal grasslands along the Baltic Sea? Ann Bot Fennici 38: 181–200.

Kahlert J, Fox AD & Ettrup H (1996) Nocturnal feeding in moulting graylag geese *Anser anser* – an anti-predator response? Ardea 84: 15–21.

Kauppi M (1965) Laiduntamisen vaikutuksista Liminganlahden rantaniittyjen kasvillisuuteen. MSc. thesis, Univ Oulu, Dept Biology.

Kautsky L & N Kautsky N (2000) The Baltic Sea, including Bothnian Sea and Bothnian Bay. In Sheppard C (ed) Seas at the millennium, an environmental evaluation. Volume I, Regional Chapters: Europe, the Americas and West Africa. Pergamon, Elsevier Sciences, Oxford: 121–134.

Kauppila P & Bäck S (2002) The state of Finnish coastal waters in the 1990s. Ambio 31: 260–261.

Kemppainen E & Eeronheimo H (2008) Promoting conservation of vascular plants in Finland. Summing up regional negotiations intended to prioritize conservation measures and present status of the species. Reports of the Finnish Environment Institute 34/2008. Finnish Environment Institute, Helsinki. URI: http://www.ymparisto.fi /julkaisut.

Kemppainen R & Lehtomaa L (2009) Perinnebiotooppien hoidon tila ja tavoitteet. Valtakunnallinen kooste perinnebiotooppien alueellisista hoito-ohjelmista. Lounais-Suomen ympäristökeskuksen raportteja 2/2009. Lounais-Suomen ympäristökeskus, Turku.

Kleyer M, Feddersen H & Bockholt R (2003) Secondary succession on a high salt marsh at different grazing intensities. J Coast Conservat 9: 123–134.

Koivula K, Pakanen V-M, Rönkä A & Belda E-J (2008) Steep past and future population decline in an arctic wader: dynamics and viability of Baltic Temminck's stints *Calidris temminckii*. J Avian Biol 39:329–340.

Kreivi M (2009) Conservation genetics and phylogeography of endangered boreoarctic seashore plant species. Ph.D. thesis, Univ Oulu, Dept Biology.

Kreivi M, Huttunen S & Aspi J (2006) Isolation and characterization of polymorphic microsatellite markers from *Primula nutans* (Primulaceae). Molec Ecol Notes 6: 334–336.

Kreivi M, Rautiainen P, Aspi J & Hyvärinen M (2005) Genetic structure and gene flow in an endangered perennial grass, *Arctophila fulva* var. *pendulina*. Conserv Genet 6: 683–696.

Kuijper DPJ, Nijhoff DJ & Bakker JP (2004) Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecologia 141: 452–459.

Kunin WE, Vergeer P, Kenta T, Davey MP, Burke T, Woodward FI, Quick P, Mannarelli M-E, Watson-Haigh NS & Butlin R (2009) Variation at range margins across multiple spatial scales: environmental temperature, population genetics and metabolic phenotype. Proc R Soc B 276: 1495–1506.

Kuussaari M, Heliölä J, Tiainen J & Helenius J (eds) (2008) Maatalouden ympäristötuen merkitys luonnon monimuotoisuudelle ja maisemalle: MYTVAS-loppuraportti 2000–2006. Suomen ympäristö 4/2008. Suomen ympäristökeskus, Helsinki.

Kuussaari M, Hyvärinen M & Luoto M (2004) Ympäristön laatu ja populaatioiden elinvoimaisuus. In Tiainen J, Kuussaari M, Laurila IP & Toivonen T (eds) Elämää pellossa – Suomen maatalousympäristön monimuotoisuus. Edita Publishing Oy, Helsinki: 234–247.

Köster T, Kauer K & Kõlli R (2005) The grazing of livestock on coastal grasslands in Estonia. Grassland Science in Europe 10: 376–379.

Leiviskä I (1908) Über die Vegetation an die Küste des Bottnischen Meerbusens zwischen Tornio und Kokkola. Fennia 27: 1–209.

Lenssen JPM, van de Steeg HM & de Kroon H (2004) Does disturbance favour weak competitors? Mechanisms of changing plant abundance after flooding. J Veg Science 15: 305–314.

Lindberg H (1929) *Puccinellia phryganodes* (Trin.) Scribn. & Merr. vid Bottniska viken, ny för Finlands flora. Mem Soc F Fl Fenn 5: 77–78.

