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Forest & Landscape
Research
No. 34 • 2004

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Forest & Landscape Research is issued by the *Danish Centre for Forest, Landscape and Planning* (in short *Forest & Landscape Denmark*) which is an independant centre for research, education, and extension concerning forest, landscape and planning at the Royal Veterinary and Agricultural University (KVL).

The journal accepts Ph.D. theses, D.Sc. theses, and other major research reports of scientific standard concerning forest, park, landscape, and planning research written in Danish or English. The content of the journal undergoes a scientific peer-review process.

Forest & Landscape Research is to be considered the continuation of *Forskningsserien - The Research Series* (ISSN: 1398-3423).

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Series-title, no.:	Forest & Landscape Research, No. 34-2004
Author:	Søren Ugilt Larsen
Citation:	Larsen, Søren Ugilt (2004): A study of factors affecting germination, establishment, and competition of the turfgrass species red fescue (*Festuca rubra* L. spp. *litoralis* Vasey), perennial ryegrass (*Lolium perenne* L.), and Kentucky bluegrass (*Poa pratensis* L.) - Forest & Landscape Research, No. 34-2004. Danish Centre for Forest, Landscape and Planning, Hørsholm. 141 pp.
ISBN:	87-7903-202-8
ISSN:	1601-6734
Printed by:	Kandrups Bogtrykkeri, DK-2100 København Ø
Number printed:	200
Price:	DKK 250 (incl. 25% VAT in Denmark)

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SUMMARY

Turfgrass is an important crop, which requires intensive cultivation during establishment and management. Proper cultivation must be based on thorough knowledge about the biology and dynamics of the turfgrass ecosystem. This thesis is concerned with germination, establishment, and competition of turfgrass mixtures consisting of slender creeping red fescue (*Festuca rubra* L. ssp. *litoralis* Vasey), perennial ryegrass (*Lolium perenne* L.), and Kentucky bluegrass (*Poa pratensis* L.). The main conclusions are mentioned below.

A two-year field study confirmed that Kentucky bluegrass establishes poorly in mixtures with red fescue and perennial ryegrass, i.e. a large proportion of Kentucky bluegrass in the seed mixture results in a relatively small proportion of shoots in the established turf. When seeds of Kentucky bluegrass were sown prior to seeds of red fescue and perennial ryegrass, the proportion of Kentucky bluegrass shoots in the established turf was increased. This shows that the time factor is important for the competitive balance between the species during establishment.

A number of laboratory experiments were done to study differences in germination behaviour between the three grass species. A part of the thesis is concerned with methodology in germination studies. Three different germination criteria, which were compared with the normal seedling criteria, provided similar results but tended to overestimate the germination percentage compared to the proportion of normal seedlings. Germination time courses were effectively summarized by a generalized hyperbolic multinomial distribution. Germination response to reduced water potential could be described by the hydrotime model, using repeated probit analysis. Germination response to temperature could be described by the thermal time model, but a non-linear regression analysis based on the Weibull function was superior to the repeated probit analysis. There were interacting effects of water potential and temperature, which affected the use of the hydrothermal time model. Finally, another important methodological conclusion is that seed lots of the same cultivar may differ considerably in seed weight and germination characteristics, and in germination studies each cultivar should, therefore, be represented by more than one seed lot.

The germination studies revealed distinct differences between the three grass species. Seeds of Kentucky bluegrass require a longer thermal time for germination compared to seeds of red fescue and perennial ryegrass. At reduced water potential, germination percentage is more reduced and time to germination is more increased for Kentucky bluegrass seeds than for seeds of the other species. The results strongly suggest that poor establishment of Kentucky bluegrass in mixture with red fescue and perennial ryegrass is related to the slower germination and lower germination percentage of Kentucky bluegrass seeds, which is particularly pronounced at low temperatures and at reduced water potentials.

Within the three grass species, germination characteristics differ between cultivars, between seed lots within cultivars, and even between seeds of a single seed lot, with heavy seeds germinating better than light seeds. The effect of choosing a fast germinating cultivar or removing light seeds of a seed lot of Kentucky bluegrass was, however, relatively small compared to the required difference in sowing time to improve the establishment of this species. Variation in seed weight between cultivars and seed lots within cultivars is distinct. When considering a seed mixture of a specific species composition by weight, seed mixture composition by number may, therefore, vary markedly depending on the seed weight of the applied cultivars and seed lots.

Key words: Cultivar differences, differential sowing time, seed germination, germination modelling, plant competition, seed weight, species mixtures, temperature and germination, turgrass establishment, water potential and germination, *Festuca rubra* ssp. *litoralis*, *Lolium perenne*, *Poa pratensis*

SAMMENDRAG (DANISH SUMMARY)

Plænegræs er en vigtig afgrøde, der kræver intensiv pleje både i etableringsfasen og efter etableringen. Forudsætningen for god pleje er grundlæggende viden om biologien og dynamikken i plænegræssets økosystem. Denne afhandling omhandler spiring, etablering og konkurrenceforhold i plænegræsblandinger bestående af rødsvingel med korte udløbere (*Festuca rubra* L. ssp. *litoralis* Vasey), alm. rajgræs (*Lolium perenne* L.) og engrapgræs (*Poa pratensis* L.). De væsentligste konklusioner nævnes i det følgende.

Et toårigt markforsøg bekræftede, at engrapgræs etableres dårligt i blandinger med rødsvingel og alm. rajgræs. En stor andel af engrapgræs i frøblandingen resulterer i en relativt lille andel skud i den etablerede plæne. Når frø af engrapgræs blev sået tidligere end frø af rødsvingel og alm. rajgræs, steg andelen af engrapgræs i den etablerede plæne. Dette tyder på, at tidsfaktoren er vigtig for konkurrenceforholdet mellem arterne under etablering.

En række laboratorieforsøg blev udført for at undersøge forskelle i spiring mellem de tre græsarter. En del af afhandlingen vedrører metodikken i spiringsundersøgelser. Tre forskellige spiringskriterier blev sammenlignet med kriteriet "normal kimplante". De tre kriterier gav næsten ens resultater, men alle tre kriterier gav for høj spireprocent i forhold til andelen af normale kimplanter. Spiringskurver kunne effektivt opsummeres med en generaliseret hyperbolsk multinomialfordeling. Virkningen af reduceret vandpotentiale på spiring kunne beskrives af *hydrotime*-modellen vha. *repeated probit analysis*. Temperaturens virkning på spiring kunne beskrives af *thermal time*-modellen, men ikke-lineær regressionsanalyse baseret på Weibullfunktionen fungerede bedre end *repeated probit analysis*. Der var vekselvirkning mellem vandpotentiale og temperatur, hvilket påvirkede analysen med *hydrothermal time*-modellen. Endnu en metodemæssig konklusion er, at frøpartier af den samme sort kan variere betragteligt i både frøvægt og spiringsegenskaber. I spiringsundersøgelser bør hver sort derfor repræsenteres ved mere end et frøparti.

Spiringsstudierne viste markante forskelle mellem de tre græsarter. Sammenlignet med rødsvingel og alm. rajgræs kræver engrapgræsfrø længere *thermal time* ('varmesum') for at spire. Reduceret vandpotentiale reducerede spireprocenten og øgede tiden til spiring i højere grad for engrapgræsfrø end for frø af de andre arter. Resultaterne tyder meget på, at dårlig etablering af engrapgræs hænger sammen med den langsommere spiring og lavere spireprocent for engrapgræs, hvilket er mest udtalt ved lave temperaturer og ved reduceret vandpotentiale.

