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IMPACT OF GRAZING ON VEGETATION AND ON SELECTED PLANT SPECIES OF CALCAREOUS FENS

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PREFACE – VORWORT

Diese Arbeit ist „kummulativ“ entstanden. Da Veröffentlichungen in Fachzeitschriften oft einem breiteren Fachpublikum zugänglich sind als monografische Dissertationen, bearbeitete ich die einzelnen Themen meiner Doktorarbeit in Form von einzelnen Artikeln für Fachjournale und daher in der Fachsprache Englisch. Da ich das Thema der Beweidung als Alternativnutzung zur Streumahd nicht nur für die Wissenschaft, sondern auch für die praktische Naturschutzarbeit als sehr wichtig empfinde, schrieb ich Einleitung und Abschlussdiskussion auf deutsch, so dass sich keiner durch das Englisch abschrecken lassen muss. In diesen beiden Teilen sind die wichtigsten Aussagen der Arbeit zusammengefasst und diskutiert.

Natürlich sind am Entstehen dieser Arbeit viele Personen beteiligt gewesen, denen ich allen meinen herzlichen Dank aussprechen möchte. Zunächst meinem Doktorvater Professor Jörg Pfadenhauer für die Möglichkeit zur Mitarbeit und Promotion an seinem Lehrstuhl, insbesondere für die hilfreichen Diskussionsbeiträge, die diese Arbeit sehr verfeinert haben. Besonderer Dank geht an Frau Dr. Kathrin Kiehl, die mich seit der Diplomarbeit im Erlernen des wissenschaftlichen Arbeitens an die Hand genommen hat. Vielen Dank für zahlreiches Korrekturlesen, auch im Urlaub, für die hilfreichen Diskussionen, die immer möglich waren, für die Hilfestellung bei statistischen und anderen Problemen, für den Endspurt am Schluss, für vieles. Weiter geht der Dank an die Kollegen des Lehrstuhls, insbesondere dem „POP AK“, der manche Probleme löste, den Gießkolonnen im Gewächshaus, dem „Arbeitsamt“ für ein schönes Arbeitsklima, nicht nur während der Teepausen, Heike für Beistand, Diskussion und Korrekturlesen, Ingrid und Frau Tork für alle technischen und organisatorischen Auskünfte; den IAESTE-Praktikanten Lena und Maria und den Zivis Manu und Stephan für die Mithilfe bei der Feld- und Laborarbeit; Martina Brudi für das überlassen ihrer Diplomarbeit für weitere Auswertungen, Elisabeth Mair für das Korrekturlesen der englischen Arbeiten.

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Meinen Eltern möchte ich herzlich danken für das Domizil während der Feldarbeit, die Unterstützung und das Interesse an meiner Arbeit, z.B. beim Kuhfuß-Basteln. Ganz besonders danke ich natürlich meiner Mutter für die geduldige Hilfe bei der Feldarbeit bei jedem Wetter. Dank schulde ich aber vor allem Volker, der sich nicht davon hat abbringen lassen, mich trotz Doppelbelastung und Abgabestreß zu heiraten und mir immer den Rücken frei hielt.

