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The process of plant invasion with focus on the effects of plant disease

PhD thesis

Marianne Erneberg

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2002

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Abstract:	<p>The invasion process of non-indigenous plants is influenced by abiotic, biotic and human-mediated factors that each plays a role for the invasion success. The main aim of this project was to study the effect of pathogenic fungi on non-indigenous plants in different phases of the invasion process. Experimental studies in natural communities of three model systems, <i>Lolium perenne-Puccinia coronata</i>, <i>Brassica napus-Sclerotinia sclerotiorum</i>, and <i>Heracleum mantegazzianum-S. sclerotiorum</i>, showed that the pathogens had no effect on the plants in the establishment phase when the populations were small. The pathogens had greater impacts in large naturalised host populations. Infections by <i>P. coronata</i> resulted in increased shoot growth of <i>L. perenne</i> and indications were that shoot growth was traded-off by reproduction. Studies with <i>H. mantegazzianum</i> and <i>S. sclerotiorum</i> strongly indicated that infected plants produced smaller seeds and had a higher risk of complete reproductive failure. A second aim of the project was to study the link between plant naturalisation and mode of introduction. The results showed that the majority of naturalised plants in selected regions of the United States were likely introduced deliberately for the purpose of food and medicine production, horticulture etc.</p>		
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Preface

The work included in this Ph.D. thesis was carried out during a three-year period at Department of Terrestrial Ecology, the National Environmental Research Institute (NERI), Silkeborg; Department of Ecology, The Royal Veterinary and Agricultural University (KVL), Copenhagen; and School of Biological Sciences, Washington State University, Pullman, WA, USA. My research supervisors were Senior Scientist Beate Strandberg (NERI) and Professor Jacob Weiner (KVL). The Ph.D. project was commenced in March 1998 and interrupted for 15 months due to maternity leave. The thesis was submitted in July and defended in September 2002.

The Ph.D. project was initiated as part of an inter-disciplinary research project set up by Centre for Effects and Risks of Biotechnology in Agriculture (Theme I and II) and financed by The Strategic Environmental Research Programme. The title of the Theme II project was "Ecological effects and risks associated with the use of transgenic, disease-resistant crops". The aims were to investigate aspects of (1) the pathogenicity of two pathogenic fungi *Puccinia coronata* and *Sclerotinia sclerotiorum* on the crop plants *Lolium perenne* (perennial ryegrass), *Brassica napus* subsp. *napus* (oilseed rape) and *Daucus carota* (carrot), (2) the gene flow of the plants and the formation of possible hybrids, and (3) the effect of the fungi on the invasiveness of the plants. The three selected model plant species are widely cultivated in Denmark and genetically modified cultivars with increased disease resistance may be approved for cultivation in the future. From a risk assessment perspective it is important to gain knowledge about factors affecting the potential spread of these plant species into natural plant communities. The thesis is directed to goal (3) above: the effects of the fungi on the invasiveness of the plants. *L. perenne* and *B. napus* were used as model plants for studies of host-pathogen interactions in the early stages of plant invasion while a non-crop species, *Heracleum mantegazzianum* (giant hogweed), was included as a real invading species for host-pathogen studies in the outbreak stage. Genetically modified seed material was not used in any of the experiments described in this thesis.

I would like to thank all the people who inspired, helped and encouraged me during my project period. I highly acknowledge and thank my supervisors, Beate Strandberg and Jacob Weiner, for their supervision and encouragement in all steps of the working process. Brita Dahl Jensen patiently guided me into the world of pathogenic fungi and inspired me with her energy and enthusiasm. I am very grateful to Beate and Brita for valuable scientific discussions and for their constructive comments to my thesis. I spent six exciting months with Professor Richard Mack and his research group at Washington State University in Pullman, WA, USA. I was overwhelmed by Richard and Nancy Mack's hospitality and support, which I greatly appreciate. I would also like to thank the very skilful people in Richard Mack's research group, particularly Lynn Kinter, Robert Pattison and Mark Minton, for scientific discussions.

Most of my project work was carried out at Department of Terrestrial Ecology, NERI, and I would like to thank all my colleagues for their support and help. I am particularly indebted to Morten Strandberg for helping me in the field and for sharing his botanical knowledge with me. I am very grateful to John Rytter who provided the muscle power during the set-up of most of the experiments and to Lise Lauridsen for skilful and engaged technical assistance. Lise Lauridsen overtook part of my field activities towards the end of my pregnancy and I thank her (and her understanding family) for her flexibility.

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Summary

The invasion process of non-indigenous plants can be divided into four phases: introduction, establishment, naturalisation and outbreak. Abiotic, biotic and human-mediated factors in the recipient plant community as well as factors intrinsic to the plant determine its success in each step. A large number of propagules of new plant species is continuously being moved into new geographical ranges, but only a fraction of the species become naturalised. By studying the modes of introduction of plant species introduced into selected regions of the United States we showed that more than 50 percent of naturalized species are likely to have been introduced deliberately to produce primarily food, seasoning, medicine, forage and fibre and for landscape and gardening purposes. Post-immigration cultivation provides a possible explanation for the high naturalisation success of deliberately introduced plants. Nursing (provision of shelter, water, nutrients, pesticides) may reduce the environmental stochasticity and thereby increase the plant's probability of reaching reproductive maturity.

The impact of pathogenic fungi on plants in the establishment and naturalisation steps was studied in field experiments with the grass *Lolium perenne* and the biotrophic fungus *Puccinia coronata* causing crown rust of *L. perenne*. The fungus has a very narrow host spectrum. It is common in Denmark and is known to reduce the yield of cultivated *L. perenne*. Seeds of the species were added to plots with factorial combinations of presence and absence of soil disturbance and inoculum of the pathogen. Seed addition of *L. perenne* to two sites that did not have a prior population of the species resulted in the establishment of small populations. Generally, exposure to *P. coronata* did not result in attack in the two small, newly established populations. This suggests that this pathogen does not affect establishment of *L. perenne* upon introduction to a new area. At the site where *L. perenne* was subjected to intense competition from established plants, the population did not persist.

The pathogen developed well on large naturalised populations of *L. perenne*, but the effect of the pathogen on *L. perenne* was very different from what has been observed in agroecosystems. Infected plants were either not measurably affected or showed enhanced shoot growth in response to attack. At one of the study sites the seed to shoot ratio was decreased on infected plants, suggesting that there may be a trade-off between reproduction and shoot growth. Overall, the study showed that disease development is more severe on large naturalised plant populations than on small, newly established populations, but the level of disease development and the impact of the disease on plant performance is also site specific. The results also show that disease may have positive effects on plants in natural plant communities.

To investigate the relationships between susceptibility of *L. perenne*, attack by *P. coronata* and crown rust development, a field experiment in a simulated natural plant community was set up. Disease incidence and severity developed faster and to higher levels on susceptible than on partially resistant *L. perenne*. The disease also reached higher levels on plants grown in short than in tall vegetation. Shoot biomass was not affected by the presence of disease.

The interaction between an invasive plant species, *Heracleum mantegazzianum*, and a generalist pathogen, *Sclerotinia sclerotiorum* was studied in natural plant populations of *H. mantegazzianum* and in field experiments where seedlings were transplanted into either pathogen susceptible or resistant vegetation and exposed to sclerotia placed in the topsoil. Plants infected by windspreed ascospores developed dry lesions on the inflorescence-bearing stems, but on most of the plants the lesion development stopped early in the growth season and no significant fecundity effects were measured. When plants were infected by mycelia developed from sclerotia placed adjacent to the plants in the soil, the plants developed soft root rot, premature senescence and reduced seed size. However, due to two important plant attributes, high seed production and a long-lived seed bank, this pathogen may have no long-term effect on the plant dynamics.

Dansk resumé

Fremmede planters invasionsproces kan inddeles i fire faser: introduktion, etablering, naturalisering og udbrud. Abiotiske, biotiske og menneskeskabte faktorer i det nye plantesamfund samt karaktertræk ved planten bestemmer dens succes i hvert enkelt invasionsstadium. Store mængder af frø fra nye plantearter bliver konstant introduceret til nye geografiske områder, men kun en lille andel af arterne bliver naturaliseret. Ved at undersøge måderne hvorpå nye plantearter er blevet introduceret til udvalgte områder i USA, har vi vist at mere end 50 procent af de naturaliserede arter med stor sandsynlighed er blevet indslæbt med henblik på produktion af mad, krydderier, medicin, foder og fibre og med henblik på brug indenfor landskabsarkitektur og havebrug. At planterne er blevet dyrket og plejet efter deres immigration er en mulig forklaring på deres naturaliseringssucces. Dyrkningsfaktorer (læhegn, vand, næringstoffer, pesticider) kan reducere den miljømæssige stokasticitet og derved øge sandsynligheden for, at planten overlever til den reproduktive alder, og at arten med tiden bliver naturaliseret.

Betydningen af patogene svampe for etableringen og naturaliseringen af fremmede planter, blev undersøgt i felteksperimenter med almindelig rajgræs, *Lolium perenne*, og en biotrofe svamp *Puccinia coronata* f.sp. *lolii*. Svampen forårsager kronrust på *L. perenne* og har et meget snævert værtsspektrum. Den er almindeligt forekommende i Danmark og er kendt for at reducere udbyttet af dyrket *L. perenne*. Rajgræsfrø blev tilført forsøgsfelter med og uden henholdsvis jordforstyrrelser og svampeinokulum. Frøtilførsel til to forsøgsområder uden tilstedeværelsen af en rajgræspopulation resulterede i, at arten etablerede sig og dannede små populationer. Eksperimentel tilførsel af svampesporer medførte generelt ingen svampeangreb på de to små, nyetablerede populationer. Dette tyder på, at svampen ikke påvirker etableringen af *L. perenne* i nye udbredelsesområder. På den ene af de to forsøgslokaliteter, var *L. perenne* udsat for massiv konkurrence fra de eksisterende planter, og populationen var derfor ikke vedvarende.