Indenfor alle tre græsarter varierer spiringsegenskaberne mellem sorter, mellem frøpartier af samme sort og endda mellem frø af samme frøparti, idet tunge frø spirer bedre end lette frø. Virkningen af at vælge en hurtigt-spirende sort eller af at fjerne de letteste frø fra et parti af engrapgræs var dog beskeden sammenlignet med den forskel i såtidspunkt mellem arterne, der var nødvendig for at forbedre etableringen af engrapgræs. Frøvægten varierede betydeligt mellem sorter og mellem frøpartier indenfor samme sort. En frøblanding med en given sammensætningen målt i vægt-procent kan derfor variere markant i sammensætningen målt i antal-procent, afhængig af frøvægten i de benyttede sorter og frøpartier.

Nøgleord: Sortsforskelle, forskudt såtidspunkt, frøspiring, modellering af spiring, plantekonkurrence, frøvægt, artsblandinger, temperatur og spiring, etablering af plænegræs, vandpotentiale og spiring, *Festuca rubra* ssp. *litoralis*, *Lolium perenne*, *Poa pratensis*

PREFACE

Having consulted a number of Ph.D. theses for inspiration while writing this, it appears to me that the preface is usually the only section, which reveals a few details about the human being behind the scientific substance – with overwhelming gratitude to him and her and that, and with no requirement of reliable documentation! This preface will not be an exception from this.

A reviewer of one of the manuscripts in this thesis noted that the message was about to disappear in the 'verbiage'. The Concise Oxford Dictionary revealed that verbiage is 'needless accumulation of words' and made me aware that I'm suffering from 'verbosity' – which one of my supervisors has also hinted now and then! I shall try to restrain myself in this section.

When entering USA from Canada after the IXth International Turfgrass Conference in Toronto in July 2001, the official at the border wanted to know about my doings in Canada. He was clearly suspicious: 'And you say that 350 people were talking about turfgrass for a week?' Five years ago, I would probably have been just as amazed myself; at that time I was not aware of the importance of turfgrass as a crop. Although realizing that turfgrass science may not save lives in the third world, I have now perceived that knowledge about turfgrass is valuable, and that turfgrass does play a role – major or minor – in many peoples life. Just listen to Tom Waits (from 'What's He Building?', 1999): 'He has no dog and he has no friends and his lawn is dying…'. The ultimate misfortune!

This thesis work has given me a great opportunity to get into the field of turfgrass biology and to unite this with my long-standing interest in seed biology. This has been a very interesting challenge.

Finally, the thanksgiving. To those who have contributed in various ways – also to those I may have forgotten – I wish to express my sincere thanks:

- The Danish Forest and Landscape Research Institute (DFLRI), The Royal Veterinary and Agricultural University (RVAU), and The Danish Research Agency (DRA) – for funding the project.
- My supervisor, Associate Professor Christian Andreasen, Department of Agricultural Sciences, RVAU, and my co-supervisor, Senior Advisor Palle Kristoffersen, Department of Park and Landscape, DFLRI, – for great supervision, ranging from advice on how to grow Japanese Ivy to advice concerning back-ache.

- My Principal, Vice-director Dr. Kjell Nilsson, Department of Park and Landscape, DFLRI – for supporting my activities and allowing me the required time.
- Professor Francoise Corbineau, Professor Daniel Côme, and Associate Professor Christophe Bailly, Laboratoire de Physiologie Végétale Appliquée, Université Pierre et Marie Curie, Paris – for inviting me to their lab and for collaboration on Paper V.
- Associate Professor Bo Martin Bibby, Department of Mathematics and Physics, RVAU – for giving a broad range of advise on statistics and for collaboration on Paper IV and VI.
- Olaf Bos, Lars Arne Jensen, Jim Lynge, and Vibeke Kragsig Mortensen – for technical assistance during the germination experiments and field trials.
- My father, Poul Larsen – for collaboration on the construction of the custom built roller for the field trials – and on many other projects.
- Photographer Torben Eskerod – for teaching me in the art of portraying seeds.
- Plant breeder Niels Christian Nielsen, DLF Trifolium A/S, and Agronomist Asbjørn Nyholt, Prodana Seeds A/S – for supplying seeds and for useful discussions and advice.
- Dansk Jordforbedring A/S – for supplying topdressing sand for the field trials.
- Professor Jens C. Streibig, Department of Agricultural Sciences, RVAU – for statistical support and encouraging shouts.
- Professor emeritus Erik Nymann Eriksen, Department of Agricultural Sciences, RVAU – for introducing me to seed science and for encouraging a scientific career.
- My colleague, Senior Advisor Jørgen Fischer, DFLRI – for introducing me to turfgrass science.
- My other colleagues at DFLRI and RVAU – for various sorts of support.
- Chris Kvisthøj – for technical assistance during the preparation of illustrations and for designing the layout.
- Chris Kvisthøj – yes, her again – for various other reasons such as sharing apartment with the seeds and myself.

Enjoy the verbiage!

Søren Ugilt Larsen

FORORD (DANISH PREFACE)

Efter at have søgt inspiration til dette forord i andre Ph.D.-afhandlinger synes det klart, at forordet ofte er det eneste sted i afhandlingen, der giver et indtryk af personen bag graferne og de videnskabelige formuleringer – gerne med en overvældende taknemlighed overfor både den ene og den anden og uden henvisning til nogen form for pålidelig kilde! Dette forord bliver ikke nogen undtagelse fra dette mønster.

Ved bedømmelsen af en af artiklerne i denne afhandling bemærkede en tidsskriftredaktør, at budskabet i artiklen var ved at forsvinde i 'the verbiage'. Hjemmets opslagsværker afslørede, at 'verbiage' er en betegnelse for 'overflødig ophobning af ord' (og sågar er synonymt med 'ordflom', 'ordskvalder' og vidtløftighed!), og at jeg således lider af 'ordgyderi' – et faktum som min ene vejleder også har bemærket! Jeg skal forsøge at begrænse mig lidt i dette afsnit.

På vej fra Den Niende Internationale Plænegræskonference i Toronto i juli 2001 ville grænsekontrolløren ved grænsen mellem Canada og USA høre nærmere om mine gøremål i Canada. Han var tydeligvis mistænksom: "Og du siger, at 350 mennesker snakkede om plænegræs i en uge?" For fem år siden ville jeg nok også selv have været forbløffet; på det tidspunkt kendte jeg ikke til, hvor betydningsfuld en afgrøde plænegræs egentlig er. Selvom jeg ikke forestiller mig, at plænegræs vil redde liv i den tredje verden, er jeg dog overbevist om, at viden om plænegræs er værdifuld, og at plænegræs spiller en rolle – større eller mindre – for mange mennesker. Lyt blot til Tom Waits (fra 'What's he building?', 1999): "Han har ingen hund og han har ingen venner og hans plæne er ved at gå ud…". Den ultimative ulykke!

Denne afhandling har givet mig en fin mulighed for at få indsigt i biologien i plænegræs og for at forene denne med min gamle interesse for frøbiologi. Det har været en meget interessant udfordring.

Til sidst taksigelserne. Jeg vil gerne udtrykke min store tak til alle dem, der på forskellig måde har bidraget undervejs – og også til dem jeg måtte have glemt:

- Forskningscentret for Skov og Landskab (FSL), Den Kgl. Veterinær- og Landbohøjskole (KVL) og Forskeruddannelsesrådet (FUR) – for at have finansieret projektet.
- Min vejleder, lektor Christian Andreasen, Institut for Jordbrugsvidenskab, KVL, og min medvejleder, seniorrådgiver Palle Kristoffersen, Afdeling for Park og Landskab, FSL – for fremragende vejledning om alt lige fra dyrkning af rådhusvin til pleje af en dårlig ryg.