CHAPTER 1

KAPITEL 1

IMPACT OF GRAZING ON VEGETATION AND ON SELECTED PLANT SPECIES OF CALCAREOUS FENS

AUSWIRKUNGEN DER BEWEIDUNG AUF DIE VEGETATION UND AUF AUSGEWÄHLTE PFLANZENARTEN VON MAGERWIESEN KALKREICHER NIEDERMOORE

EINE EINFÜHRUNG

IMPACT OF GRAZING ON VEGETATION AND ON SELECTED PLANT SPECIES OF CALCAREOUS FENS

AUSWIRKUNGEN DER BEWEIDUNG AUF DIE VEGETATION UND AUF AUSGEWÄHLTE PFLANZENARTEN VON MAGERWIESEN KALKREICHER NIEDERMOORE

EINFÜHRUNG

Oligo- bis mesotrophe, kalkreiche Niedermoore sind im Alpenvorland durch die Vegetation der Kleinseggenrieder (Caricion davallianae) und Kalk-Pfeifengraswiesen (Molinion caeruleae) gekennzeichnet (Oberdorfer 1998). Primär kommen Kleinseggenrieder nur kleinflächig im Verlandungsbereich oligotropher Seen oder um helokrene Hangquellen vor (Braun 1968). Ihre sekundäre Ausweitung verdanken sie der Beweidung von Erlen-Eschen- oder Erlen-Bruchwäldern, in denen so die Waldverjüngung unterdrückt wurde (Pfadenhauer 1989). Als der Bedarf an Einstreu in der Mitte des 19. Jahrhunderts durch vermehrte Stallhaltung stieg und die Streunutzung in Wäldern gesetzlich eingeschränkt wurde, wurden sekundäre Kleinseggenrieder durch eine im Herbst erfolgende Streumahd weiter ausgedehnt (Quinger et al. 1995). Zur Steigerung der Ernteerträge wurden die Kleinseggenrieder oftmals leicht entwässert, wodurch sie sich zu Pfeifengraswiesen entwickelten (Ellenberg 1996, Biewer & Poschlod 1997). Begrifflich wird im folgenden unterschieden zwischen dem Lebensraum für Pflanzen (kalkreiches Niedermoor), dem Nutzungstyp (Streuwiese, Herbstmahd) und dem Vegetationstyp (Kleinseggenried, Kalk-Pfeifengraswiese).

1 GEFÄHRDUNG DER ARTENVIELFALT VON MAGERWIESEN AUF KALKREICHEN NIEDERMOOREN

Generell bieten halbnatürliche Wiesen und Weiden in West- und Mitteleuropa Lebensraum für artenreiche Pflanzengemeinschaften (Pykälä 2000), so auch Streuwiesen auf kalkreichen Niedermooren (Quinger et al. 1995). Besonders bedeutend für die Koexistenz zahlreicher Arten sind die geringe Produktivität im Vergleich zu nährstoffreichen, intensiv genutzten Flächen und die regelmäßige, aber schwache Störung. Grace (1999), Tilman & Pacala (1993) und Waide et al. (1999) gehen von einer unimodalen Beziehung zwischen Produktivität und Artenvielfalt aus, da Pflanzen bei Nährstoffmangel unterirdisch um Bodennährstoffe konkurrieren, bei ausreichender Versorgung dagegen oberirdisch um Licht. In extensiv genutzten Wiesen und Weiden kommt es außerdem zu regelmäßigen, im Vergleich zum Intensivgrünland aber nur zu geringen anthropogenen bzw. zoo-anthropogenen Störungen. Auch zwischen Störung und Artenvielfalt besteht ein unimodaler Zusammenhang (Pickett & White

1985, White & Jentsch 2001): ohne Störung werden wenige Arten dominant und unterdrücken konkurrenzschwache Arten, bei häufiger Störung dagegen sind nur noch wenige Arten fähig, diese zu kompensieren oder zu vermeiden.

Der Wandel in der Landwirtschaft einerseits hin zur Intensivierung ertragreicher Standorte und andererseits hin zur Nutzungsaufgabe auf ertragsschwachen Standorten führt in Mitteleuropa im Verlauf des 20. Jahrhunderts zum Rückgang halbnatürlicher Wiesen (Bakker & Berendse 1999, Lavorel et al. 1998). Auch viele Magerwiesen auf kalkreichen Niedermooren wurden entweder intensiviert oder fielen brach. Seit dem Ende des zweiten Weltkriegs wurde der Bedarf an Einstreu durch Veränderungen in der Stallhaltung (d.h. Schwemmmistverfahren) geringer, weswegen ein Großteil der Streuwiesen durch Entwässerung und Düngung in Futterwiesen oder Ackerland umgewandelt wurde. Insbesondere die Eutrophierung – auch durch Nährstoffeintrag von umliegenden Fettwiesen, aus der Luft oder durch eutrophiertes Grundwasser - gefährdet Pflanzenarten der Streuwiesen und damit die Artenvielfalt der Vegetation, da sich hochwüchsige Pflanzenarten mit einem höheren Nährstoffbedarf ausbreiten und die weniger konkurrenzstarken Arten der Magerwiesen verdrängen (Bollens & Ramseier 2001, Egloff 1987). Durch Renaturierungsmaßnahmen wird heute versucht, artenreiche Pfeifengraswiesen auf ehemals intensiv genutzten Niedermoorstandorten durch Wiedervernässung, Aushagerung durch Sommerschnitt oder Bodenabtrag und Ansaat oder Pflanzungen wieder zu etablieren (Biewer & Poschlod 1997, Maas 1988, Kapfer 1997, Patzelt & Pfadenhauer 1998, Pfadenhauer et al. 2000). Einige der Maßnahmen sind erfolgreich, dennoch konnte bisher nie die Artenvielfalt ursprünglicher Streuwiesen erreicht werden, da sich in den Versuchen nicht alle Arten ansiedeln ließen. Deswegen ist die Erhaltung der Artenvielfalt noch traditionell genutzter Streuwiesen besonders wichtig (vgl. Young 2000). In Deutschland verbieten heute die Naturschuzgesetze (z.B. BayNatSchG Art. 13d) die Entwässerung und Düngung seggenreicher Nassstandorte. Deswegen bedroht heute nicht mehr die Intensivierung, sondern die Nutzungsaufgabe der ertragsschwachen, unrentablen Standorte die Artenvielfalt der Vegetation sekundärer Kleinseggenrieder und Kalk-Pfeifengraswiesen (Diemer et al. 2001, Thorn 2000): Durch den fehlenden Abtransport des Aufwuchses kommt es zunächst zur Bildung einer dichten Streuschicht und zu einer starken Dominanz weniger Grasartiger (z.B. *Molinia caerulea*, *Schoenus ferrugineus*), was die Verdrängung niedrigwüchsiger Arten und insgesamt die Abnahme der Artenzahl zur Folge hat.