På naturaliserede planter, som voksede i store populationer, udviklede svampen sig derimod godt, men svampens effekt var anderledes end det, man har observeret i dyrkede landbrugssystemer. Skudvæksten hos smittede planter blev enten øget eller ikke påvirket i forhold til planter, som ikke var smittede. På den ene forsøgslokalitet havde inficerede planter en reduceret frøbiomasse i forhold til skudbiomasse, hvilket tyder på, at der er en "trade-off" mellem den biomasse, som allokeres til henholdsvis reproduktion og skudvækst. Samlet viste undersøgelsen, at sygdomsniveauet var højere i store, naturaliserede populationer end i små, nyetablerede populationer. Desuden viste resultaterne, at plantesygdomme kan have en positiv påvirkning på planter i naturlige plantesamfund.

Med henblik på at undersøge forholdet mellem *L. perenne*'s modtagelighed overfor *P. coronata*, svampens angrebsrate og sygdomsudviklingen, udførtes et feltforsøg i et simuleret naturligt plantesamfund. Sygdomsudviklingen, der var baseret på frekvensopgørelser (incidence) og dækningsgrader (severity), var hurtigere og opnåede et højere niveau på modtagelige planter end på delvis resistente planter. Desuden blev sygdomsudviklingen yderligt forstærket, når vegetationshøjden blev reduceret. Skudbiomassen blev ikke påvirket af tilstedeværelsen af sygdom.

Sammenspillet mellem en invasiv planteart, *H. mantegazzianum* (kæmpe-bjørneklo), og en patogen svamp med et bredt værtsspektrum, *Sclerotinia sclerotiorum*, blev undersøgt i naturlige *H. mantegazzianum* populationer samt i felteksperimenter, hvor planter voksede i vegetation, som var enten modtagelig eller resistent overfor svampen. Svampesklerotier blev placeret i jorden, hvor de dannede to typer af inokulum: apothecier med ascosporer eller mycelium i jorden. Planter, der blev smittet af vindspredte ascosporer, udviklede tørre læsioner på blomsterstandsstænglen, men på hovedparten af planterne gik sygdomsudviklingen i stå tidligt i vækstsæsonen, og der var ingen målbar reduktion af planternes fekunditet. Andre planter blev smittet via svampemycelium i jorden. Disse planter udviklede råd i roden, tidlig ældning og dannede mindre frø. På trods af dette, har *P. coronata* ikke nødvendigvis har en langtidseffekt på *H. mantegazzianum*'s populationsdynamik pga. plantens store frøproduktion og opbyggelsen af en langvarig frøbank.

Objectives and structure of the thesis

The overall objective of this thesis is to study and discuss how plant disease may affect non-indigenous plants in different phases of the invasion process. The process of plant invasion can be divided into the introduction, establishment, naturalisation and outbreak steps. When a plant species advances from one step to another its population structure changes (e.g. plant density and population size), and this may have profound effects on the interaction between the plant species and the surrounding community such as host-parasite interactions. Our understanding of host-parasite interactions in natural plant communities is still not well developed (Burdon 1987), and apart from the literature on biological control, evidence of the possible effects of parasites on the process of plant invasion is almost non-existent.

The introduction of propagules (seeds, rhizomes) to a new area is the first step in the invasion process of non-indigenous plants. Anthropogenic factors may strongly influence the spread of species to new areas and the probability of subsequent establishment and naturalisation may be tightly linked to the mode of introduction and post-immigration conditions such as cultivation. These issues are discussed in a literature study in Paper A.

According to the "biotic resistance hypothesis", biotic factors such as native plant competitors, herbivores, and parasites (e.g. bacteria, virus, fungi, protozoans) may hinder establishment or naturalisation of new plant species (Crawley 1987, Mack 1996, Maron & Vila 2001). The importance of pathogenic fungi on plants in the establishment phase is studied in paper C and D for two model systems: *Lolium perenne*-*Puccinia coronata* and *Brassica napus*-*Sclerotinia sclerotiorum*. *S. sclerotiorum* failed to establish at the experimental sites with *B. napus* so paper D, which will not be submitted for publication, sums up the rather limited results that can be extracted from this study by discussing seed and microsite limitation of *B. napus* in Danish grassland ecosystems.

S. sclerotiorum and *P. coronata* may severely reduce plant productivity of their hosts in agroecosystems (Simons 1970, Purdy 1979), and it is tempting to assume that they have a similar effect on hosts which have escaped from cultivation and naturalised in natural plant communities. However, agroecosystems are relatively simple ecosystems, and the greater variation of environmental factors in natural ecosystems may strongly affect the outcome of the host-pathogen interactions. For example, the varying height of neighbouring plants in natural communities may affect the dissemination of spores and thus disease development. The degree of disease susceptibility and genotypic variation within a population of naturalised plants may also play a role for disease development and the subsequent effect on host performance in natural ecosystems. Plants with a high level of resistance to a certain pathogen may potentially experience ecological release and become more

competitive in natural communities than individuals with a high level of susceptibility. These aspects were studied in paper B and C with an approach that integrates the biology of both the host and the pathogen.

It seems intuitive that non-indigenous plants that become invasive in a new range are either little affected by the prevailing pathogens or may be able to escape from the pathogens in some areas of its new range, but experimental evidence is lacking. Results on the pathogen spread, disease development and the effect of *S. sclerotiorum* attack on the performance of the invasive plant *H. mantegazzianum* are reported in paper E.

The thesis consists of a synopsis and five papers (A-E). Literature relevant to the topic is presented in the synopsis and results obtained in the five papers are integrated and discussed. All papers except Paper A are based on experimental studies. Paper A is published in *Annals of the Missouri Botanical Garden* (vol. 89, 2002). It is included in the thesis as the page proofs. Paper B and C are under preparation for submission in international refereed journals. Paper E has been accepted for publication with minor revisions in the refereed proceeding from the 6th International Conference on the Ecology and Management of Alien Plant Invasions (EMAPi). The present version of Paper E is the revised version.

1 Synopsis

1.1 Introduction

During the last 100 years the number of naturalised non-indigenous plant species has rapidly escalated primarily due to the increased deliberate and accidental transport of plant propagules by humans in most regions of the world (Sykora 1990, Rejmánek & Randall 1994, Mack & Lonsdale 2001, Pimentel *et al.* 2001, Paper A). This escalation and the associated environmental and economical problems have raised awareness and concern among scientists, management practitioners, conservationists, politicians and the general public (e.g. Ruesink *et al.* 1995, Hindar 1999, Weidema 2000, Mack & Lonsdale 2001, Pimentel *et al.* 2001, Reichard & White 2001).

Perspectives on alien species are strongly biased by economic and environmental interests. Large numbers of plant species are deliberately transported across borders for the purpose of agriculture, horticulture, medicine, food and fodder and "hitch-hiking" plant species are accidentally introduced with them (e.g. Sykora 1990, Mack 1991, Mack & Lonsdale 2001, Reichard & White 2001, Paper A). Most of these introduced species fail to establish due to unfavourable environmental conditions (Mack 1996) and in every step of the invasion process the number of species is progressively reduced (Williamson & Fitter 1996). However, those species that successfully establish and spread in new ranges may have great impact and cause many environmental and economic problems. For example, non-indigenous plants, animals, and microbes are believed to be among the greatest causes of loss in native biodiversity (D'Antonio & Vitousek 1992, Wilcove *et al.* 1998). One total estimate of the economic losses alien species inflict in the United States, United Kingdom, Australia, South Africa, India and Brazil is more than 314 billion US dollars per year (Pimentel *et al.* 2001). This estimate includes costs related to the introduction of non-indigenous organisms causing livestock and human diseases, losses in crop systems, and environmental damages. Eliminating all introductions of alien species is neither a feasible nor a desirable goal for the global human society, however. A more meaningful and realistic goal is to obtain efficient control of deliberately introduced species and prevent accidental introductions (Weidema 2000) by developing efficient methods for risk assessment and early detection of problematic alien species (Kolar & Lodge 2001). In order to reach these goals, information about alien species and the factors influencing their invasion process must be gathered, and experiments and monitoring must be carried out to fill out the large gaps in our knowledge.

1.1.1 The invasion process of plants

The invasion process of plants has intensively been described and discussed among researchers, and various sub-divisions of the process have been proposed (di Castri 1989, Williamson 1989, Kornas

1990, Williamson & Fitter 1996). A recently developed model of the idealised plant invasion (Heger 2001) is appealing in its approach because of its logical sub-division of the process and because it distinguishes between the stages in the plant invasion and the steps (processes) leading to each stage (Figure 1). The first step is immigration, in which propagules of the species are deliberately or accidentally introduced to a new area (stage 1). If at least one propagule is able to grow and reproduce unaided by humans, the species is defined as being spontaneously established (stage 2). Some species are able to form a population and if the population reaches a minimum viable population size (MVP), it is more resistant to environmental, demographic, and genetic stochastic forces, and is described as being permanently established (stage 3). Some of the permanently established plant species are able to spread into new localities of the new range (stage 4).

There is not yet agreement among researchers on the terminology for describing the status of non-indigenous plants and the steps in the invasion process (Richardson *et al.* 2000). In the present context I will use the terms *introduction*, *establishment*, *naturalisation* and *outbreak/invasion* for the steps in invasion (step 1-4 *sensu* Heger) and the terms *introduced*, *established*, *naturalised* and *invasive* for describing the status of the plant species (stage 1-4 *sensu* Heger). These terms closely correspond to those used by most plant invasion biologists (for discussion see Richardson *et al.* 2000). The terms *non-indigenous* and *alien* are used interchangeably to describe plants that occur in areas outside of their place of origin.