- Min chef, Vicedirektør og forskningschef Kjell Nilsson, Afdeling for Park og Landskab, FSL – for opbakning og for at bevillige mig den fornødne tid.
- Professor Francoise Corbineau, professor Daniel Côme og lektor Christophe Bailly, Laboratoire de Physiologie Végétale Appliquée, Université Pierre et Marie Curie, Paris – for at invitere mig til deres laboratorium og for samarbejde i forbindelse med Artikel V.
- Lektor Bo Martin Bibby, Institut for Matematik og Fysik, KVL – for alsidig vejledning om statistiske emner og for samarbejde i forbindelse med Artikel IV og VI.
- Olaf Bos, Lars Arne Jensen, Jim Lynge og Vibeke Kragsig Mortensen – for teknisk hjælp i forbindelse med spiringsforsøg og markforsøg.
- Min far, Poul Larsen – for samarbejde ved fremstilling af den specialbyggede tromle til markforsøgene – og ved mange andre projekter.
- Fotograf Torben Eskerod – for at undervise mig i portrættering af frø.
- Planteforædler Niels Christian Nielsen, DLF Trifolium A/S, og salgschef Asbjørn Nyholt, Prodana Seeds A/S – for forsyning af frø og for gode diskussioner og råd.
- Dansk Jordforbedring A/S – for forsyning af topdressingsand til markforsøgene.
- Professor Jens C. Streibig, Institut for Jordbrugsvidenskab, KVL – for statistiske tips og opmuntrende tilråb.
- Professor emeritus Erik Nymann Eriksen, Institut for Jordbrugsvidenskab, KVL – for at indføre mig i frøforskningens verden og for at opmuntre til en videnskabelig uddannelse.
- Min kollega, seniorrådgiver Jørgen Fischer, FSL – for at introducere mig til fagområdet for plænegræs.
- Mine øvrige kolleger på FSL og KVL – for diverse former for hjælp og opmuntring.
- Chris Kvisthøj – for teknisk hjælp ved fremstilling af illustrationer og for at udforme afhandlingens layout.
- Chris Kvisthøj – ja, hende igen – af forskellige andre årsager såsom for at dele hjem med frøene og mig.

God fornøjelse med ordflommen!

Søren Ugilt Larsen

1. INTRODUCTION

1.1 Turfgrass and seed mixtures

Despite its lack of nourishing value, turfgrass is now considered an agronomic crop of large importance – at least where nourishment is not a problem. In addition to its prevalence in private gardens and parks etc., turfgrass is used extensively as playing surface in various sports such as football, golf, cricket and rugby. Practice of many sports requires a playing surface of a certain minimum quality standard, including wear tolerance and a high percentage ground cover. Consequently, establishment and management of turfgrass areas have become subjects of increasing professional and economic importance and as a result, research in turfgrass science has also become increasingly relevant. Accordingly, this work was done to gain more knowledge about one aspect of turfgrass science.

Turfgrass is in certain cases established by vegetative propagation, but generally establishment is done by seeding (Turgeon, 1991). The seed material is often a mixture of two or more grass species, and a species is often represented by more than one cultivar.

The use of species mixtures is a means of obtaining genetic diversity and higher adaptive potential (Beard, 1973). The mixture acts as insurance; if one species (or cultivar) performs poorly within the given growth conditions another species (or cultivar) with different requirements is likely to perform better. Besides, different species may exploit different niches in the turfgrass community, allowing them to co-exist. This increases the tolerance to pests and other environmental stresses compared to monostands (Beard, 1973).

1.2 Establishment of Kentucky bluegrass in species mixtures

In temperate areas, seed mixtures often include the grass species Kentucky bluegrass (*Poa pratensis* L.), perennial ryegrass (*Lolium perenne* L.), and subspecies of red fescue, e.g. slender creeping red fescue (*Festuca rubra* L. ssp. *litoralis* Vasey) (subsequently just termed red fescue) in various proportions. These species possess various characteristics, which allow them to coexist and supplement each other, which make them desirable as turfgrass species. Kentucky bluegrass is, for instance, convenient due to its production of rhizomes (Etter, 1951) and high tolerance to wear (Shearman and Beard, 1975).

When sown in mixture with red fescue and particularly perennial ryegrass, Kentucky bluegrass is often found to establish very poorly (e.g.

(Adams and Bryan, 1974; Niehaus, 1976). This is clearly illustrated by Fig. 1, based on results in Paper I. A large proportion of Kentucky bluegrass in the seed mixture resulted in a rather small proportion of Kentucky bluegrass shoots in the established turf. Although the proportion of shoots may not be identical to the proportion of plants of a species, Kentucky bluegrass obviously has a lower establishment success than red fescue and perennial ryegrass (see discussion in Paper I). This represents a practical problem; seeds of Kentucky bluegrass are expensive (by weight, the price may be more than twice the price of perennial ryegrass), and the use of them does not result in the desired proportion of Kentucky bluegrass in the turf.

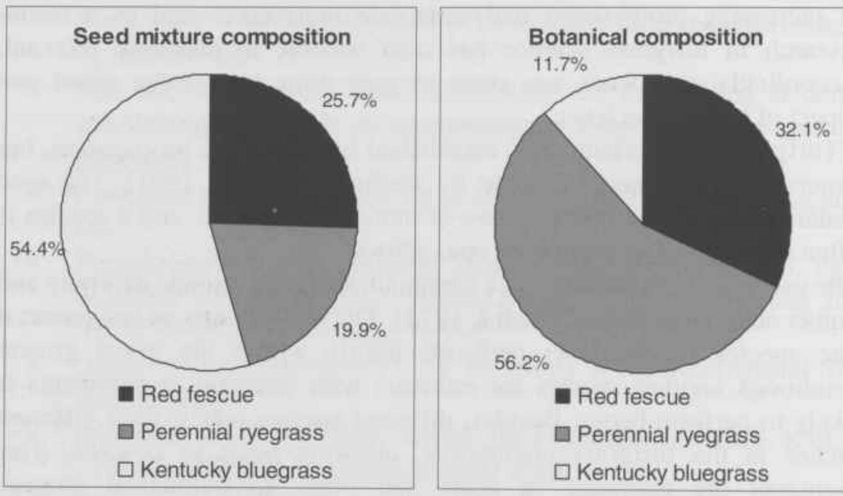

Figure 1. *Relationship between species composition in the seed mixture (% seeds by number) and in the established turf (% shoots) based on data from Paper I. Seed mixture composition was calculated as mean percentage pure viable seeds of the three species in the seed mixture sown in the two years. Botanical composition was estimated as percentage shoots of each species when sown at the same time. The composition was estimated by the non-linear regression method as a mean of the four field trials.*

1.3 Hypotheses – potential reasons for poor establishment of Kentucky bluegrass

Why is there such a difference between the proportion of Kentucky bluegrass in the seed mixture and the proportion in the established turf? Unsuccessful establishment can – no matter which species – potentially be due to a range of causes in the sequence from seed to established plant:

- *Dead and empty seeds*. A seed lot usually contains a proportion of dead and/or empty seeds. If seed mixture composition is based on pure viable seeds rather than total number of seeds, this factor is irrelevant. The calculation of pure viable seeds sown per area unit, however, requires that thousand-seed weight is considered, as demonstrated in Paper II.
- *Viable seeds that do not germinate in the soil*. Although a seed is able to germinate at optimal conditions in a germination test, it may not do so in the seedbed (Perry, 1980). This can be due to low seed vigour, and the effect is often most pronounced under suboptimal germination conditions, e.g. in cold and wet soil (ISTA, 1995).
- *Germinated seeds that die prior to emergence*. A seed may germinate in the soil but the seedling may never manage to emerge from the soil. Again, this may be due to low seed vigour. Alternatively or additionally, the seeds may have been sown too deeply (Riordan *et al.*, 1981), have been exposed to temporary drought (Turgeon, 1991) although this does not necessarily cause seedling mortality (Allen *et al.*, 1993), or a soil crust may inhibit seedling emergence (Frelich *et al.*, 1973).
- *Germinated seeds that die after emergence*. After a seedling has emerged from the soil, it may die due to various environmental factors, e.g. attack form diseases (Gooding *et al.*, 1989). Alternatively, seedling mortality may be due to competition from other species or from other plants of the same species. Mortality due to competition can be caused by slow emergence or slow growth after emergence, both causing a reduced competitive ability, especially at high plant densities (Begon *et al.*, 1996).