Da in den meisten süddeutschen Gebieten der Bedarf an Einstreu gering ist (Quinger et al. 1995), stellt die Streumahd kalkreicher Niedermoore häufig nur noch eine zielorientierte, mit staatlichen Mitteln geförderte Pflegeform dar. Eine handlungsorientierte Naturschutzstratgie dagegen, die versucht die magere Feuchtwiesenvegetation durch eine Kopplung an das Landnutzungssystem zu erhalten, bietet langfristige Perspektiven (Pfadenhauer 1996). Daher wird für die Offenhaltung wirtschaftlich unbedeutender, produktionsschwacher, aber artenreicher Magerwiesen immer öfter bei Interesse der Landwirte die Beweidung vorgeschlagen, da sie weniger kostenintensiv ist (Riecken et al. 1999).

Da Beweidung in Abhängigkeit von der Art und Anzahl der Weidetiere und der Weideführung unterschiedliche Auswirkungen auf den Artenbestand haben kann, wird sie hinsichtlich ihrer Bedeutung für den Naturschutz kontrovers diskutiert (u.a. Luick 1996, Kapfer 1995, Jedicke et al. 1996).

2 UNTERSCHIEDLICHE AUSWIRKUNGEN VON WEIDE UND MAHD AUF DIE VEGETATION

Arten der Magerwiesen kalkreicher Niedermoore haben durch die späte Mahd im September Vorteile im Vergleich zur Brache oder zu einer früheren Mahd (Maas 1988, Schopp-Guth 1993). Spätblühende, hochwüchsige Arten haben durch den späten Mahdzeitpunkt die Möglichkeit, reife Samen auszubilden. Zusätzlich verfügen manche Arten über die Fähigkeit, Nährstoffe in Speicherorgane, die von der Mahd nicht erfasste werden, zu verlagern (Pfadenhauer 1989). Die geringe Nährstoffversorgung und der hohe mittlere Grundwasserstand (7-40 cm unter Geländeoberkante) limitieren die Produktivität der Streuwiesen (zwischen 10 und 40 dt/ha), so dass die Pflanzendecke ausreichend Licht für niedrigwüchsige Arten durchlässt (Quinger et al. 1995). Die Mahd im Herbst fördert die meisten Arten indirekt, da sie bereits ihre Wachstumsperiode abgeschlossen haben und nicht durch den Schnitt geschädigt werden. Durch den Biomasseentzug im Herbst wird aber die Bildung einer Streuschicht verhindert, die im Frühjahr das Wachstum konkurrenzschwacher Pflanzenarten und auch die Keimung neuer Individuen behindern würde.