The number of plant species in the different stages of the invasion process is progressively reduced. Based on empirical studies of British plants, Williamson & Fitter (1996) proposed the "tens rule" stating that approximately ten percent of the species proceed from one stage in the invasion process to the next. Other researchers have

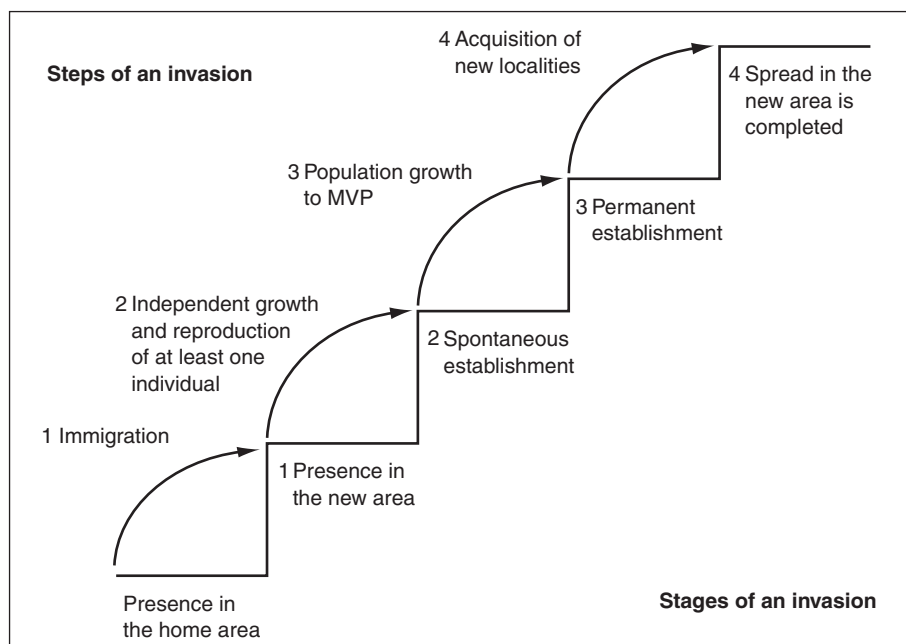


Figure 1. Steps and stages in the invasion process of plants. MVP: minimum viable population size. (Heger 2001).

suggested percentages of varying magnitudes (Crawley 1987, di Castri 1989). However, since we will never know the exact number of species that has arrived to a new area and failed, and since some plant species may establish and perish without being noticed, such estimates must be considered with caution.

1.1.2 Factors influencing the invasion process

A number of biotic, abiotic and human-mediated factors may affect the process of invasion. Some factors may facilitate invasion (Weiss & Milton 1984, Fox & Fox 1986, Burke & Grime 1996, Mack 2000, Paper A), whereas other factors may slow it down or even prevent invasion (Mack 1996, Richardson *et al.* 2000). The factors may have different effects depending on their scale and frequency. Furthermore, the relative importance of these factors may change during the process of invasion.

Geographic barriers such as oceans and mountains are the first barriers that limit the introduction of new species. Subsequent barriers that act after the introduction event are abiotic and biotic (Richardson *et al.* 2000). They may hinder establishment or naturalisation of new species at the site of introduction or may hinder the species from spreading into new areas. Important abiotic factors are photoperiod, temperature, toxic or deficient levels of nutrients and drought. Examples of biotic barriers that may hinder naturalisation or reduce plant performance in the new range ("biotic resistance") are herbivores, parasites (e.g. bacteria, virus, fungi, protozoans), and plant competitors (Crawley 1987, Mack 1996, Maron & Vila 2001). Among these factors, the interaction between parasites and non-indigenous hosts seem to have received the least attention from ecologists. It may none-the-less play an important role for the distribution and abundance of plants world-wide (Mack 1996).

Several factors may also promote plant invasions. Natural and human-mediated disturbances are generally acknowledged to facilitate alien plants in the early stages of the invasion process (Fox & Fox 1986, Crawley 1987, Hobbs 1989, di Castri 1990). Soil disturbances that increase the number of safe sites (*sensu* Harper *et al.* 1961) by creating gaps of competitor-free ground and by increasing the availability of limiting resources, enable many immigrant species to become established (Hobbs 1989, Burke & Grime 1996). "Biotic release", the release of immigrant species from the constraints imposed by their native co-evolved natural enemies upon introduction to a new area ("natural enemy hypothesis", Maron & Vila 2001) may have a facilitating effect on plants in several steps of the invasion process. Non-indigenous plants that experience biotic release show increased growth and reproduction due to reduced damages or reduced allocation to defence (Weiss & Milton 1984). Plants that perform a novel function in a new area may also become more competitive. This was observed in Hawaii where non-indigenous N-fixing plants had a competitive advantage in nitrogen-poor environments that did not possess native N-fixers (Vitousek & Walker 1989). In addition, non-indigenous N-fixing plants are likely to facilitate the invasion of other plant species if the nutrient

availability in the soil is altered (Carino & Daehler 2002). There are many other examples showing synergistic interactions among invaders (Simberloff & Holle 1999). Some non-indigenous plant species increase the amount of flammable litter, burn at high relative humidities and are capable of rapid regrowth following fires. They promote fires and facilitate the invasion of other plant species (Hughes 1991).

The importance of cultivation in the early invasion steps has been underestimated in the past (Mack 2000, Reichard & White 2001, Paper A). Plant species that are introduced into new ranges and subsequently cultivated include species of agricultural, medicinal and horticultural interest, species used in landscaping and forestry, and species accidentally introduced with seeds and pot soil (Mack 2000, Reichard & White 2001, Paper A). A large number of propagules (seeds, rhizomes) are introduced for these purposes and multiple introductions of the species will often take place; both circumstances increase the probability of establishment (Kolar & Lodge 2001). Furthermore, nursing (provision of water, nutrients, shelter and pesticides) protects small populations from environmental stochasticity and may thus increase the probability of a plant immigrant surviving to reproduction and eventually reaching a minimum viable population size (Mack 2000, Paper A).

A major difference between crops introduced today and in the 19th century is the intensity of selection they have been through. Most cultivars on the market today have intensively been selected and bred for in order to increase the yield, the ability to resist diseases and herbivores (food and fodder plants), the colour, numbers and sizes of flowers (horticultural plants) *etc.* Competitive ability, which may be more crucial for the survival and establishment of plants in most natural communities, may have been impaired in many crops during the selection. Competitive ability is a less important attribute for crops in agroecosystems where competition is reduced, soil resources and pesticides are applied and each plant competes with plants of a similar genotype and at the same phenological stage. Most crops cultivated today may therefore have less potential to become invasive than plants introduced for commercial reasons 100 years ago.

1.2 Grasslands

Grasslands are in the present context defined as ecosystems dominated by perennial grasses with varying proportions of intermixed short-lived herbs. Grasslands range from being natural to man-made (van Andel *et al.* 1987), and they are diverse in plant and faunal diversity and composition (Crawley 1983, Elberse *et al.* 1983), water and nutrient availability (Burke *et al.* 1998) and disturbance regime (Grubb 1985). Herbivory is often the factor that prevents the transition from grassland to shrub land and forest (Lawrence 1989).

Permanent, temperate grassland ecosystems in Denmark were used as recipient systems for the non-indigenous plant species studied in the experiments in this project (Table 1). The grasslands have a mean

annual precipitation of 781 mm (Frich *et al.* 1997) and are considered to be "indeterminate dominance" grasslands. Such grasslands have intermediate precipitation levels between 700 and 1200 mm, continuous above- and belowground plant cover, and temporal and spatial variation in the resources that may limit plant growth, primarily water, nitrogen and light (Lauenroth & Coffin 1992, Burke *et al.* 1998). Grasslands with precipitation below 700 mm are typically characterised by intense belowground competition for water, high root to shoot ratio and discontinuous plant cover whereas grasslands with more than 1200 mm precipitation are generally dominated by aboveground competition for light (Burke *et al.* 1998). Due to the large sand content in the soil at most of the experimental sites (Table 2), the potential of the soils for retaining soil water and nutrients may be low.

Nutrient availability and carbon storage in grassland soils are strongly influenced by the prevailing composition of plant species (Wedin & Tilman 1990, 1996). Grasslands are characterised by a diverse, small-scale heterogeneity in resource availability due to organic matter that accumulates beneath the perennial grasses ("resource islands"; Burke *et al.* 1998). The amount and quality of organic matter that accumulates under individual plants depend on plant longevity, growth form, biomass allocation and litter quality (Vinton & Burke 1995, Burke *et al.* 1998). For instance, larger amounts of organic matter will accumulate in the soil beneath plants with long life spans than under plants with short life spans (Vinton & Burke 1995) and higher soil nitrogen contents are found beneath N-fixing legumes than grasses (Robles & Burke 1997).

1.2.1 Disturbances in grasslands

Disturbances can be characterised according to their type (Lavorel *et al.* 1998), scale, intensity, frequency (Grubb 1985, Coffin & Laurenroth 1988), and timing (Hobbs & Mooney 1985) as well as factors such as presence of litter (Bergelson 1990). These characteristics determine the effect of the disturbance on the dynamics of the community (Hobbs & Mooney 1985, van Andel & van den Berg 1987, Coffin *et al.* 1998). Continual disturbances may result in distinct, long-persistent vegetation types (e.g. vegetation characteristic of sand dunes or pastures) while periodic disturbances may open gaps for regeneration (Grubb 1985) of both existing and new species and thereby increase local species diversity (Lavorel *et al.* 1998). Gaps may be created in numerous ways by plant mortality, trampling, flooding, wind, erosion (White 1979), but disturbances that create gaps of bare soil increase recruitment more than mortality events (Aguilera & Laurenroth 1995). Seedling emergence and survival in grasslands are highly dependent on the gap dynamics (Aguilera & Laurenroth 1995) due to the strong asymmetric competition between adult plants and seedlings in established, undisturbed perennial vegetation (Grubb 1977, Fenner 1978, Fowler 1986, Gurevich 1986). The probability of reaching reproductive maturity for selected non-indigenous plants was shown to be positively correlated with gap size (McConnaughay & Bazzaz 1987). The spread of an invading species, *Senecio vulgaris*, from one generation to the next was

Table 1. Location, management and history of experimental sites described in Papers B-E. Brat: abbreviation for Brattingsborg.