The possible explanations of poor establishment may as mentioned apply to many plant species. When sowing different species together, the species will experience the same conditions in the growth environment but may respond differently to these conditions. Accordingly, it is of vital interest to know the differences between species in a mixture and particularly their potentially different response to various factors. In the present study, it is of particular interest to know, if Kentucky bluegrass responds markedly different to various factors compared to red fescue and perennial ryegrass. Such knowledge may improve the understanding of the establishment process and may, furthermore, offer possibilities for improving the establishment by cultural practices.

Previous studies have shown that Kentucky bluegrass has lower emergence percentage (Davies, 1927; Skirde, 1967), slower emergence (Skirde, 1967; Pommer, 1972; Bø, 1989), as well as slower seedling growth (Arnott and Jones, 1970; Henderlong, 1971) compared to red fescue and particularly perennial ryegrass. Thus, poor establishment of Kentucky bluegrass appears to be caused by a combination of more than one factor.

1.4 Objectives of the study

The primary field of this investigation is the role of seed and germination characteristics in the establishment of red fescue, perennial ryegrass, and Kentucky bluegrass when sown in mixture. Most parts of the thesis represent comparative studies where various sources of differences between the three species were studied. Specifically, the studies had the following purposes:

- To study the effect of the time factor on the competitive relationship between the three species during establishment and to evaluate the possibility of affecting the species composition in the established turf by differential sowing time (Paper I).
- To study the variation in thousand-seed weight within each species and to quantify the potential effect on seed mixture composition when thousand-seed weight is not taken into account (Paper II).
- To study certain aspects of the methodology in germination studies, viz. to compare three different germination criteria (Paper III) and to evaluate different methodologies for analysing germination data to describe various germination patterns (Papers IV, V and VI).
- To study the variation in germination characteristics between and within each species and to evaluate the possibility of affecting the relative establishment success by choosing specific cultivars and/or seed lots (Paper IV).
- To study the effect of water potential and temperature on germination of two cultivars of each of the three species (Papers V and VI).
- To study the relationship between seed weight and germination characteristics within seed lots of the three species and to

evaluate the possibility of improving seed lot performance by seed grading (Paper VII).

2. EFFECT OF THE TIME FACTOR ON COMPETITION BETWEEN ESTABLISHING GRASS SPECIES

One of the hypotheses for the poor establishment of Kentucky bluegrass is that slow germination and emergence and/or slow seedling growth leads to a low competitive ability. To test if the time factor is involved in the competition between species during the establishment, a field trial with differential sowing time was conducted, i.e. where seeds of Kentucky bluegrass were sown at various intervals prior to sowing of red fescue and perennial ryegrass. The results reported in Paper I strongly indicate that the time factor is involved in the competition between Kentucky bluegrass, red fescue and perennial ryegrass. The predicted linear relationships indicated that the proportion of Kentucky bluegrass could be increased from 0.016% to 0.077% per °day sowing time advantage, and a minimum sowing time advantage of 60 to 450 °days was required to increase the proportion of Kentucky bluegrass significantly. Thus, despite large variability, the proportion of Kentucky bluegrass in the established turf was clearly increased when increasing the time advantage for this species. The field trial reported in Paper I, however, does not distinguish between the effect of slow emergence and slow seedling growth. As will be discussed in subsequent sections, both slow emergence and slow seedling growth are likely to be involved.

From a practical point of view, the results of the field trial demonstrate that the botanical composition of a turf can be altered by differential sowing time of the species. The field trial was primarily established in periods when soil temperature was relatively high, i.e. in May and August to mid-September. When considering the mean daily soil temperature through the growing season and the germination response to soil temperature (see subsequent section and Fig. 6 and 7), it is evident that a longer actual difference in sowing time would be required in e.g. April or October to obtain the same difference in thermal time. It is, therefore, relevant to aim at sowing mixtures with Kentucky bluegrass at a time with relatively high soil temperature. Furthermore, effort should be made to ensure sufficient soil moisture for germination (Fig. 4), either by irrigation or by aiming at sowing just prior to rainfall. Although differential sowing time may offer a means for improving the establishment of Kentucky bluegrass in mixtures, the two sowing occasions bring along practical circumstances that need to be handled. Besides, an advantage of the fast emerging species in mixtures is that they prevent weed invasion (Juska *et al.*, 1956). In the field trial, a larger invasion of annual bluegrass (*Poa annua* L.) was noticed in field plots where sowing of red fescue and perennial ryegrass was delayed the most. Thus, allowing Kentucky bluegrass more space during establishment also provides more niches for establishment of weeds, and this problem also needs a solution for differential sowing time to be applicable.

3. THOUSAND-SEED WEIGHT AND SEED MIXTURE COMPOSITION

Thousand-seed weight (*TSW*) varies considerably within a species. Thus, Paper II illustrates that *TSW* can vary up to 31%, 38%, and 69% within red fescue, perennial ryegrass, and Kentucky bluegrass, respectively, due to differences between cultivars and/or differences between seed lots within cultivars. The variation in *TSW* can potentially have a large impact on both seed mixture composition and total seed number per weight unit of seed mixture. Fig. 2 demonstrates how seed mixture composition may vary, depending on *TSW* of the applied seed lots in the mixture. The example is based on the same seed mixture composition as used in Fig. 1 (Paper I), which is commonly used for turfgrass on football pitches. The example in Fig. 2 does not take into account differences in seed viability and vigour, and these factors as well as the applied seed rate (Engel and Trout, 1980) may affect the composition of the established turf. Moreover, (Ebdon and Skogley, 1985) found that the number of Kentucky bluegrass shoots in mixtures with perennial ryegrass was first significantly reduced when the proportion of perennial ryegrass in the seed mixture was increased from 20 to 50%. Nevertheless, the proportion of the species in mixture 1 and mixture 2 are likely to result in different species compositions in the established turf. Therefore, in contrast to common practice, *TSW* as well as seed viability should always be taken into account when considering seed mixtures and the establishment of mixtures.

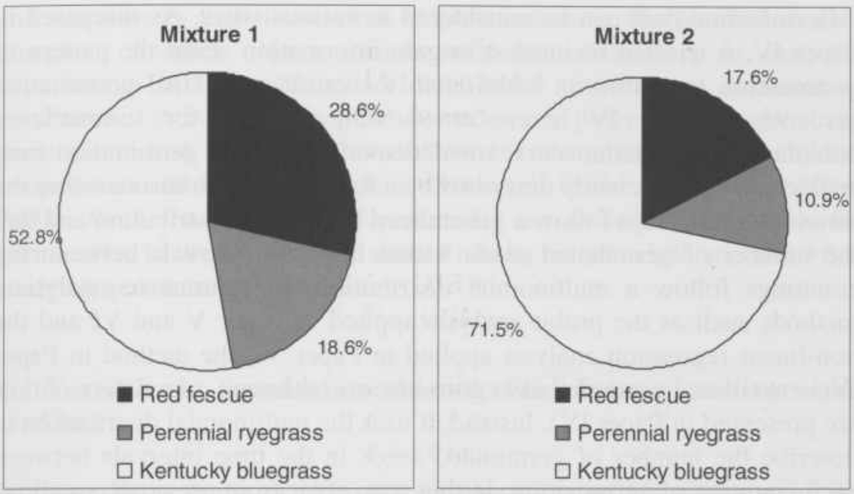

Figure 2. *The effect of variation in thousand-seed weight (TSW) within a species on the composition of turfgrass seed mixtures (% seeds by number). Mixtures 1 and 2 both include 30%, 40%, and 30% by weight of red fescue, perennial ryegrass, and Kentucky bluegrass, respectively. Mixture 1 includes seeds of red fescue and perennial ryegrass with the lowest TSW and seeds of Kentucky bluegrass with the highest TSW found in the experiment in Paper II. Mixture 2 includes seeds of red fescue and perennial ryegrass with the highest TSW and seeds of Kentucky bluegrass with the lowest TSW found in the same experiment.*