Während es in Streuwiesenbrachen durch die Akkumulation der Streu zu einem Artenrückgang kommt, verhindert die Beweidung durch den Verbiss des Aufwuchses die Bildung einer Streuschicht. Unter Beweidung kommt es aber im Gegensatz zur Streumahd nicht zu einer einmaligen Störung im Herbst, sondern zu einer kontinuierliche Störung während der Weidezeit (Peintinger 1999). Neben diesen zeitlichen Unterschieden zwischen Beweidung und Mahd findet Störung auf der Weide auch räumlich differenziert statt, da Teile der Weide vom Weidevieh oft besucht werden (z.B. am Zaun, in der Nähe der Tränke), während andere ungenutzt bleiben (Olff & Ritchie 1998). Zusätzlich unterscheidet sich die Art der Störungen in Form von Tritt, Verbiss oder Dung auf der Weide vom Schnitt auf der Streuwiese (Mulder 1999). So wird der Schaffung von Offenstellen durch Tritt Bedeutung für die Erhaltung der Artenvielfalt beigemessen (Bullock et al. 2001, Isselstein et al. 2002, Schläpfer et al. 1998).

Die Reaktion von Pflanzengemeinschaften auf Beweidung wurde in anderen Habitaten mit Hilfe von “response groups” beschrieben, d.h. Gruppen von Arten, die aufgrund ihrer Eigenschaften (z.B. Wuchsform, Ausbreitungsfähigkeit) ähnlich auf Beweidung reagieren (Bullock et al. 2001, Lavorel et al. 1997). Arten, die Beweidung aufgrund ihrer Arteigenschaften vermeiden oder tolerieren können, werden in Weiden gefördert (Crawley 1997). Grasartige können Beweidung tolerieren, da sie in der Lage sind, Biomasseverluste schnell zu kompensieren, niedrigwüchsige Rosettenpflanzen und Arten mit Abwehrstoffen, da sie den Verbiss durch ihre Wuchsform oder ihre Inhaltsstoffe vermeiden können (z.B. Lavorel et al. 1998, McIntyre et al. 1999). Das Vorkommen von Artengruppen auf Weiden aufgrund bestimmter Arteigenschaften wurde bisher nur im Vergleich zu Brachen oder zu Exclosures untersucht, nicht jedoch im Vergleich zu gemähten Wiesen (Bullock et al. 2001).

3 DIE BEDEUTUNG POPULATIONSBIOLOGISCHER MERKMALE FÜR DAS VORKOMMEN VON ARTEN UNTER BEWEIDUNG

Auf der Ebene der Population kann die Beweidung ebenfalls das Vorkommen von Pflanzenarten beeinflussen, z.B. hinsichtlich der Alters-Entwicklungsklassen-Struktur (Bühler & Schmid 2001, Oostermeijer et al. 1994). So kann eine auf der Weide im Vergleich zur Streuwiese veränderte Etablierungsrate, Lebensdauer oder Reproduktionsrate die Populationsdichte von Arten verändern (Mulder 1999). Beispielsweise bildet *Primula farinosa* unter Beweidung mehr Fruchtstände aus als unter Streumahd (Schopp-Guth 1993), die Art keimt in durch mehrfache Mahd niedrig gehaltener Vegetation besser als in nur im Herbst gemähten Streuwiesen (Maas 1988). Insbesondere das vermehrte Auftreten von Offenstellen in Weiden durch Tritt (Bullock 2001) kann eine Beschleunigung des Kreislaufs aus Extinktion und Wiederbesiedlung, und damit eine Veränderung der Alters-Entwicklungsklassen-Struktur hin zu einem höheren Anteil an Keimlingen bewirken (Grubb 1977, van der Maarel & Sykes 1993, Zobel et al. 2000). Für gefährdete Arten werden sowohl die Alters-Entwicklungsklassen-Struktur als auch die Lebensdauer zur Bewertung des Aussterberisikos einer Population herangezogen (Oostermeijer et al. 1994, Colling et al. 2002, Hegland et al. 2001). Anhand dieser demografischen Merkmale ist es möglich, Managementstrategien für die Naturschutzarbeit, z.B. über die Eignung der Beweidung als Alternative für die Mahd ab zu leiten (Cornelius 1991).