Loonen MJJE & Bos D (2000) Geese in the Wadden Sea: an effect of grazing on habitat preference. In: Wolff WJ, Essink K, Kellermann A & van Leeuwe (eds) Challenges to the Wadden Sea. Proceedings of the 10th International Scientific Wadden Sea Symposium, Groningen 2000. Ministry of Agriculture, Nature Management and Fisheries / University of Groningen: 107–119.

Lorentsen SH, Øien IJ, Aarvak T, von Essen L, Farago S, Markkola J, Morozov V, Syroechkovsky EE Jr & Tolvanen P (1999) Lesser white-fronted goose Anser erythropus. In Madsen J, Fox T & Cracknell J (eds) Review of goose populations wintering in the western Palearctic. Wetlands International, Cambridge, UK.

Luh Huang C-Y & Schulte EE (1985) Digestion of plant tissue for analysis by ICP emission spectrometry. Common Soil Sci Plant Anal 16: 943–958.

Lumijärvi K, Tuohimaa M & Vilppola P (2002) Erityistuet lisäävät maisemalaiduntamista – luonnonlaitumet sopivat hiehoille ja lihakarjalle. KM Vet 8: 36–39.

Lundberg C (2005) Eutrophication in the Baltic Sea. Ph.D. thesis, Environmental and Marine Biology, Department of Biology, Åbo Akademi University.

Manninen, M., Huhta, H., 2001. Influence of *pre partum* and *post partum* plane of nutrition on the performance of crossbred suckler cows and their progeny. Agricultural and Food Science in Finland 10: 3–18.

Manninen M, Virkajärvi P & Jauhiainen L (2005) Effect of whole-crop barley and oat silages on the performance of mature suckler cows and their progeny in outdoor winter feeding. Anim Feed Sci Technol 121: 227–242.

Markkola J (2001) Spring staging of lesser white-fronted geese on the Finnish Bothnian Bay coast in 2000. In Tolvanen P, Oien JJ & Ruokolainen K (eds) Fennoscandian lesser white-fronted goose conservation project report. Annual repport 2000. WWF Finland Report 13, NOF Rapportserie, Report no. 1-2001: 12–16.

Markkola J (2007) Rönsysorsimon (*Puccinellia phryganodes*) tilanne vuonna 2007. Report of the North Ostrobothnia Regional Environment Centre, Oulu.

Markkola J, Luukkonen A & Leinonen A (2004) The spring migration of the lesser white-fronted goose on Bothnian Bay coast, Finland, in 2001-2003. In Aarvak T & Timonen S (eds) Fennoscandian lesser white-fronted goose conservation project report 2001–2003. WWF Finland Report 20, Norwegian Ornithological Society NOF Rapportserie Report no. 1-2004: 14–18.

Markkola J & Merilä E (1998) Hailuodon Ison Matalan – Härkäsäikän luonnonsuojelualueen käyttö- ja hoitosuunnitelmaehdotus. Liminganlahti Life-Nature -projekti, Painotupa Ky, Oulu.

Markkola J, Merilä E & Siira J (1989) Rönsysorsimon (*Puccinellia phryganodes*) suojelusuunnitelma. Perämeren tutkimusaseman monisteita 20, Oulun yliopisto.

Markkola J, Ohtonen A & Karvonen R (1998) Spring staging areas of the lesser white-fronted goose *Anser erythropus* on Bothnian Bay coast: features of spring migration in 1997. In Tolvanen P *et al.* (eds) Finnish lesser white-fronted goose conservation project. Annual report 1997. WWF Finland Rep. 9: 9–15.

Marvier MA (1998) Parasite impacts of host communities: Plant parasitism in a California coastal prairie. Ecology 79: 2616–2623.

Mikkola-Roos M (1995) Lintuvesien kunnostus ja hoito. Metsähallituksen luonnonsuojelujulkaisuja, Sarja A 45. Metsähallitus, Helsinki.

Mikkola-Roos M & Niikkonen T (eds) (2005) Kosteikkojen kunnostuksen ja hoidon parhaat käytännöt kuudella Life-kohteella Suomessa – Life CO-OP -hankkeen tulokset. Metsähallituksen luonnonsuojelujulkaisuja, Sarja A 149. Metsähallitus, Helsinki.

MTT (2006) Rehutaulukot ja ruokintasuositukset (The Feed Tables and Feeding Recommendations 2006). Maa- ja elintarviketalous 106, MTT Agrifood Research Finland, Jokioinen.