4. COMPARATIVE GERMINATION STUDIES

4.1 Methodology in germination studies

Since a major part of this thesis concerns seed germination, the methodology in germination studies is of great importance. Previous germination studies within grass species have applied different criteria when evaluating germination, but the correlation between these criteria was scantily studied. Paper III demonstrates that the three criteria radicle germination, coleoptile germination, and cotyledon germination resulted in similar results in all of the three grass species, although all three criteria tended to overestimate the percentage of normal seedlings. Whereas the normal seedling criterion is certainly a more precise predictor of seedling vigour, all three alternative criteria appear to give information closely related to those given by the normal seedling criterion. Choice of germination criterion is, therefore, not crucial for conclusions of germination studies, at least for studies carried out at optimal germination conditions.

Germination data can be considered in various ways. As discussed in Paper IV, it is often of interest to gain information about the pattern of germination over time in addition to the estimate of final germination percentage. Paper IV is concerned with methods for summarizing cumulative germination curves and demonstrates that germination time courses can be efficiently described by a function, which assumes that the times to germination follow a generalized hyperbolic distribution and that the number of germinated seeds within the time intervals between the countings follow a multinomial distribution. In contrast to analytical methods such as the probit analysis applied in Paper V and VI and the non-linear regression analysis applied in Paper VI, the method in Paper IV is not based on cumulative germination (although cumulative curves are presented in Paper IV). Instead, it uses the multinomial distribution to describe the number of germinated seeds in the time intervals between each counting of germination. In this way, error from previous countings of germination is not accumulated in subsequent observations, as is the case for methods based on cumulative germination. A general problem when analysing germination data is that the observations of germination percentages are not independent when subsequent countings are made in the same experimental unit, which is common practice. Although common practices may not be correct, it has been reported that consecutive countings in the same experimental unit and independent counting in separate experimental units gives identical results (Bradford, 1995). It therefore seems reasonable to ignore the lack of independence between observations in germination studies.

Paper IV illustrates the variation in germination between individual seed lots of the same cultivar and emphasizes the importance of representing a cultivar by more than one seed lot. This is equivalent to the situation in Paper II where seed weight was also variable between seed lots of a cultivar. In studies of seed biology, it is therefore essential to distinguish between genetic variation and physiological variation due to other factors than genetics.

In seed biology, much attention has been paid to the quantification of germination response to environmental factors such as water potential and temperature. Paper V and VI apply the concepts of thermal time, hydrotime, and hydrothermal time and demonstrate that these concepts have some potential for describing germination behaviour. Paper VI illustrates that thermal time to germination is often skewed and shows that skewed germination data are better described by the Weibull function than a symmetric function. A complication for the modelling of germination response to environmental factors is that the effect of one factor may interact with the effect of other factors, as discussed in Paper V. Such interactions illustrate the dynamic nature of seed germination and emphasizes that the control of germination in the seedbed is very complex. Another aspect, which must be considered, is that the experiments in Paper V and VI are based on constant germination conditions, i.e. constant temperature and water potential throughout the germination test. However, the seed zone is characterised by the widest temperature and water fluctuations that occur in the soil profile (Allen, 2003). Such fluctuations may potentially act as important signals for germination in the seedbed and should ideally be taken into account when studying germination behaviour.

4.2 Variation in germination characteristics between cultivars and seed lots

In paper IV, a range of cultivars and seed lots within cultivars of red fescue, perennial ryegrass, and Kentucky bluegrass were germinated at optimal conditions, and the three species were found to differ markedly in their germination characteristic (Fig. 3). Kentucky bluegrass generally had a lower final germination percentage (*FGP*) than red fescue and particularly perennial ryegrass (Paper IV). If such differences between species are not accounted for when considering establishment of species mixtures, they may – at least partly – contribute to the poorer establishment of Kentucky bluegrass. Besides, low germination percentage is often accompanied by low seed vigour (Roberts, 1986), and this may amplify the species differences. Kentucky bluegrass also had a higher mean germination time (*MGT*) and time from 25% to 75% germination ($T_{25\text{-}75}$) than the other species, illustrating that this species generally germinates more slowly and over a longer period of time (Fig. 3). This is consistent with reports of more slowly emergence for Kentucky bluegrass (DeFrance and Simmons, 1951; Bø, 1989). The species differences in germination characteristics (Fig. 3) are therefore all likely to be involved in the poorer establishment of Kentucky bluegrass.

The screening of a range of cultivars (Paper IV) revealed some significant genetic differences in germination characteristics within species, but *MGT* only differed up to one day between the cultivars of Kentucky bluegrass. Considering the applied germination temperature, this difference is equivalent to approximately 18 °days with a base temperature of 0°C. Compared to the minimum difference in sowing time of 60 to 450 °days required to improve the proportion of Kentucky bluegrass (Paper I), the cultivar difference is relatively small. Therefore, choosing the most rapidly germinating cultivar rather than the slowest one in the screening experiment would presumably only improve the establishment of Kentucky bluegrass slightly. In contrast, individual seed lots within cultivars of Kentucky bluegrass differed up to six days in *MGT*, equivalent to 110 °days. Thus, if a Kentucky bluegrass seed lot of particular low vigour and high *MGT* is sown in a seed mixture, this is likely to result in a pronounced competitive disadvantage. To facilitate establishment of Kentucky bluegrass in mixtures, it is, therefore, important to use seed lots of high quality to avoid slow germinating seeds.

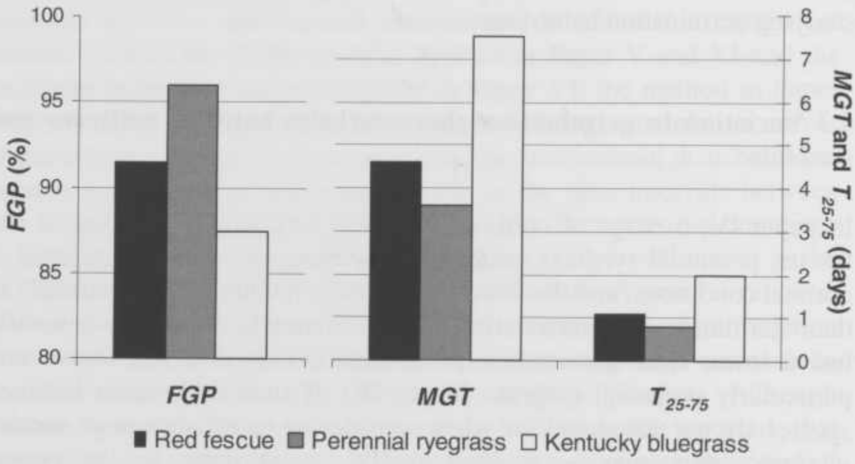

Figure 3. *Final germination percentage (FGP), mean germination time (MGT), and time from 25% to 75% germination ($T_{25\text{-}75}$) for red fescue, perennial ryegrass, and Kentucky bluegrass when germinated in a standard germination test at 15/25°C for 16/8 hours per day. Values are estimates from Paper IV, based on germination of 20, 19, and 16 seed lots of the three species, respectively.*

4.3 Water potential and germination

In Paper V, the use of PEG solutions is assumed to mimic the effect of drought stress on germination. Reduced water potential, i.e. water potential below 0 MPa, has a pronounced decreasing effect on germination percentage and an increasing effect on time to germination (Fig. 4). The results demonstrate that Kentucky bluegrass responds more strongly to reduced water potential, with a larger reduction in germination percentage and a larger increase in time to germination (Fig. 4) at a given water potential compared to red fescue and perennial ryegrass.