4 ZIEL DER ARBEIT

In dieser Arbeit möchte ich den Einfluss der Beweidung auf die Vegetation der Magerwiesen auf kalkreichen Niedermooren im Vergleich zur Streumahd, aber auch zur Brache analysieren. Dabei werden zunächst die Unterschiede zwischen den Pflanzengemeinschaften beweideter und gemähter Niedermoorwiesen betrachtet. Um aber die Mechanismen zu verstehen, die zur Veränderung der Artenzusammensetzung führen, sind zusätzlich Untersuchungen auf der Ebene des Individuums und der Population notwendig. Die Fragestellungen für diese Arbeit sind daher:

(1) Läßt sich das Vorkommen von Arten auf Weiden und Streuwiesen durch Arteigenschaften (species traits) erklären?

(2) Gibt es zwischen Weiden und Streuwiesen Unterschiede hinsichtlich der Populationsdichte und Frequenz häufiger Kennarten von Kalk-Pfeifengraswiesen und Kleinseggenrieden des Alpenvorlands?

(3) Kommt es auf Weiden im Vergleich zu Streuwiesen zu einer Veränderung in der Alters-Entwicklungsklassen-Struktur der Pflanzenpopulationen?

(4) Wie wirken sich Beweidung, Brache und Streumahd auf einzelne Lebensphasen (z.B. Keimung) verschiedener Arten aus?

(5) Gibt es Arten, die auf Sonderstandorten der Weiden (z.B. Trittstellen) gefördert werden?

(6) Welche Faktoren der Weide (Tritt, Verbiss, Dung) limitieren das Vorkommen der Pflanzenarten am stärksten, so dass deren negative Auswirkungen durch das Weidemanagement minimiert werden müssen, um die Arten auf Weiden zu erhalten?

5 FLÄCHENAUSWAHL

Bei den Untersuchungsflächen handelt es sich einerseits um traditionell im Herbst gemähte Streuwiesen und andererseits um langjährig genutzte Weiden auf Niedermooren im bayerischen Alpenvorland. Die Weidenutzung konnte dort auf Allmendeflächen überdauern, da die häufig große Zahl der Nutzungsberechtigten Intensivierungsmaßnahmen oder die Umwandlung zu Streuwiesen verhinderte (Radlmair et al. 1999). Auch heute werden dort Tiere verschiedener Landwirte auf die Flächen getrieben, auf manchen Flächen gibt es allerdings nur wenige Nutzungsberechtigte, die ihre Weiderechte noch ausführen (Brudi n.p.). Die Viehweiden werden von Mai bis August/September beweidet, überwiegend mit Rindern (meist Jungvieh); nur eine der Untersuchungsflächen (Nr. 9 bei Ettal; Abb. 1) war eine Pferdeweide. Der größte Teil der einzelnen Weideflächen liegt jeweils auf mineralischem Boden, während Niedermoorböden nur kleine Bereiche (im Mittel 20 % der Gesamtfläche) einnehmen. Der Weidedruck auf den Niedermoorbereichen ist demnach gering und entspricht nach einer Berechnung von Brudi (n.p.) einem Besatz von weniger als einer Großvieheinheit pro Hektar. Für den Vergleich von Mahd und Beweidung wurden 18 Flächenpaare ausgewählt (Abb. 1), bei denen langjährige Weide und Streumahd direkt benachbart und nur durch einen Zaun getrennt waren. Dadurch wurden die standörtlichen und kleinklimatischen Unterschiede innerhalb der Flächenpaare möglichst gering gehalten. Für experimentelle Untersuchungen (siehe folgender Abschnitt „Aufbau der Arbeit“) wurden in Pfefferbichl (Landkreis Ostallgäu, Nr. 8 in Abb. 1) eine Brachfläche, eine Weide und eine Streuwiese ausgewählt, die direkt benachbart waren. Die Vegetation der Flächen wurde von Brudi (n.p.) den Kleinseggenrieden (Caricion davallianae) oder den Kalk-Pfeifengraswiesen (Molinion caeruleae) zugeordnet.