Paper	Experimental sites	Location	Present management	Management History
Paper B	Funder	56°9'N, 9°23'E	None	No management for min. 30 years
Paper C	Brat I	56°23'N, 9°21'E Up-slope relative to Brat II	Extensive cattle grazing	Cultivated field up to the late 1980s
	Brat II	56°23'N, 9°21'E Down-slope relative to Brat I	Extensive cattle grazing	Cultivated field up to the late 1980s
	Dollerup	56°22'N, 9°19'E	None	No cultivation or grazing for min. 50 years, vegetation is occasionally cut
	Hald	56°24'N, 9°21'E	Vegetation cut annually but not removed	No recent record of cultivation or grazing
Paper D	Brat	56°23'N, 9°21'E	Extensive sheep grazing	Cultivated field
	Dollerup	56°22'N, 9°19'E	None	No cultivation or grazing for min. 50 years, vegetation is occasionally cut
	Hald	56°24'N, 9°21'E	Vegetation cut annually but not removed	No recent record of cultivation or grazing
Paper E	Brat	56°23'N, 9°21'E	None	Cultivated field up to the 1990s
	Hald	56°24'N, 9°21'E	Vegetation cut annually but not removed	No recent record of cultivation or grazing
	Viborg South	56°20'N, 9°21'E	None	Unknown
	Århus	56°12'N, 10°10'E	None	No recent record of cultivation or grazing

Table 2. pH, soil texture, and nutrient availability at experimental areas described in Papers C-E. The sand, silt and clay contents in the soil were determined by the particle size: coarse sand: 2.0-0.2 mm; fine sand: 0.20-0.02 mm; silt: 0.020-0.002 mm; clay: <0.002 mm. Plant available N, P and K contents were determined from dried soil samples. Analyses were carried out by Miljø-kemi, Dansk Miljø Center, Viborg. Brat: abbreviation for Brattingsborg.

	Paper C		Paper C and D		Paper D		Paper E	
	Brat I	Brat II	Hald	Dollerup	Brat (sheep)	Brat (no sheep)	Brat	Hald
pH _(CaCl2)	5.4	5.4	5.5	5.6	5.9	5.4	5.3	5.4
Coarse sand (%)	68.7	68.8	68.7	59.1	69.7	74.3	71.0	62.7
Fine sand (%)	21.2	22.4	17.0	21.8	20.0	17.2	16.2	22.6
Silt (%)	3.2	2.8	4.6	7.8	2.8	2.0	4.6	4.4
Clay (%)	4.3	5.9	7.1	7.4	5.8	5.1	5.2	7.5
Humus (%)	2.6	2.1	2.6	3.9	1.7	1.4	3.0	2.8
Nitrate-N (mg • kg ⁻¹)	3.1	5.1	2.7	5.2	3.4	3.8	4.1	4.5
Phosphate (mg • 100g ⁻¹)	3.1	2.5	3.1	1.2	3.4	3.3	4.1	3.2
Potassium (mg • 100g ⁻¹)	15.7	12.3	15.7	5.6	6.3	5.9	12.9	12.1

enhanced both by increasing gap size and by uniformly rather than patchily distributed gaps (Bergelson *et al.* 1993).

Although the soil is enriched beneath recently dead plants (Vinton & Burke 1995, Burke *et al.* 1998), seedling establishment may be low due to a drier topsoil in soil currently occupied by plants (Aguilera & Laurenroth 1995) or the presence of litter from the dead plants (Bergelson 1990). The nutrient-enriched zone under dead plants persists for less than 36 months following plant death (Kelly & Burke 1997). Plant morphological attributes and regeneration strategies differ for plants colonising different types of disturbances (Grubb 1985, Lavorel *et al.* 1998) and for plants colonising disturbed soil formed at different times of the year (Hobbs & Mooney 1985).

One of the most frequently cited hypotheses concerning plant diversity, "the intermediate disturbance hypothesis", states that species diversity is highest under intermediate levels of disturbances (Connell 1978). A common problem, often not considered in the literature on disturbance, is that intermediacy of the various components of a disturbance, i.e. type, scale, intensity and frequency, may affect a plant community differently (Pickett & White 1985). The impact of a disturbance also depends on the structure of the community, which can be divided into shoot-biased, root-biased, surface-attached and substrate-contained communities (Pickett & White 1985). For example, disturbances that only affect the aboveground vegetation may have a lower effect in root-biased than in shoot-biased communities (Pickett & White 1985).

Experimental studies have shown that soil disturbance generally facilitates plant invasion in grassland (Hobbs 1989, Bergelson *et al.* 1993, Kotanen 1997). For example, gopher mounds may increase the abundance of non-indigenous annual grasses more than the naturally occurring perennial grasses (Kotanen 1997). Combined soil disturbance and nutrient addition often have a larger facilitating effect on plant invaders than soil disturbance alone (Akinola *et al.* 1998). Invasion of annual grasses into perennial grasslands may affect the soil nutrient status and the spatial heterogeneity of soil resource availability (Vinton & Burke 1995).

1.2.2 Natural herbivory and livestock grazing in grasslands

One important source of disturbance in grassland ecosystems is herbivory. Many, if not most, temperate grassland communities are not climax communities, but the colonisation of woody species is prevented by herbivory. Numerous studies have demonstrated that natural herbivores, particularly arthropods, molluscs and rodents, may modify grassland communities by affecting plant performance and the competitive balance between plant species (Crawley 1988, Brown 1990, Brown *et al.* 1988, Hulme 1994, 1996, Wilby & Brown 2001). Molluscs, for example, may cause high mortalities of herbaceous seedlings in grassland ecosystems (Hulme 1994, Wilby & Brown 2001, Paper D) and by their selective feeding change the community composition towards a less herb- and more grass-dominated community (Wilby & Brown 2001).

Livestock grazing is the most important management tool in preventing the transition from grassland into shrub land and forest in Denmark. Livestock grazing may reduce plant biomass and fecundity, alter allocation patterns (Polley & Detling 1989, Grigulis *et al.* 2001, Mikola *et al.* 2001) and plant competitive interactions (Archer & Detling 1984), and increase species diversity (Collins *et al.* 1998) in grassland ecosystems. Grazing may increase seedling establishment of both native and non-indigenous species (Oesterheld & Sala 1990, Grigulis *et al.* 2001, Paper D) by creating gaps in the soil by trampling (Bergelson *et al.* 1993), by removing the litter layer that develops in the absence of grazing (Grigulis *et al.* 2001), by reducing the adult-seedling competition (Fenner 1978), and by incorporating the seeds into the soil (Paper D).

The intensity of grazing influences the species composition and abundance in a community. Some species, like *Lolium perenne*, are very tolerant to livestock grazing and are typical indicators of grazed grasslands (Elberse *et al.* 1983). *L. perenne* produced more shoot biomass in grazed than in ungrazed grassland communities, presumably due to depression of co-occurring species that are less tolerant to grazing (Mikola *et al.* 2001). Its competitive ability is decreased if management practices are changed from pasture to hay production, sometimes resulting in total extinction from the fields within ten years (Elberse *et al.* 1983).

Livestock grazing also modifies the plant-soil interactions. Grazing increases the nitrogen concentrations in plant litter and reduces microbial immobilisation. It thereby increases the nitrogen availability in the soil and thus plant productivity (Polley & Detling 1989, Holland & Detling 1990, Holland *et al.* 1992, McNaughton *et al.* 1997). Plants that are able to effectively deplete the plant available nitrogen in the soil generally have a competitive advantage (Tilman & Wedin 1991).

1.2.3 The experimental sites

Different grassland communities were used as experimental sites for the studies in the present thesis. Some were relatively pristine in character (Dollerup, Funder, Århus), others were abandoned from cultivation (Brattingsborg, Hald), and a single site was situated between a cultivated field and a roadside (Viborg) (Table 1, Figure 2). The abandoned fields, with the exception of some parts of Brattingsborg, were managed either by extensive sheep and cattle grazing or by occasionally cutting of the vegetation to prevent successional changes. Pesticides, fertilisers or other chemicals were not used at any of the sites prior to or during the experimental period. The Hald, Dollerup and Brattingsborg sites were used for several of the experiments (Table 1). Within the Brattingsborg site different management practices were carried out (Table 1).

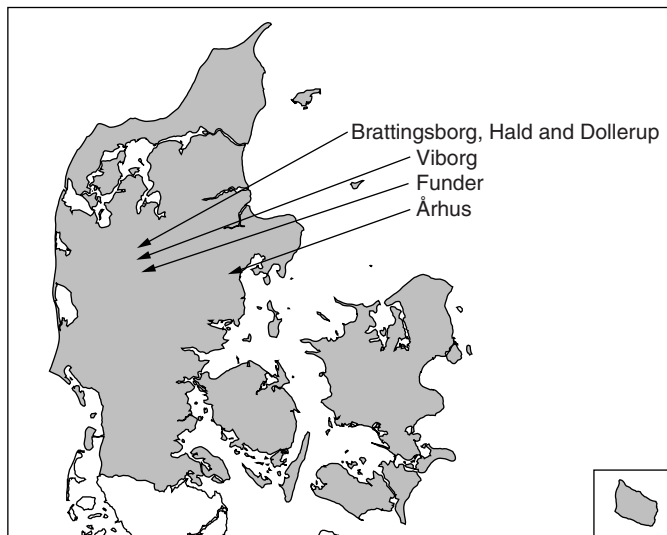


Figure 2. Map of Denmark showing the location of the experimental sites described in Papers B-D.

At selected sites (Hald, Dollerup, Brattingsborg), soil samples were analysed for pH, texture and plant available N, P and K (Table 2). These soils were well-drained and coarse-textured, so the vegetation may presumably suffer from drought in dry summers. pH values were within a range of 5.4 to 6.0. Nutrient availability varied between sites (Table 2) and may primarily reflect the time since they were last fertilised. For a description of the plant species composition and abundance at the different sites see the papers.

1.3 Study organisms

Two crops, *Lolium perenne* L. (perennial ryegrass) and *Brassica napus* subsp. *napus* L. (oilseed rape), and the invasive plant *Heracleum mantegazzianum* Somm. and Lev. (giant hogweed), were studied in the experiments. In Denmark, each of these species occurs in a different stage in the invasion process (Figure 1): *B. napus* is established and forms spontaneous populations (stage 2), *L. perenne* is naturalised and forms permanent populations (stage 3), and *H. mantegazzianum* is invasive and is presently expanding its distribution in Denmark (stage 4).