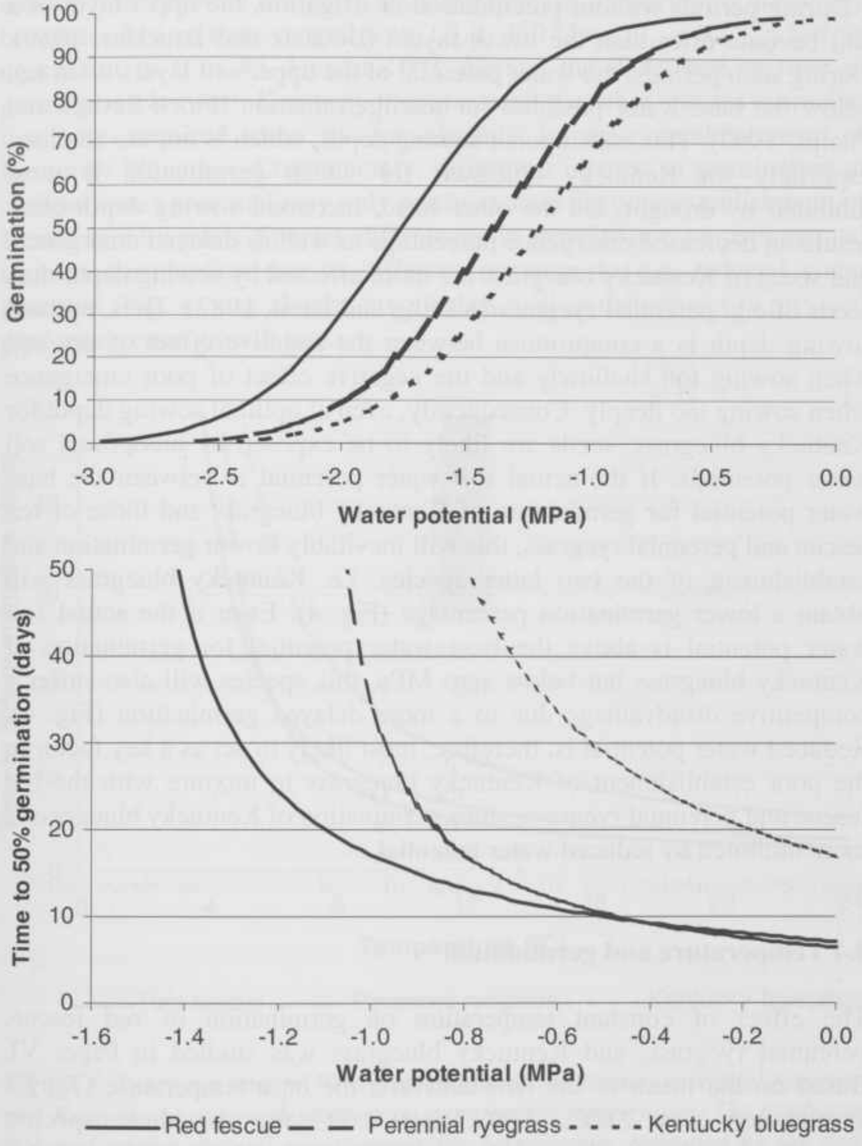

Figure 4. Predicted final germination percentage (upper figure) and time to 50% germination (lower figure) for red fescue, perennial ryegrass, and Kentucky bluegrass depending on water potential in the germination medium. The prediction is based on the hydrotime requirements for germination at 10°C, estimated by the hydrotime model in Paper V. The prediction is calculated as a mean of two cultivars of each species. Note different scales on the x-axis.

During periods without precipitation or irrigation, the upper layer of a soil become drier than the lower layers (Bouaziz and Bruckler, 1989). During such periods, the water potential of the upper soil layers often fall below the base water potential for seed germination (Finch-Savage and Phelps, 1993). This calls upon a sowing depth, which is not too shallow, especially for Kentucky bluegrass for which germination is most inhibited by drought. On the other hand, increased sowing depth often results in decreased emergence percentage as well as delayed emergence, and seeds of Kentucky bluegrass are more affected by sowing depth than seeds of e.g. perennial ryegrass (Käding and Kreil, 1982). Thus, optimal sowing depth is a compromise between the negative effect of dry soil when sowing too shallowly and the negative effect of poor emergence when sowing too deeply. Consequently, even at optimal sowing depth for Kentucky bluegrass, seeds are likely to be exposed to suboptimal soil water potentials. If the actual soil water potential is between the base water potential for germination of Kentucky bluegrass and those of red fescue and perennial ryegrass, this will inevitably favour germination and establishment of the two latter species, i.e. Kentucky bluegrass will obtain a lower germination percentage (Fig. 4). Even if the actual soil water potential is above the base water potential for germination of Kentucky bluegrass but below zero MPa, this species will also suffer a competitive disadvantage due to a more delayed germination (Fig. 4). Reduced water potential is, therefore, most likely to act as a key factor in the poor establishment of Kentucky bluegrass in mixture with the red fescue and perennial ryegrass, since germination of Kentucky bluegrass is more inhibited by reduced water potential.

4.4 Temperature and germination

The effect of constant temperature on germination of red fescue, perennial ryegrass, and Kentucky bluegrass was studied in Paper VI. Based on the mean of the two cultivars, the base temperature (T_b) for germination was 2.6°C, 3.6°C, and 2.6°C for the three species, respectively, whereas thermal time to 50% germination ($\theta_T(50)$) was 64, 44, and 116 °days, respectively. Thus, T_b is not very different for the three species whereas $\theta_T(50)$ is considerably higher for Kentucky bluegrass than the other species. Accordingly, Kentucky bluegrass takes a longer time to obtain 50% germination, and the actual time difference is prominent at lower temperatures (Fig. 5). At 10°C, for instance, the predicted time to 50% germination is 8.6 days for red fescue, 6.9 days for perennial ryegrass, and 15.7 days for Kentucky bluegrass. Results from Paper I indicated that the minimum difference in sowing time required to significantly increase the proportion of Kentucky bluegrass in a mixture ranged from 60 to 450 °days (T_b = 0°C), which is equivalent to 6 to 45 days at 10°C. Hence, the difference in time to germination between Kentucky bluegrass and the other species is smaller than the required time to considerably improve establishment of Kentucky bluegrass. Consequently, difference in time to germination at optimal water potential may only partly explain the poor establishment of Kentucky bluegrass. Species differences in germination percentage and time to germination due to different response to e.g. reduced water potential (Fig. 4) may also be involved as well as differences in pre- and post-emergence growth rate.