Mulder CP (1999) Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. Perspect Plant Ecol Evol Syst 2: 29–55.

Mäkinen L & Mäkinen Y (1964) The distribution ecology, morphology and taxonomy of *Primula nutans* Georgi ssp. *finnmarchica* (Jacq.) Löve & Löve. Ann Bot Fennici 1: 273–291.

Ngai JT & Jefferies RL (2004) Nutrient limitation of plant growth and forage quality in Arctic coastal marshes. J Ecol 92: 1001–1010.

Niemelä M (1999) Kiljuhanhen (*Anser erythropus*) ravinnonvalinta ja kevätlevähdysalueen kasvillisuus. MSc. thesis, Univ Oulu, Dept Biology.

Niemelä M, Huuskonen A, Jaakola S, Nevalainen R, Kiljala J & Joki-Tokola E (2006a) Perämeren rantalaidunten eläintuotos, rehuntuotantokyky ja rehun laatu. In Huuskonen A (ed) LUMOLAIDUN Maisemalaiduntaminen luonnon monimuotoisuuden lisääjänä – tasapaino monimuotoisuuden ja tuottavuuden välillä, Maa- ja elintarviketalous 79, MTT Agrifood Research Finland, Jokioinen: 110–135.

Niemelä M, Pessa J, Hägg M, Timonen S & Huuskonen A (2006b) Ohjeita ja suosituksia rantalaidunnuksen toteuttamiseen. In Huuskonen A (ed) LUMOLAIDUN Maisemalaiduntaminen luonnon monimuotoisuuden lisääjänä – tasapaino monimuotoisuuden ja tuottavuuden välillä, Maa- ja elintarviketalous 79, MTT Agrifood Research Finland, Jokioinen: 136–142.

Norderhaug A, Ihse M & Pedersen O (2000) Biotope patterns and abundance of meadow plant species in a Norwegian rural landscape. Landscape Ecol 15: 201–218.

Olff H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ & de Munck W (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology 85: 799–814.

Owen M (1975) An assessment of faecal analysis technique in waterfowl feeding studies. J Wildl Manage 39: 271–279.

Pennings SC & Callaway RM (1992) Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73: 681–690.

Pennings SC & Callaway RM (1996) Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. Ecology 77: 1410–1419.

Pennings SC & Callaway RM (2002) Parasitic plants: Parallels and contrasts with herbivores. Oecologia 131: 479–489.

Pessa J & Anttila I (2000) Conservation of habitats and species on wetlands. A case of Liminganlahti LIFE Nature-project in Finland. The Finnish Environment 389. North Ostrobothnia Regional Environment Centre, Oulu.

Pessa J, Timonen S, Sjöholm J & Holmström H (2006) Laiduntamalla ja niittämällä hoidettujen Perämeren rantaniittyjen linnusto. In Huuskonen A (ed) LUMOLAIDUN Maisemalaiduntaminen luonnon monimuotoisuuden lisääjänä – tasapaino monimuotoisuuden ja tuottavuuden välillä, Maa- ja elintarviketalous 79, MTT Agrifood Research Finland, Jokioinen: 66–109.

Prach K, Pyšek P & Šmilauer P (1993) On the rate of succession. Oikos 66: 343–346.

Press MC & Phoenix GK (2005) Impact of parasitic plants on natural communities. New Phytol 166: 737–751.

Price PW, Westoby M, Rice B, Atsatt PR, Fritz R, Thompson JN, & Mobley K (1986) Parasite mediation in ecological interactions. Annu Rev Ecol Syst 17: 487–505.

Prop J & Deerenberg C (1991) Spring staging in brent geese *Branta bernicla*: feeding constrains and the impact of diet on the accumulation of body reserves. Oecologia 87: 19–28.

Puustinen S & Mutikainen P (2001) Host-plant-herbivore interactions: implications of host cyanogenesis. Ecology 82: 2059–2071.

Puustinen S & Salonen V (1999) The effect of host defoliation on hemiparasitic-host interactions between *Rhinanthus serotinus* and two *Poa* species. Can J Bot 77: 523–530.

Pykälä J (2007) Maintaining plant species richness by cattle grazing: mesic semi-natural grasslands as focal habitats. Ph.D. thesis, Univ Helsinki, Dept Biological and Environmental Sciences.

Pywell RF, Bullock JM, Walker KJ, Coulson SJ, Gregory SJ & Stewenson NJ (2004) Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. J Appl Ecol 41: 880–887.