L. perenne is a host for the pathogen *Puccinia coronata* Corda., and *B. napus* and *H. mantegazzianum* are hosts for the pathogen *Sclerotinia sclerotiorum* (Lib.) de Bary. Both pathogens are biotrophic fungi i.e. fungi that depend on living host tissue to obtain nutrients (Parbery 1996). Due to poor results from the study on the *B. napus*-*S. sclerotiorum* interaction (Paper D), this host-pathogen interaction will not be further described and discussed.

Agricultural studies of *P. coronata* and *S. sclerotiorum* and their hosts show that plant growth and reproduction are negatively affected by pathogen attack (Simons 1970, Purdy 1979). Due to the economical importance of *L. perenne*, there has been much focus on crown rust of

L. perenne. In comparison, Paper E reports the only experimental study on *H. mantegazzianum* and *S. sclerotiorum*.

1.3.1 Model system: *Lolium perenne* - *Puccinia coronata*

L. perenne is a perennial bunchgrass, presumably native to Central Europe, the Mediterranean countries and Southwest Asia (Pedersen 1974). It is grown in most cool, moist regions of the world (Beddows 1967) for fodder, silage and seed production, and it is also an important component of grass seed mixtures used to seed pastures, golf courses, lawns and roadsides due to its resistance to trampling (Pedersen 1974). *L. perenne* was intentionally introduced to Denmark in late 1700 presumably for cultivation (Christiansen 1977). Today it is commonly found naturalised in semi-natural grasslands (Figure 2d), in urban areas, and along roadsides (Pedersen 1974, Frederiksen 1981).

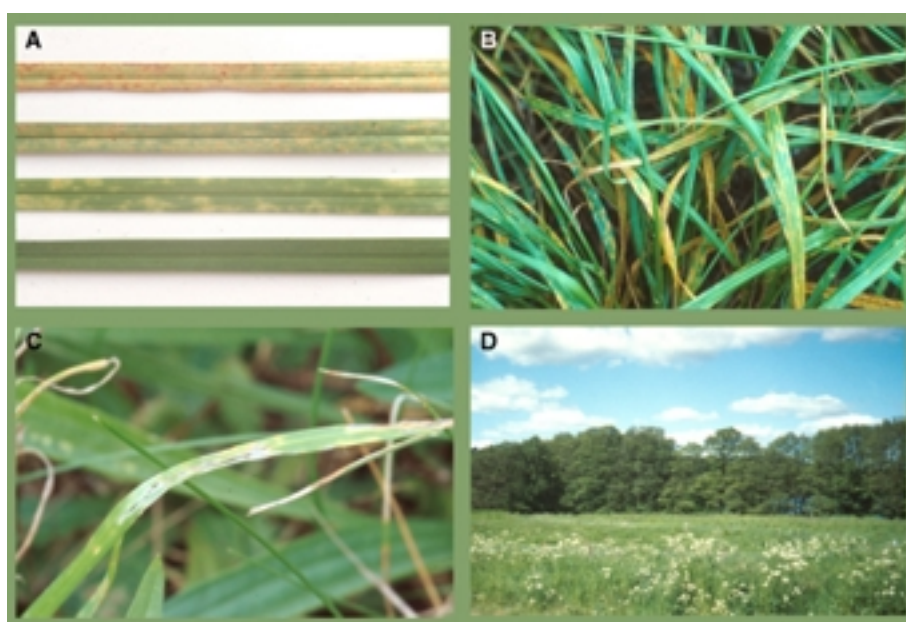


Figure 2. Disease symptoms on *Lolium perenne* infected by *Puccinia coronata*. (A) Leaves with different levels of disease severity. (B) Infected plants grown in monoculture. (C) Mollusc herbivory on plant tissue with pustules. (D) Permanent population of *L. perenne* in a semi-natural grassland community (Site: Hald).

L. perenne is 20-60 cm tall and develops seeds in spikelets, which are attached to 4-30 cm long inflorescences (Christiansen 1977). It is self-incompatible and therefore dependent on cross-pollination (Cornish *et al.* 1979). Populations are genetically diverse (Cooper 1959). *L. perenne* is an indicator species of grazed pastures where it produces the highest shoot biomass on fertilised soil (Elberse *et al.* 1983). Grazing and trampling by livestock increase the life span of *L. perenne*, perhaps because they prevent the development of inflorescences (Beddows 1967). Natural seed dispersal is of very limited importance (Beddows 1967) compared to the continuous, human-mediated seed dispersal. Seeds kept in storage may remain viable for up to eight years (Beddows 1967).

Crown rust is considered one of the most severe yield-reducing diseases of cultivated *L. perenne* in Denmark (Ghita Cordsen Nielsen, personal communication). One of the important means of disease control in agroecosystems is to choose cultivars with disease resistance. Studies of the genetic background and inheritance of crown rust resistance in *L. perenne* have led to several hypotheses. Some studies show that resistance to crown rust is controlled by a large number of genes with minor effects, while other studies indicate that the trait is controlled by one or few single genes (for review, Kimbeng 1999). Furthermore, inheritance patterns ranging from complete dominance to recessiveness have been suggested (Kimbeng 1999).

P. coronata is a macrocyclic, heteroecious fungus that requires both a grass host and a host from the genus *Rhamnus* in order to complete an entire life cycle (Holliday 1998; Figure 3). The uredial stage occurs on the gramineous host and may give rise to several generations of uredia with uredospores during the summer (Hawksworth *et al.* 1995). This stage of *P. coronata* has an almost worldwide distribution, presumably due to efficient long-distance dispersal of uredospores by the wind (Simons 1970). Despite its high dispersal potential, profound differences in pathogen development may occur locally due to differences in host susceptibility and structure and size of the surrounding vegetation (Paper B). Telia and overwintering teliospores are formed in autumn on mature, slowly drying leaves of the grass host (Smiley *et al.* 1992). The teliospores are released from the grass host in autumn. They produce basidia with basidiospores, which infect leaves of the alternate rhamnaceous host (Hawksworth *et al.* 1995). This stage has a much more limited global distribution since alternate hosts may be absent from some areas and winters may be too mild to break the dormancy of the teliospores (Simons 1970). Aecia and aeciospores, that are able to infect the gramineous host, are formed on the alternate host in the following spring, and the life cycle is thus completed (Simons 1970, Dinooor *et al.* 1988). In areas with mild winters the uredial stage may last throughout the winter and enable the fungus to survive although the alternate host is lacking (Simons 1970). In Denmark the uredial stage of *P. coronata* was recorded in 1890 on 22 species of grasses and the telial stage on three relatively rarely occurring species of *Rhamnus* (Rostrup 1890).

Crown rust appears on the leaves of the gramineous host (Simons 1970). Uredia and uredospores appear as rusty-coloured pustules surrounded by chlorotic or necrotic leaf areas (Figure 2a-b), or they may only appear as small light-coloured flecks if the host possesses a high degree of resistance (Simons 1970). Host plants generally show little visual damage in the first few weeks after infection, as mycelium of the fungus spreads intercellularly and absorbs nutrients through haustoria that invaginate the host cells without degrading the tissue to any great extent (Schumann 1991).

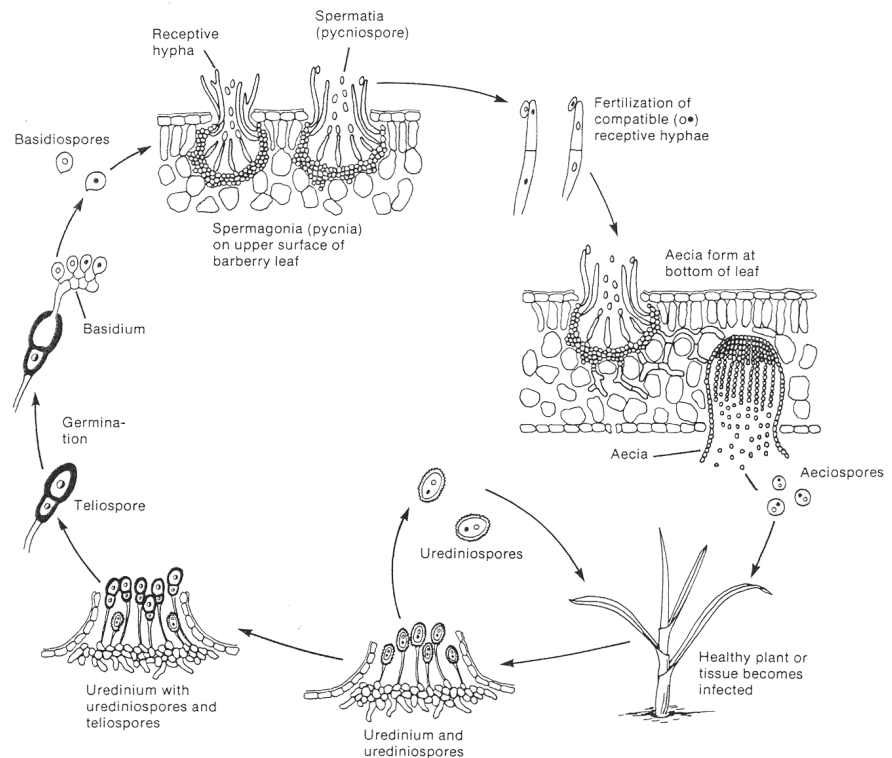


Figure 3. Disease cycle of a macrocyclic, heteroecious rust fungus exemplified by the cycle of *Puccinia graminis* (Smiley et al. 1992).

During sporulation, the plant epidermis is ruptured, transpiration is increased (Littlefield 1981), and the infected leaves begin to wither and senesce (Plummer *et al.* 1992). In autumn, irregular oblong, brown to black telia covered by epidermis are formed (Simons 1970).

The species *P. coronata* has been divided into special forms, *formae specialis* (f.sp.) identified on the basis of their host range (Simons 1970). The forms are named according to the host genera they originally were found to attack; species of the genera *Lolium* are hosts for *P. coronata* f.sp. *lolii*, species of the genera *Avena* are hosts for *P. coronata* f.sp. *avena* etc. The special form used for the experiments was undoubtedly *P. coronata* f.sp. *lolii* since the uredospores of *P. coronata* were collected on a *L. perenne* population and subsequently maintained on *L. perenne*. Five of the most dominating grasses at the experimental sites (*Festuca rubra*, *Poa pratensis*, *Agropyron repens*, *Bromus hordeaceus*, *Dactylis glomerata*) were tested for susceptibility to the *P. coronata* inoculum under controlled conditions, but none of them became infected (unpublished data).