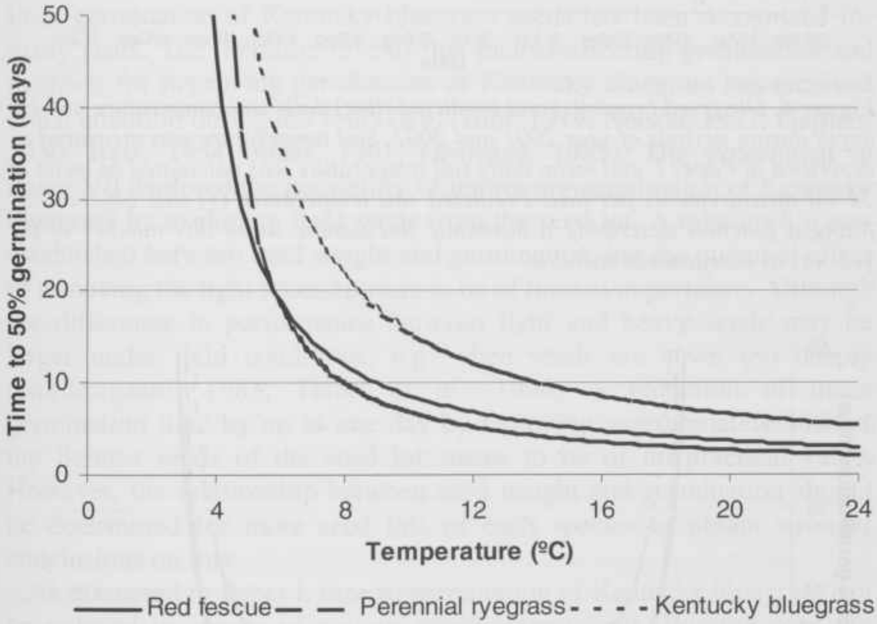

Figure 5. *Predicted time to 50% germination of red fescue, perennial ryegrass, and Kentucky bluegrass depending on germination temperature. The prediction is based on the thermal requirements for germination, estimated by the non-linear regression method in Paper VI. The prediction is calculated as a mean of two cultivars of each species.*

Soil temperature is, of course, an important factor for time to germination in the soil. Fig. 6 shows the fluctuation in mean daily soil temperature at 1 cm depth during periods of two years. When combining the predicted daily soil temperature with estimates of T_b and $\theta_T(50)$ from

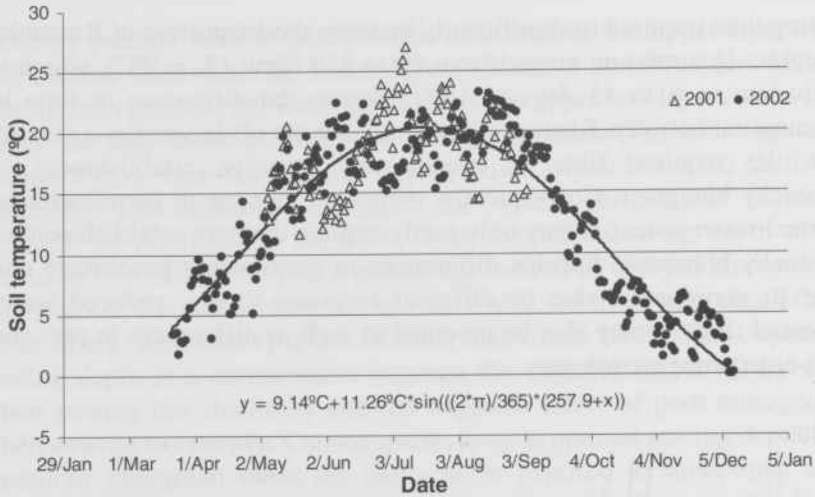

Figure 6. *Observed (symbols) and predicted (line) daily soil temperature at 1 cm depth during periods of year 2001 and 2002. Soil temperature was measured as described in Paper I, and mean daily soil temperature was calculated as mean of 24*60 measurements per day. Predicted soil temperature (y) was obtained by fitting a function describing a harmonic fluctuation, using day number of the year (x) as independent variable.*

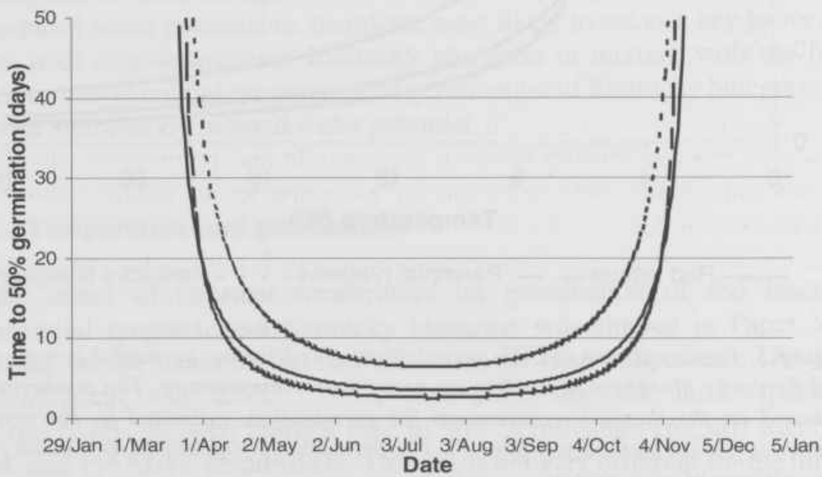

Figure 7. *Predicted time to 50% germination of red fescue, perennial ryegrass, and Kentucky bluegrass depending on time of the year. The prediction is based on the thermal requirements for germination, estimated by the non-linear regression method in Paper VI, and the mean daily soil temperature at 1 cm depth, predicted from the soil temperature data from 2001 and 2002. The prediction is calculated as a mean of two cultivars of each species.*

Paper VI, the time to 50% germination in the soil can be predicted as a function of sowing date (Fig. 7). There is evidently a large day-to-day variation in soil temperature due to changing weather conditions which is not accounted for by the predicted function (Fig. 6). Estimates of T_b and $\theta_T(50)$ are also associated with some variation. Nevertheless, Fig. 7 clearly illustrates that sowing date is of great importance for the time to germination, and that actual time to germination differs more between the three species in early spring and in late autumn.

4.5 Seed treatments and germination

Poor germination of Kentucky bluegrass seeds has been recognized for many years. The literature reveals that factors affecting germination and methods for improving germination of Kentucky bluegrass has received much attention during the years (e.g. (Hite, 1919; Nelson, 1927; Gaβner, 1930; Bass, 1954; Jonas, 1961; Grimstad, 1985). The experiment in Paper VII explored the possibility of improving germination of Kentucky bluegrass by excluding light seeds from the seed lot. A relationship was established between seed weight and germination, but the potential effect of removing the light seeds appears to be of limited importance. Although the difference in performance between light and heavy seeds may be larger under field conditions, e.g. when seeds are sown too deeply (Nordestgaard, 1983; Tamet *et al.*, 1996), a reduction of mean germination time by up to one day by removing approximately 50% of the lightest seeds of the seed lot seems to be of no practical value. However, the relationship between seed weight and germination should be determined for more seed lots of each species to obtain stronger conclusions on this.

As discussed in Paper I, time to germination of Kentucky bluegrass can be reduced by means of various priming treatments. Priming does not speed up the germination by the magnitude needed to enhance the establishment of Kentucky bluegrass in mixtures with perennial ryegrass and red fescue, as determined in Paper I (Pill and Necker, 2001). Nevertheless, the use of primed seeds of Kentucky bluegrass may contribute to a better establishment. However, the effect of priming is often reduced to some extent by desiccation of the treated seeds, resulting in a practical challenge when storing and handling primed seeds. An alternative seed treatment for improving germination of Kentucky bluegrass involves removal of the *glumellae*. A preliminary experiment, which was carried out in this study, showed that the removal of *glumellae* can reduce time to germination by several days (Fig. 8). The effect suggests that germination of Kentucky bluegrass is somehow restrained by the *glumellae*. A possible mechanism of this restraint may be physical resistance against germination, or the *glumellae* may delay germination by oxygen consumption, as is the case in barley (*Hordeum vulgare* L.) (Lenoir *et al.*, 1986). The role of the *glumellae* in germination and the possibility of improving germination of Kentucky bluegrass by removing the *glumellae* need to be explored further.