Pöyry J, Luoto M, Paukkunen J, Pykälä J, Raatikainen K & Kuussaari M (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos 115: 401–412.

Rassi P, Alanen A, Kanerva T & Mannerkoski I (eds) (2001) Suomen lajien uhanalaisuus 2000. Uhanalaisten lajien II seurantatyöryhmä. (Summary: The 2000 Red List of Finnish species). Ministry of the Environment, Helsinki.

Rautiainen P, Aikio & Hyvärinen M (2007) Growth and disturbance in the spatial dynamics of an endangered seashore grass *Arctophila fulva* var. *pendulina*. Ecol Model 207: 145–154.

Rautiainen P, Laine A-L, Aikio S, Aspi J, Siira J & Hyvärinen M (2004) Seashore disturbance and management of the clonal *Arctophila fulva*: Modelling patch dynamics. Appl Veg Sci 7: 221–228.

Rook AJ, Dumont B, Isselstein J, Osoro K, WallisDeVries MF, Parente G & Mills J (2004) Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biol Conserv 119: 137–150.

Rowcliffe JM, Watkinson AR & Sutherland WJ (1998) Aggregative responses of brent geese on salt marsh and their impact on plant community dynamics. Oecologia 114: 417–426.

Ruokonen M, Kvist L, Aarvak T, Markkola J, Morozov VV, Øien IJ Syroechkovsky EE, Tolvanen P & Lumme J (2004) Population genetic structure and conservation of the lesser white-fronted goose *Anser erythropus*. Conserv genet 5: 501–512.

Ryttäri T & Kettunen T (eds) (1997) Uhanalaiset kasvimme. Suomen ympäristökeskus, Kirjayhtymä Oy, Helsinki.

Ryttäri T, Rautiainen V-P, Kemppainen E & Alanen A (2001) Putkilokasvit, In: J Ilmonen J, Ryttäri T & Alanen A (ed) Finnish plants and invertebrate animals in the EU Habitats Directive. A scientific evaluation of the Finnish Natura 2000 –proposal, The Finnish Environment 510, Finnish Environment Institute, Helsinki: 17–71.

Rönkä A (1996) Distribution, status and population trends in the Temminck's stint Calidris temminckii in the Finnish Bothnian Bay. Ornis Fenn 73: 1–11.

Salminen P & Kekäläinen H (eds) (2000) Perinnebiotooppien hoito Suomessa. Suomen ympäristö 443. Ympäristöministeriö, Helsinki.

Schulman A, Alanen A, Hæggström C-A, Huhta A-P, Jantunen J, Kekäläinen H, Lehtomaa L, Pykälä J & Vainio M (2008) Perinnebiotoopit. In Raunio A, Schulman A & Kontula T (eds) Suomen luontotyyppien uhanalaisuus – Osa 2: Luontotyyppien kuvaukset. Suomen ympäristökeskus, Helsinki. Suomen ympäristö 8/2008: 397–465.

Sedinger JS & Raveling DG (1984) Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. Auk 101: 295–306.

Siira J (1970) Studies in the ecology of the sea-shore meadows of the Bothnian Bay with special reference to the Liminka area. Aquilo Ser Bot Tom 9: 1–109.

Siira J (1984) On the vegetation and ecology of the primary saline soils of the Bothnian Bay. Aquilo Ser Bot 20: 1–13.

Siira J (1985) Saline soils and their vegetation on the coast of the Gulf of Bothnia, Finland. Ann Bot Fennici 22: 63–90.

Siira J (1994) The occurrences and ecology of *Arctophila vulva* (Poaceae) on the Liminka Bay (the Gulf of Bothnia). Aquilo Ser Bot 33: 107–120.

Siira J Rönsysorsimo (*Puccinellia phryganodes*) Suomessa vuosina 1926–2000. Manuscript.

Siira J & Haapala H (1969) Studies in the distribution and ecology of *Puccinellia phryganodes* (Trin.) Scirbn. & Merr. in Finland. Aquilo Ser Bot 8: 1–24.

Siira J & Merilä E (1985) *Puccinellia phryganodes* (Poaceae) in Finland: Occurrences and ecology up to 1983. Ann Bot Fennici 22: 281–290.

Siira J & Merilä E (1997) Rönsysorsimon esiintymät ja hoitokokeilut Suomessa vuonna 1996. Oulun yliopisto, Perämeren tutkimusaseman julkaisuja 10: 1–28.