Studies in the laboratory and in agroecosystems have shown that infected *L. perenne* plants may have reduced tiller and leaf biomass (Lancashire & Latch 1966, Potter 1987, Plummer *et al.* 1990), reduced root growth (Lancashire & Latch 1966), fewer tillers due to increased tiller death rate (Plummer *et al.* 1990) and a lower competitive ability (Latch & Lancashire 1970, Potter 1987). In contrast, the present studies of *L. perenne* in natural communities show that the fungus may have no (Paper B) or even a positive effect (Paper C) on plant growth, presumably due to a change in allocation of biomass from reproduction to shoot or due to other indirect effects. Interaction with

other organisms may also play an important role in natural communities e.g. some herbivores have a "cleansing" effect by feeding selectively on the spores and on host leaf tissues with pustules (Figure 2c; Ramsell & Paul 1990, Ericson & Wennström 1997).

Virulence of *P. coronata* on oats can be explained by the gene-for-gene concept (for review, Dinooor *et al.* 1988) in which each resistance gene in the host interacts with a corresponding avirulence gene in the pathogen (Holliday 1998). A consequence of this is that a single-gene mutation may change the virulence of the pathogen (Dinooor *et al.* 1988) and thereby result in a compatible interaction on a previously resistant cultivar. Whether this concept applies for *L. perenne* and *P. coronata* has not yet been tested (Kimbeng 1999). Evidence suggests that the pathogen has enough genetic variability to enable rapid adaptation to overcome host resistance (Wilkins 1978).

1.3.2 Model system: *Heracleum mantegazzianum* - *Sclerotinia sclerotiorum*

H. mantegazzianum is a monocarpic, biennial or short-lived perennial herb native to the Caucasus (Tiley *et al.* 1996). Presently it is found in most temperate regions of Europe (Tutin *et al.* 1968) and Central Russia (Tiley *et al.* 1996) and in some regions of Canada and the United States (Morton 1978). *H. mantegazzianum* was introduced to Denmark as an ornamental plant in the middle of the 18th century (Weidema 2000) but has subsequently spread into many plant communities (Hansen 1981, Tiley *et al.* 1996).

The plant develops a leaf rosette of up to 150 cm long leaves in the years prior to flowering (Hansen 1981, Otte & Franke 1998). After a threshold amount of nutrients is accumulated in the roots (Otte & Franke 1998), a 2-4 m tall compound umbel is formed (Hansen 1981). Seed production varies between 10,000 and 30,000 seeds per plant, and plant vigour determines the seed size and weight (Tiley & Philp 1997). The seeds remain viable in the soil for up to 7 years (Andersen & Calov 1996).

Due to its vigorous growth and high seed production, *H. mantegazzianum* may locally out-compete native plants, reduce species diversity, and form monocultures (Tiley *et al.* 1996). In Denmark it is most abundant in riparian areas where it may form large dense monocultures (Figure 4e; personal observation). Plausible hypotheses for explaining its high abundance in riparian habitats are that seed germination requires moist conditions, the plant tolerates poorly drained soils (Tiley *et al.* 1996), and seeds are effectively dispersed in water (Clegg & Grace 1974).

S. sclerotiorum is a broad-spectrum pathogenic fungus that has been reported to attack 408 plants species from 75 different families (Boland & Hall 1994). Most host species are herbaceous dicots, only few hosts are monocots, while no woody hosts have been recorded. *S. sclerotiorum* is a monocyclic pathogen that overwinters as sclerotia in the soil (for disease cycle see Paper E, p. 116). The sclerotia



Figure 4. Disease symptoms on *Heracleum mantegazzianum* infected by *Sclerotinia sclerotiorum*. (A) Dry stem lesion on stem above soil level. (B) Lesion and immature, white sclerotia at stem base. (C) Close-up of sclerotia of variable shapes formed beneath epidermis and in stem cavities. (D) Bisected section of a plant stem showing stem and root rot and mature sclerotia. (E) Population of *H. mantegazzianum* along a stream in a natural grassland community near Århus. Photos A, B and D are included in Paper E. (Photos C and D by Brita Dahl Jensen)

germinate in spring and develop into either mycelia or ascospore-producing apothecia. These two possible sources of primary inoculum will typically infect different parts of the plant. The wind-dispersed ascospores cause infection of above-ground plant parts (Figure 4a; Purdy 1979) while the mycelia, formed directly from germinating sclerotia in the soil, initiate disease in the stem-root interface or in the roots of nearby hosts (Figure 4b, 4d; Huang & Hoes 1980, Kohn 1995, Paper E). Towards the end of the growing season, sclerotia of variable sizes and shapes are formed in cavities or on tissue surfaces (Figure 4c) (Purdy 1955, 1979, Paper E). They are either discharged or remain within the plant until decomposition. They can remain viable in the soil seed bank for at least 4-5 years (Adams & Ayers 1979).

The fungus is widely distributed in cool and moist areas on most continents (Purdy 1979). In New Zealand the fungus has been shown to have a greater prevalence in natural habitats than in agricultural fields when analysing the percentage of sites infected. Sixty and ten percent of the sampled sites were infected in natural and agricultural systems, respectively (Bourdôt *et al.* 2000). However, an attempt to estimate the sclerotia density in the soil revealed that natural habitats had only 9 sclerotia per m² while up to 400 sclerotia per m² were found in agricultural fields (Bourdôt *et al.* 2000).

It is unknown how factors such as nutritional status of the host, temperature and other interacting organisms may influence this plant-pathogen interaction. It is also uncertain whether resistance to this pathogen exists within *H. mantegazzianum*. We know from other host species that resistance has been detected, and that resistance to *S. sclerotiorum* is a polygenic trait in sunflower (Mestries *et al.* 1998) and cauliflower (Baswana *et al.* 1991). Typical resistance reactions are breakdown of plant tissue, formation of phytoalexins, and physical barriers that may impede penetration and fungal development (Lumsden 1979).

The level of resistance to *S. sclerotiorum* of each plant part may differ. For instance, leaves of *Brassica napus* subsp. *napus* were resistant to penetration while damaged or healthy petals were susceptible (Jamaux *et al.* 1995), and leaves of *H. mantegazzianum* were resistant to attack, while undamaged inflorescence-bearing stems were susceptible (Paper E). Mycelium from a germinated spore may, under suitable environmental conditions, infect new host tissue throughout the growing season and result in the destruction of parenchymatous tissues as well as vascular and structural elements of the host (Purdy 1979). The pathogen may spread from an infected to an uninfected host if the aboveground parts of the plants have physical contact (Huang & Hoes 1980).

The diseases caused by *S. sclerotiorum* are known under different names (e.g. cottony soft rot, white mould, watery soft rot), and the symptoms vary depending on the specific host and the tissue attacked. Watery soft rot or white mould develop on leaves, stems or roots on some hosts, while on other hosts, dry lesions are formed (Purdy 1979, Hoes & Huang 1975).

The results of the study reported in Paper E showed that the mode of infection played an important role for the development of *S. sclerotiorum* and the associated effect on *H. mantegazzianum*. Infection initiated by wind-dispersed ascospores on the inflorescence-bearing stems of *H. mantegazzianum* resulted in dry stem lesions (Figure 4a). On most of these infected plants, lesion development stopped early in the growth season and did not support the development of sclerotia. In contrast, all plants infected in the roots or in the stem-root interface by mycelium from germinating sclerotia in the soil developed soft root rot (Figure 4d). On some of these plants the pathogen subsequently spread from the roots to the lower parts of the inflorescence-bearing stems resulting in the formation of dry stem lesions (Figure 4b). Experiments combined with observations indicated that plant fecundity was unaffected by stem lesion, but root rot appeared to cause premature wilting and reduced seed size. More severe effects of sclerotinia disease have been observed for plant survival and productivity of crops in agroecosystems (Purdy 1979, Jacobs *et al.* 1996, Yang *et al.* 1999).

Comparison of weight and size measures of sclerotia, asci and ascospores of isolates selected from different host species suggests that the isolates constitute a continuous series (Price & Colhoun 1975) i.e. no physiological specialisation takes place on separate host species. This was confirmed by a recent molecular study that was unable to show greater similarity between isolates from the same host species compared to isolates from two different hosts species (Carpenter *et al.* 1999). Other studies have shown that weeds in infected canola fields are infected with the same *S. sclerotiorum* genotypes as the canola plants (Kohli *et al.* unpublished data: cited in Kohli & Kohn 1996). Furthermore, *H. mantegazzianum* were successfully infected by sclerotia originally developed on *Daucus carota* (Paper E). Populations of *S. sclerotiorum* on wild plants growing adjacent to cultivated fields may thus act as a reservoir of inoculum infecting crops.

Many natural populations are more spatially isolated and protected from immigration of new genotypes than agricultural populations. This may explain why some wild populations of *S. sclerotiorum* are highly differentiated from agricultural populations (Kohli & Kohn 1996). Agricultural populations of *S. sclerotiorum* have a world-wide spatial distribution of many of the same genotypes (Kohli & Kohn 1996), most likely due to the long-distance transport of inoculum with agricultural seed as new genotypes with similar genetic background are repeatedly introduced into cultivated fields around the world.

1.4 Discussion of results and research methods

1.4.1 Experimental methods: pathogen and disturbance treatments

Pathogen-mediated effects were the prime focus in this project while the main purpose of including the soil disturbance treatment in the

experiments was to ensure competitor-free gaps for recruitment. In the present context, soil disturbance was defined as a change in conditions that creates competitor-free, transient gaps in the vegetation. The results from paper C and D confirmed earlier studies showing that soil disturbances in established, perennial vegetation increase the number of safe sites available for seedling emergence and growth (Hobbs & Mooney 1985, Aguilera & Lauenroth 1995, Burke & Grime 1996).