An alternative approach to speeding up the slow-germinating species may be to slow down the fast-germinating species in a seed mixture, i.e. increasing the time to germination for red fescue and perennial ryegrass. This can be done by inducing varying degrees of dormancy which can increase the time to emergence without influencing seedling density (Khan, 1996). As discussed earlier, slow emergence may result in increased weed invasion, and it is, therefore, more desirable to reduce the time to germination for the slow species rather than increasing the time to germination for the fast species.

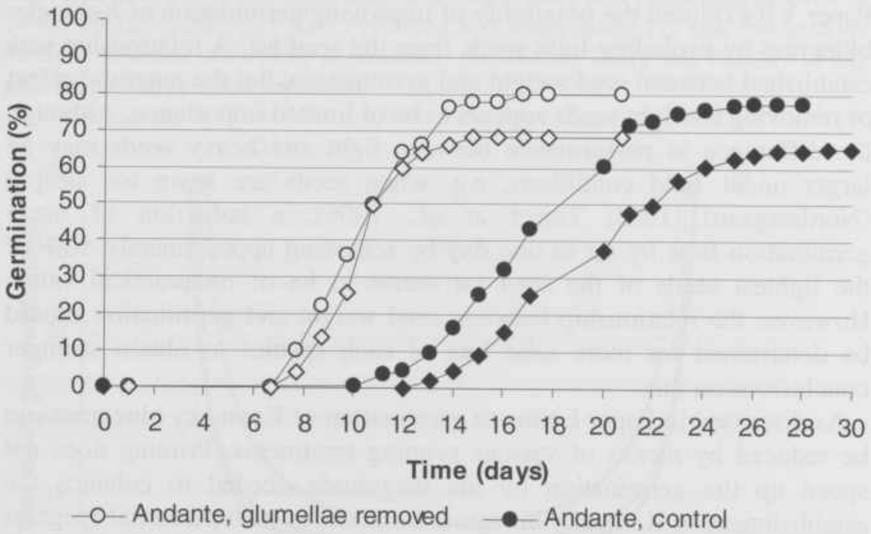

Figure 8. *The effect of removing glumellae on germination of two cultivars of Kentucky bluegrass. The glumellae were removed under microscope after 24 hours of imbibtion, and seeds were germinated at 10°C in darkness. The cumulative germination curves are based on 4*50 seeds per cultivar for the control treatments and 2*25 seeds for the removal of glumellae.*

5. CONCLUDING REMARKS

The present work has lead to a number of conclusions, which will be summarized in the following:

- It has been confirmed that Kentucky bluegrass establishes poorly when sown in mixture with red fescue and perennial ryegrass (Paper I). Since Kentucky bluegrass is a desirable turfgrass, it is relevant to study possible causes and solutions for this problem.
- The time factor is important for the competitive relationship between Kentucky bluegrass and the other grass species during establishment (Paper I). The present experiment does not distinguish between the effect of slow emergence and the effect of slow seedling growth, and considering previous studies both factors are likely to be involved. The results illustrate that species composition in the established turf can be modified by means of differential sowing time, i.e. it is possible to obtain a larger proportion of Kentucky bluegrass if sown prior to red fescue and perennial ryegrass (Paper I). Various practicalities have to be considered if applying differential sowing time, e.g. to carry out the second sowing without burying and damaging germinated seeds of Kentucky bluegrass. Besides, weed invasion may be a problem if Kentucky bluegrass is sown alone.
- Thousand-seed weight varies considerably between cultivars and even between seed lots of a single cultivar (Paper II). Variation in thousand-seed weight can potentially have a large effect on the composition of seed mixture by number. Thousand-seed weight as well as seed purity and viability should, therefore, always be taken into account when considering composition and establishment of seed mixtures.
- In germination studies of the three grass species, the choice of germination criterion is of low importance; radicle germination, coleoptile germination, and cotyledon germination are similarly and closely related to the criterion based on normal seedlings (Paper III). In contrast, the choice of method for analysing germination data may be of larger importance when analysing population behaviour. A generalized hyperbolic multinomial distribution summarized individual germination time courses effectively (Paper IV). The repeated probit analysis provided a reasonable description of germination response to reduced water potential, using the hydrotime concept (Paper V). Conversely, a non-linear regression analysis based on the Weibull function

provided a better description of germination response to temperature than the repeated probit analysis, when using the thermal time model (Paper VI). Interacting effects of temperature and water potential on germination affected the application of the hydrothermal time model (Paper V).

- When germinating at optimal conditions, final germination percentage was generally lower and mean germination time and time from 25 to 75% germination were generally higher for Kentucky bluegrass than for red fescue and perennial ryegrass (Paper IV). This suggests that differences in germination characteristics between the three species may be involved in the poor establishment of Kentucky bluegrass. Germination characteristics varied between cultivars within the three species and even between seed lots of a single cultivar. However, choosing a fast germinating cultivar of Kentucky bluegrass appeared to be of little practical impact compared to the required difference in sowing time to improve establishment of Kentucky bluegrass (Paper IV).
- Germination of Kentucky bluegrass seeds requires a longer thermal time and is more inhibited by reduced water potential compared to red fescue and perennial ryegrass (Papers V and VI). The results suggest that these differences in germination response to environmental factors may contribute considerably to the poor establishment of Kentucky bluegrass, particularly when seeds germinate in a cold and/or dry soil.
- Within a seed lot, heavy seeds of all three grass species generally had a higher germination percentage and a faster germination compared to light seeds (Paper VII). This enables a quality separation of seeds by their weight, but the effect of removing light seeds from a seed lot appear to be of limited practical value.

In conclusion, the results suggest that species differences in germination characteristics play a key role in the poor establishment of Kentucky bluegrass when sown in mixture with red fescue and perennial ryegrass. To get further insight into the establishment of Kentucky bluegrass and to achieve possibilities for improving the establishment, it is suggested that future work should focus on the following areas:

- Experimental work should aim at separating the effects of species differences in field germination percentage, field emergence percentage, time to field emergence, and post-emergence growth rate. A quantification of the relative contribution of these factors may aid in understanding the competitions dynamics of a turfgrass community during establishment. Moreover, this may indicate whether a solution should be based on seed-related factors or on cultural factors or both.

- Germination studies should aim at describing and understanding the combined effects of various environmental factors on germination of the grass species sown in mixtures. Studies should attempt to quantify interacting effects of the most important environmental factors, e.g. different fluctuating levels of water potential combined with fluctuating temperatures, which are often encountered in the seed bed. Besides, novel seed treatments for improving germination of Kentucky bluegrass seeds such as removal of the *glumellae* should be further explored as well as the effect of combining different seed treatments.
- From a practical point of view, research should address the potential combined effect rather than the individual effects of various cultural practices for improving germination and establishment of Kentucky bluegrass. Previous research has shown that establishment and competition of Kentucky bluegrass in mixture may be affected by a number of cultural factors, e.g. composition of the species seed mixture (Ebdon and Skogley, 1985), seed rate of the applied seed mixture (Engel and Trout, 1980), sowing depth (Käding and Kreil, 1982), fertilizer level (Schmidt and Taylor, 1981), and mowing strategy during establishment (Brede and Duich, 1984). In future studies it is relevant to study the effect of combining two or more of the factors that have been shown to improve establishment of Kentucky bluegrass. This may comprise seed treatments as well as other cultural treatments, e.g. the use of primed Kentucky bluegrass seeds sown prior to and/or at shallower sowing depth than red fescue and perennial ryegrass, followed by a fertilization and cutting strategy that also favours Kentucky bluegrass. Integrating various factors that all favour the establishment of Kentucky bluegrass will presumably aid the establishment of this species in mixtures.

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