Silliman BR and Bertness MD (2002) A trophic cascade regulates salt marsh primary production. Ecology 99: 10500–10505.

Smith D (2000) The population dynamics and community ecology of root hemiparasitic plants. Am Nat 155: 13–23.

Snogerub B (1983) Northwest European taxa of *Odontites* (Schrophulariaceae). Acta Bot Fenn 124: 1–62.

Sørensen T (1953) A revision of the Greenland species of *Puccinellia* parl. Meddelar om Grønland 136: 1–179.

Spörndly E, Olsson I & Burstedt E (2000) Grazing by steers at different sward heights on extensive pastures: a study of weight gain and fat deposition. Acta Agric Sci Sect A, Animal Sci 50: 184–192.

Srivastava DS & Jefferies RL (1996) A positive feedback: herbivory, plant growth, salinity, and the desertification of an arctic salt-marsh. J Ecol 84: 31–42.

Stampfli A (1991) Accurate determination of vegetational change in meadows by successive point quadrat analysis. Vegetatio 96: 185–194.

Strengell H (2003) Ruijanesikon populaatioekologia ja suojelu Perämeren rannikolla. MSc. thesis, Univ Oulu, Dept Biology.

Sæther NH, Sickel H, Norderhaug A, Sickel M, Vangen O (2006) Plant and vegetation preferences for one old native and one old modern Norwegian dairy cattle breed when grazing on shared semi-natural mountain pasture. Anim Res 55: 367–387.

Thomas VG & Prevett JP (1980) The nutritional value of arrow-grasses to geese at James Bay. J Wildl Manage 44: 830–836.

Tolvanen P, Aarvak T, Øien IJ & Timonen (2004) Introduction. In Aarvak T & Timonen S (eds) Fennoscandian lesser white-fronted goose conservation project report 2001-2003. WWF Finland Report 20, Norwegian Ornithological Society NOF Rapportserie Report no. 1-2004: 5–8.

Tyler G (1969a) Studies in the ecology of Baltic sea-shore meadows. II. Flora and vegetation. Opera Botanica 25: 1–101.

Tyler G (1969b) Regional aspects of Baltic shore-meadow vegetation. Plant Ecol 19: 60–86.

Ulvinen T (1997) Ruijanesikko, In Ryttäri T & Kettunen T (eds) Uhanalaiset kasvimme. Suomen ympäristökeskus, Kirjayhtymä Oy, Helsinki: 122.

Vainio M & Kekäläinen H (1997) Pohjois-Pohjanmaan perinnemaisemat. Alueelliset ympäristöjulkaisut 44. Pohjois-Pohjanmaan ympäristökeskus, Oulu.

Vainio M, Kekäläinen H, Alanen A & Pykälä J (2001) Suomen perinnebiotoopit. Perinnemaisemaprojektin valtakunnallinen loppuraportti. Suomen ympäristö 527, Suomen ympäristökeskus, Helsinki.

van der Wal R, Egas M, van der Veen A & Bakker J (2000a) Effects of resource competition and herbivory on plant performance along a natural productivity gradient. J Ecol 88: 317–330.

van der Wal R, van Lieshout S, Bos D & Drent RH (2000b) Are spring staging brent geese evicted by vegetation succession? Ecography 23: 60–69.

van der Wal R, van Wijnen H, van Wieren S, Beucher O & Bos D (2000c) On facilitation between herbivores: how brent geese profit from brown hares. Ecology 81: 969–980.

Van Eerden MR, Drent RH, Stahl J & Bakker JP (2005) Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. Global Change Biol, 11: 894–908.

Van Soest PJ 1994. Nutritional Ecology of the Ruminant. 2nd ed. Cornell University Press, Ithaca, NY.

Van Wijnen HJ & Bakker JP (2000) Annual nitrogen budget of a temperate coastal barrier salt-marsh system along a productivity gradient a low and high marsh elevation. Perspect Plant Ecol Evol Syst 3: 128–141.

Vartiainen T (1980) Succession of island vegetation in the land uplift area of the northernmost Gulf of Bothnia. Acta Bot Fenn 115: 1–105.

Vehkaoja S, Jokinen M, Herva T, Halkosaari P, Sonninen R, Eeli K & Alatalo J (2005) Suunnitelmallinen naudanlihantuotanto. AtriaNauta, Kauhava.

Virkajärvi P (1999). Suckler cows grazing on meadows and forest pastures. Forskningsnytt 2: 14–16.