I aimed at creating disturbances that in scale and intensity was similar to what is found in natural grassland ecosystems. The experimental soil disturbances in Paper C and D were artificially created before seed addition at the onset of the experiment by overturning the soil to a depth of 20 cm. Two sizes of disturbances, 25x25 cm and 5x5 cm, were created in each experimental plot. The sizes of the large and small disturbances were approximately equivalent to molehills and hoof prints, respectively. Some researchers investigate establishment of non-indigenous plants by sowing seeds into large-scaled disturbances created for instance by tilling or ploughing (e.g. Crawley *et al.* 1993, Crawley & Brown 1995). This scenario is unlikely to be found in semi-natural and natural communities, however. The soil was overturned in the artificial disturbances described in paper C and D so root parts were present on the surface of the disturbances. It is likely that exudates from the roots may have affected the colonisation events, and that plant recruitment would have been higher if the soil had been sieved and the root material removed. Furthermore, this would have mixed the soil layers and thus increased the resemblance of soil found in molehills.

Artificial disturbances have certain advantages over natural disturbances in experimental field investigations. They allow us to control the disturbances and thus reduce the variability in the experimental system, and they allow us to set up randomised experiments where disturbed and control plots can be compared. A drawback is that it is difficult to simulate natural disturbances in experiments and that the dynamic of the colonisation processes may differ in natural and man-made disturbances (Lavorel *et al.* 1998).

The occurrence, expression and severity of disease depend on three components: the pathogen (e.g. virulence, abundance), the host (e.g. susceptibility, population size and density), and the biotic and abiotic environment (e.g. chemical and physical factors, other organisms) (Burdon 1987). The interactions of these three components are generally referred to as the "disease triangle". The choices made during an experimental investigation with plant and pathogens may have implications for the results and should be carefully considered. In addition, the choices are limited to what is practically feasible when working in the field. For example, sporulating *L. perenne* individuals were used as disease foci although the number of disseminated spores was likely to vary among the plants. Also, the distance between plots was chosen by considering both the risk of spore dissemination from pathogen-treated to untreated plots, the environmental heterogeneity that may arise when plots are separated

by large distances, and finally the size of the available experimental area.

In the field experiments with *L. perenne* and *P. coronata* (Papers B and C), pathogen exposure was carried out by transplanting a sporulating plant to the centre of each of the experimental plots. The level of disease severity on each of the transplants was high and approximately similar to what I have observed on *L. perenne* grown in monoculture. Herbivory by molluscs, which appeared much more attracted to the sporulating *L. perenne* transplants than the naturally occurring *L. perenne* plants, reduced the shoot biomass of the transplants within a day or two. This reduced the amount of plant tissue with pustules and thus the dissemination of spores to a level that I later observed to be more realistic in natural communities. Although *P. coronata* is wind-dispersed and has a high dispersal potential, control plots without sporulating transplants had surprisingly low disease incidence.

Comparisons among sites of disease development and the associated effect on plant performance should be done with caution. Differences in environmental conditions, particularly humidity and temperature, may have profound effects of the interaction between rust fungi and hosts (Simons 1970, Roderick & Thomas 1997). Also differences in biotic factors, such as the presence of spore-feeding herbivores (Ramsell & Paul 1990, Ericson & Wennström 1997), may result in site-specific disease development patterns. *P. coronata* was maintained on the transplants throughout the growth season in all three study years at all experimental sites, so it seems highly plausible that the fungus is able to attack and develop on naturally occurring *L. perenne* plants even at the site of Dollerup where attack was not observed. For similar reasons to those stated above, comparison among years of disease development and its effect on host plants should also be done with care.

In the field experiments with *H. mantegazzianum* and *S. sclerotiorum* (Paper E), the pathogen treatment was carried out by adding sclerotia to the soil. At all sites, the sclerotia developed into ascospore-producing apothecia, and disseminated ascospores successfully attacked inflorescence-bearing stems of *H. mantegazzianum*. We know very little about the sclerotia density found in natural plant communities, however, one study from New Zealand reported an average of 9 and 400 sclerotia per m² in natural plant communities and cultivated fields, respectively (Bourdôt *et al.* 2000). In the study described in Paper E, 67 sclerotia per m² were applied to the soil of experimental plots. This density may likely be similar to what is found in field edges where many *H. mantegazzianum* populations grow in Denmark.

1.4.2 Differences between the pathogens studied

There are a number of different aspects in the biologies of the two fungal pathogens, *P. coronata* and *S. sclerotiorum*, that have implications for the effect they may have on their hosts in natural plant communities (Table 3). Unlike *P. coronata*, *S. sclerotiorum* has an extremely wide host range (Boland & Hall 1994) and therefore it

Table 3. Differences between the two pathogenic fungi *P. coronata* and *S. sclerotiorum*.

<i>Puccinia coronata</i> f. sp. <i>lolii</i>	<i>Sclerotinia sclerotiorum</i>
Narrow host range ¹	Wide host range ³
Polycyclic disease epidemics ⁴	Monocyclic disease epidemics ²
Rapid spread over long distances in “stepping stone” increments due to the production of multiple spore generations within a growth season ¹	Dispersal with agricultural material or in “stepping stone” increments ⁵
Heteroecious (two alternate hosts required to complete lifecycle) ⁶	Autoecious (one main host required to complete lifecycle) ²
Spends entire lifecycle on plants ¹	Spends some of its lifecycle in the soil ²

¹Simons 1970; ²Purdy 1979; ³Boland & Hall 1994; ⁴Hawksworth *et al.* 1995; ⁵Kohli & Kohn 1996; ⁶Holliday 1998.

presumably has a more ubiquitous distribution in different types of habitats. In natural habitats with *H. mantegazzianum*, *S. sclerotiorum* will not only affect *H. mantegazzianum*, but also many of the other co-occurring host species. This is in sharp contrast to the situation in natural habitats with *P. coronata* and *L. perenne*. Under most circumstances *L. perenne* will be the only species in a given local area that is infected by *P. coronata*.

P. coronata depends on two host species to complete its life cycle (Simons 1970). To survive the winter in Denmark *P. coronata* seems generally to depend on the rhamnaceous host, but when winters are mild the pathogen may also survive in the form of uredospores on the grass host (personal observation). The alternate host, *Rhamnus cathartica*, is relatively rare in Denmark (Rastad 1981) so primary inoculum spread from Southern Europe to Denmark may be responsible for initiating many of the epidemics in the spring. Unlike *P. coronata*, *S. sclerotiorum* only depends on one host to complete its lifecycle (Purdy 1979). The sclerotinia fungus spends some of its life cycle in the soil where it is exposed to hazards from many organisms (Adams & Ayers 1979).

P. coronata gives rise to polycyclic disease epidemics i.e. many ascospore generations may develop within one season. This results in a rapid build-up of an epidemic providing that the environmental conditions are adequate for the inoculum to cause infections. Ascospores of *S. sclerotiorum* are likewise dispersed with the wind but only a single pathogen generation takes place within a season (Purdy 1979), so the build-up of a disease epidemic and the spread of the pathogen from patch to patch is presumably slower. Since the pathogen has a wide host range (Boland & Hall 1994) and only require a single host species to complete its lifecycle, its prevalence in a specific area may be more stable over time.

The origins of *P. coronata* and *S. sclerotiorum* are uncertain, so it is unclear whether the pathogens are native to Denmark or introduced. The special form *P. coronata* f.sp. *lolii* was presumably introduced to Denmark at the same time or after *L. perenne*.

1.4.3 Differences between the host plants studied

L. perenne and *H. mantegazzianum* differ from each other in several ways that can be expected to affect the host-pathogen interaction (Table 4). In Denmark, *H. mantegazzianum* is an aggressive plant invader that is able to spread into both disturbed, semi-natural and some types of natural habitats. *L. perenne*, on the other hand, is naturalised but not invasive. *L. perenne* is more abundant and widely occurring outside cultivated habitats than *H. mantegazzianum*, as large amounts of *L. perenne* seeds have been dispersed deliberately during more than 200 years. In the view of the general public, *L. perenne* is accepted and probably acknowledged as being a “native” plant while *H. mantegazzianum* is considered a nuisance that is systematically destroyed both on private and particularly on public land.

Table 4. Differences between *Lolium perenne* and *Heracleum mantegazzianum*.

<i>Lolium perenne</i>	<i>Heracleum mantegazzianum</i>
Long-lived perennial grass ²	Biannual or short-lived perennial herb ⁴
Widely distributed in disturbed and semi-natural habitats ³	Clumped distribution in disturbed and semi-natural habitats and in some types of natural habitats (riparian) ⁵
Naturalised ³	Invasive ⁴
Susceptible to <i>P. coronata</i> during entire lifecycle excl. seed stage ¹	Susceptible to <i>S. sclerotiorum</i> when reproducing ⁶

¹Pedersen 1974; ²Simons 1970; ³Frederiksen 1981; ⁴Tiley *et al.* 1996; ⁵pers. observation; ⁶Paper E.

L. perenne is potentially a very long-lived species (Beddows 1967). It is susceptible to the rust pathogen during its entire life cycle except as a seed (Simons 1970). Pathogen attack may therefore potentially affect both the number of offspring produced and longevity. The potential duration of disease attack is much shorter for sclerotinia attack on *H. mantegazzianum* (Paper E). The plant is monocarpic, i.e. it reproduces only once and it dies after the reproductive event. It is only susceptible to *S. sclerotiorum* late in the life cycle when it is reproducing (Paper E) so longevity is probably not affected. Although the effect of attack is only short-term, a single infection may potentially have a large impact on the plant since it is unable to compensate for the damage before it dies.

1.4.4 Biotrophic fungi and the invasion process of plants

Population size and density, distribution, and genetic diversity of host plants are of crucial importance for the development of plant pathogens and for the damage the pathogens may inflict on their hosts (Burdon & Chilvers 1982, Burdon 1987). These plant population characteristics change during the invasion process of alien plants, so it is reasonable to expect that also the effects of plant pathogens on their hosts will change during the process. To limit the early establishment of alien plants, pathogens must be able to damage the plants while they are at low density. This seems intuitively unlikely,

as disease development is dependent on the density and proportion of hosts to non-hosts (Burdon & Chilvers 1982, Burdon 1987, Paul 1990). Thus, as has been shown in Paper C, less severe infections are expected to be found in newly established populations of alien plants due to their small size and low plant density.

The probability of being attacked upon entry into a new area is strongly dependent on the host spectrum of the pathogen in question. Due to the broad host spectrum of *S. sclerotiorum* (Boland & Hall 1994), it is more likely that *S. sclerotiorum* is present at the site of introduction of *H. mantegazzianum* than that *P. coronata* f.sp. *lolii* is present at the site of introduction of *L. perenne*. The epidemic build-up of *S. sclerotiorum* on *H. mantegazzianum* is not related to the population size of *H. mantegazzianum* itself, but to the total number of individuals of host plant species. Generalist pathogens are therefore more likely to have an effect on plants in the early invasion stages than pathogens with a narrow host range.

Later in the invasion process the alien plant population increases in size and density. This is advantageous for the development of disease epidemics (Burdon & Chilvers 1982, Burdon 1987). Some plant species will eventually spread to new localities. Part of them may only be able to invade a narrow range of habitat types, while other species, such as *L. perenne* and *H. mantegazzianum*, are more non-specific and occur in a wide range of habitats. Even if a plant species is highly susceptible to a pathogen, the plant may find refugees in some habitats where the environmental conditions are unsuitable for disease development.

In addition to population size and density, the genetic diversity of a plant population may also determine the probability of being attacked by a pathogen and the subsequent rate of disease development (Burdon 1987). The actual genetic diversity of an alien plant species in a new area depends on the genetic diversity of the introduced propagules and the species' potential for creating new genetic variation through sexual reproduction or mutation. In addition, the diversity between populations created over time depends on the isolation of the population and the potential for gene spread. The introduction of new propagules with a novel genetic background may further add to the overall genetic variation of the population lowering disease development and the risk of disease-induced changes in the population dynamics. New *L. perenne* varieties selected for crown rust resistance are continuously introduced and spread into many types of human-managed cultivated and semi-natural habitats. This reduces the susceptibility of populations and may together with the other factors mentioned in Paper B and C (resource allocation, allelopathy, height of neighbouring vegetation) be responsible for the non-significant or even slightly positive effect found on the vigour of infected *L. perenne* in the studied grassland ecosystems. Knowledge on the genetic variability of *H. mantegazzianum* is lacking, and so are observations on the occurrence of disease of *S. sclerotiorum* in natural populations of *H. mantegazzianum* and in natural native plant populations in general. Paper E demonstrates that *H. mantegazzianum* is susceptible

to *S. sclerotiorum* and strongly suggests that the pathogen may decrease seed size and promote senescence. However, this effect was only observed when sclerotia were placed close to the plants suggesting that the spatial distribution of the sclerotia is an important factor for the dynamics of this host-pathogen interaction. More large-scaled experiments must be carried out in order to get more precise estimates of the fitness consequences of attack.

Contrary to what is known from agricultural systems, experimental addition of *P. coronata* to *L. perenne* growing in natural plant communities revealed that crown rust attack may result in an increase in above-ground plant biomass (Paper C). Similar effects were observed for *Agrostis tenuis* and *A. stolonifera* infected with *Epichloe typhina* causing the disease "Choke". Infected plants were vegetatively more vigorous but showed suppressed development of inflorescences (Bradshaw 1959). Evidence showing a positive response of pathogen attack on the vegetative vigour of host plants is relatively rare. However, previous studies suggest that the increased shoot growth is traded off by either a decrease in root development (Catherall & Parry 1987) or in reproduction (Bradshaw 1959, Clay 1984, Wennström & Ericson 1991).

Damage from pathogens that decrease seed production or seed quality may have a direct effect on recruitment in future generations for monocarpic plants like *H. mantegazzianum*. Attacks occur late in the developmental stage of *H. mantegazzianum* and this hinders its ability to compensate for the damage. In contrast, *L. perenne* may be able to compensate across years for poor seed production years and it can maintain established populations by vegetative reproduction. Yet, due to two important life-history attributes of *H. mantegazzianum*, large seed production (Tiley & Philp 1997) and long-lived seed banks (Andersen & Calov 1996), the species may be buffered from pathogen-induced population impacts. Furthermore, the broad host spectrum of *S. sclerotiorum* might, under some circumstances, facilitate rather than inhibit the spread of *H. mantegazzianum* if the pathogen has a more detrimental effect on other species than on *H. mantegazzianum* itself. Such circumstances are more likely to be found in communities dominated by herbs, such as riparian areas, than in grassland communities where most plant species are non-hosts. The importance of the susceptibility of the surrounding vegetation was studied in Paper E but no significant differences in disease incidence was found between plants grown in more and less susceptible vegetation. However, more long-term experiments may be needed in order to test this hypothesis since the epidemic build-up of a monocyclic pathogen like *S. sclerotiorum* may take a long time.

Presumably, the most important factor determining the invasiveness of *H. mantegazzianum* and *L. perenne* is their ability to compete with the native plants. The competitive ability of *H. mantegazzianum* has not yet, to my knowledge, been studied experimentally, but observations and demographic studies of the species clearly show that its competitive ability and effect on other species is enormous (e.g. Tiley *et al.* 1996).

The ability of *L. perenne* to escape from cultivated fields into natural grassland communities is unclear. *L. perenne* was able to establish as seedlings when sown into established vegetation (Paper C), but in most natural plant communities this species may be unable to reach reproductive maturity before being out-competed by adult plants. *L. perenne* has a wide distribution in Denmark but most of the naturalised populations of *L. perenne* present in semi-natural grasslands in Denmark today were presumably once seeded and to some extent cultivated. These populations have become naturalised by virtue of post-seeding cultivation, and they are now able to maintain themselves primarily by vegetative propagation. This conclusion is based on several studies showing that *L. perenne* seedlings are poor competitors when they compete against adult plants. For example, in a seed addition experiment 6400 seeds of *L. perenne* were introduced into disturbed and undisturbed grassland vegetation (see Paper B for description of the vegetation), and only 11 seedlings were counted one year later (unpublished data). Furthermore, *L. perenne* was not naturally occurring at the most pristine and undisturbed sites (Dollerup and Århus). Also, a greenhouse experiment showed that when *L. perenne* was sown together with *Poa trivialis*, shoot and root growth and tillering of *L. perenne* were reduced during the first four weeks of its establishment (Haggard 1979). The effect was enhanced when *Poa trivialis* was sown before *L. perenne*. The effect of *P. trivialis* on *L. perenne* seedlings older than four weeks was considerably reduced. The importance of emergence time for the outcome of competition was also observed when *L. perenne* and *Plantago lanceolata* were sown in mixtures (Sagar 1959 acc. to Ross & Harper 1972). When the two species were sown simultaneous, *L. perenne* constituted 80% of the total biomass, but when *L. perenne* was sown three weeks later than *P. lanceolata*, it only constituted 6% of the biomass. A study with *L. perenne* and three other commonly occurring grassland species, *Festuca rubra*, *F. arundinaceae* and *Poa pratense*, showed that when well-established 3 years old plants of the four species compete against each other, the invasiveness of *L. perenne* was ranked second, only slightly lower than *F. rubra* (Silvertown *et al.* 1994). Because of *P. coronata*'s low effect on *L. perenne* in non-cultivated plant communities and its presumably irregular occurrence from year to year, it seems unlikely that the fungus has any significant long-term influence on the population dynamics of *L. perenne* in Denmark and or on *L. perenne*'s potential to be invasive. Expansion of *L. perenne* populations due to human activity appears to be much more important.

1.5 Concluding remarks

Several researchers have hypothesised that pathogens may negatively affect the invasion process of non-indigenous plants. The present studies of two host-pathogen interactions, *L. perenne*-*P. coronata* and *H. mantegazzianum*-*S. sclerotiorum*, do not support this hypothesis. In two small, newly established *L. perenne* populations, pathogen infection and development were either low or did not occur, presumably due to density-dependent effects on disease development. In large, naturalised populations of *L. perenne*, high

disease levels were found, but plant vigour, measured as shoot biomass, was not affected or was enhanced. The study illustrates that disease may affect crop species quite differently when they occur in natural communities or are grown in agroecosystems, and that we must be cautious about extrapolating knowledge about host-pathogen interactions from cultivated to natural systems. Host susceptibility appeared to be unimportant for the performance and presumably the competitive ability of infected *L. perenne*. This may not be the case for other interactions between pathogens and non-indigenous plant species. Short-lived plant species that rely on current seed production are more likely to be influenced by natural enemies (Maron & Vila 2001). The study on the invasive *H. mantegazzianum* indicated that *S. sclerotiorum* may have fitness consequences for the plant but it is uncertain whether the pathogen will affect the long-term population dynamics of the species.

Scientific knowledge is not yet adequate to predict the impact of pathogens on plants in the different stages of the invasion process. Biotic factors, including pathogens, have been integrated in plant invasion models and hypotheses, such as the biotic resistance and biotic release hypotheses (Maron & Vila 2001), but the experimental evidence needed to test these hypotheses is lacking. Individual studies, like the present project, provide glimpses of understanding but further studies are needed before we can make reliable generalisations. The importance of disease resistance for the establishment and naturalisation of non-indigenous plants is also a neglected area that must be subjected to more investigations before it can be applied in risk assessment.

1.6 References

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2 Papers

- Paper A. Mack R.N. & Erneberg M. 2002. The United States naturalized flora: Largely the product of deliberate introductions. *Annals of the Missouri Botanical Garden* 89: 176-189. 51
- Paper B. Erneberg M. Reduced height of co-occurring vegetation in a natural plant community increases the epidemic build-up of crown rust (*Puccinia coronata*) on susceptible and partially resistant *Lolium perenne* (*In preparation*). 65
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- Paper E. Erneberg M., Strandberg B. & Jensen B.D. Susceptibility of a plant invader to a pathogenic fungus: An experimental study of *Heracleum mantegazzianum* (Giant Hogweed) and *Sclerotinia sclerotiorum* (*Accepted for publication*). 113

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