Vulink JT (2001) Hungry herds. Management of temperate lowland wetlands by grazing. Ph.D. thesis, Univ Groningen, Lelystad.

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH & Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304: 1629–1633.

Wilson SD & Keddy PA (1986) Species competitive ability and position along a natural stress/disturbance gradient. Ecology 67: 1236–1242.

Zeevalking HJ & Fresco LFM (1977) Rabbit grazing and diversity in a dune area. Vegetatio 35: 193–196.

Original papers

I Niemelä M, Markkola A & Mutikainen P (2008) Modification of competition between two grass species by a hemiparasitic plant and simulated grazing. Basic and Applied Ecology 9: 117–125.

II Niemelä M, Markkola AM & Hyvärinen M (2009) Impact of goose grazing and primary succession on vegetation and threatened plant species on coastal meadows. Manuscript.

III Rautiainen P, Björnström T, Niemelä M, Arvola P, Degerman A, Erävuori L, Siikamäki P, Markkola A, Tuomi J & Hyvärinen M (2007) Management of three endangered plant species in dynamic Baltic seashore meadows. Applied Vegetation Science 10: 25–32.

IV Markkola J, Niemelä M & Rytkönen S (2003) Diet selection of lesser white-fronted geese *Anser erythropus* at a spring staging area. Ecography 26: 705–714.

V Niemelä M, Huuskonen A, Jaakola S, Joki-Tokola E & Hyvärinen M (2008) Coastal meadows as pastures for beef cattle. Agriculture, Ecosystems & Environment 124: 179–186.

Original publications are not included in the electronic version of the dissertation.

513. Laitinen, Jarmo (2008) Vegetational and landscape level responses to water level fluctuations in Finnish, mid-boreal aapa mire – aro wetland environments

514. Viljakainen, Lumi (2008) Evolutionary genetics of immunity and infection in social insects

515. Hurme, Eija (2008) Ecological knowledge towards sustainable forest management. Habitat requirements of the Siberian flying squirrel in Finland

516. Kaukonen, Risto (2008) Sulfide-poor platinum-group element deposits. A mineralogical approach with case studies and examples from the literature

517. Rokka, Aare (2008) Solute traffic across the mammalian peroxisomal membrane—the role of Pxmp2

518. Sharma, Satyan (2008) Computational Studies on Prostatic Acid Phosphatase

519. Chen, Zhijun (2008) Characterization of the 2-enoyl thioester reductase of mitochondrial fatty acid synthesis type II in mammals

520. Hilli, Anu (2009) The effect of crop quality and pre-treatment on germination in Scots pine and Norway spruce seeds

521. Kreivi, Marjut (2009) Conservation genetics and phylogeography of endangered boreoarctic seashore plant species

522. Riihijärvi, Jorma (2009) Tietojenkäsittelytieteiden koulutuksen työelämävastaavuus. Esimerkkitapauksena Oulun yliopiston tietojenkäsittelytieteiden laitoksen koulutusohjelma

523. Ilmonen, Jari (2009) Benthic macroinvertebrate and bryophyte assemblages in boreal springs: diversity, spatial patterns and conservation

524. Pujol, François (2009) Experiments on fatty acids chain elongation and glycan flipping in the ER membrane

525. Lampila, Satu (2009) The causes and consequences of population declines of two boreal forest species. The case of the willow tit (*Parus montanus*) and the Siberian flying squirrel (*Pteromys volans*)

526. Anttila, Katja (2009) Swimming muscles of wild, trained and reared fish. Aspects of contraction machinery and energy metabolism

527. Roppola, Katri (2009) Environmental applications of manometric respirometric methods

528. Arhippainen, Leena (2009) Studying user experience: issues and problems of mobile services. – Case ADAMOS: User experience (im)possible to catch?

Book orders:
OULU UNIVERSITY PRESS
P.O. Box 8200, FI-90014
University of Oulu, Finland

Distributed by
OULU UNIVERSITY LIBRARY
P.O. Box 7500, FI-90014
University of Oulu, Finland

UNIVERSITY OF OULU P.O.B. 7500 FI-90014 UNIVERSITY OF OULU FINLAND

A C T A U N I V E R S I T A T I S O U L U E N S I S

ISBN 978-951-42-9122-7 (Paperback)
ISBN 978-951-42-9123-4 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)

UNIVERSITY of OULU
OULUN YLIOPISTO