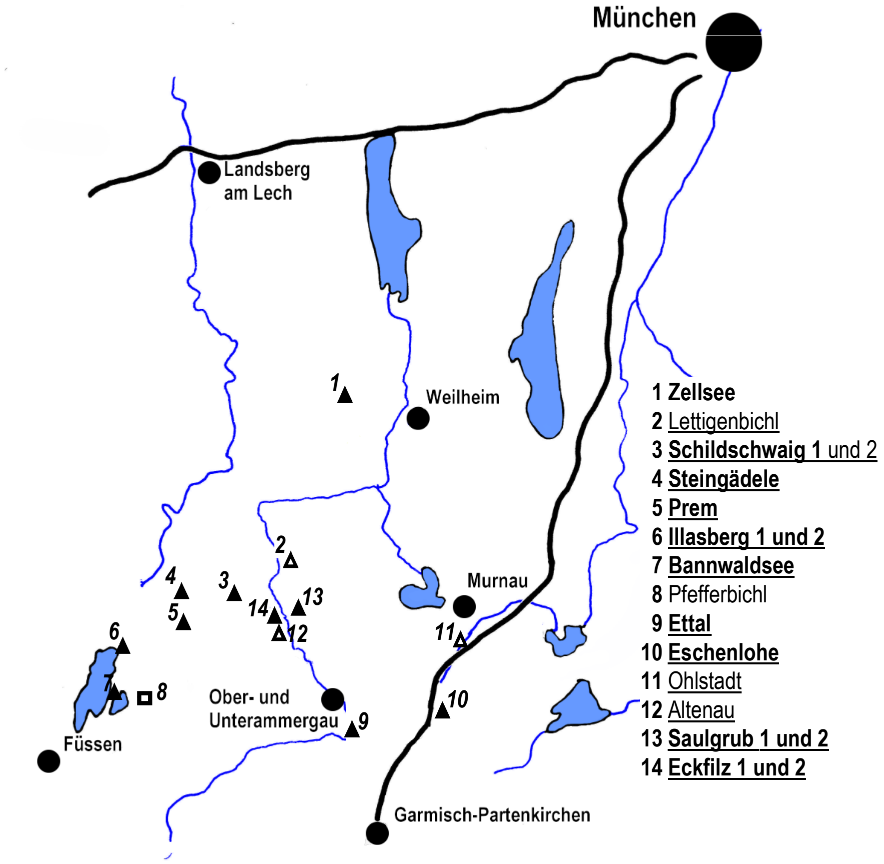

Abb. 1: Überblick über die Lage der Flächen, unterschieden in ☐ Flächen der experimentellen Untersuchungen (Kap. 4, 5), ▲ Flächenpaare der Vegetationsaufnahmen (unterstrichen, Kap. 2) und der Ermittlung der Populationsdichte (fett, Kap. 3), Δ weitere Flächenpaare der Vegetationsaufnahmen von 1995 (Kap. 2), die in den Jahren 2000-2002 nicht mehr beweidet wurden.

6 ARTENAUSWAHL

Als Arten für die populationsbiologischen Untersuchungen wurden subdominante (sensu Suding 2001) Kennarten der Magerwiesen kalkreicher Niedermoore ausgewählt. Die Reaktion häufiger Kennarten auf unterschiedliche Nutzungsweisen lässt sich leichter auf andere Arten mit ähnlichen Arteigenschaften übertragen, als die Reaktion von Arten, die bereits durch besondere Standortansprüche, durch einen speziellen Lebenszyklus oder durch eine beschränkte Ausbreitung selten sind. *Parnassia palustris*, *Pinguicula vulgaris*, *Primula farinosa*, *Serratula tinctoria*, *Succisa pratensis* und *Tofieldia calyculata* wurden ausgewählt, da sie die oben beschriebenen, für die Vegetation von Magerwiesen auf kalkreichen Niedermooren typischen Wuchsformen (niedrigwüchsig oder hochwüchsig und spätblühend) mit verschiedenen Reproduktionseigenschaften (Samenmenge, Samengewicht, klonale Vermehrung) repräsentieren. Bezüglich der unterschiedlichen Wuchsformen können Hypothesen bezüglich der Vor- und Nachteile der Arten auf Weiden formuliert werden (Tab. 1).

Tab. 1: Überblick über Wuchsform und Reproduktionseigenschaften der untersuchten Arten, über die Hypothesen bezüglich der Vor- oder Nachteil auf Weiden im Vergleich zu Streuwiesen und über die Kapitel dieser Arbeit, in denen die Arten behandelt werden (Quelle: Frank & Klotz 1988). Bei allen Arten handelt es sich um Hemikryptophyten.

	Wuchsform	Reproduktions-eigenschaften	Hypothese: Vorteil / Nachteil auf Weide	Untersucht in Kapitel
Parnassia palustris	Niedrigwüchsig, aber nicht niederliegend; Höhe ~ 10 cm	Blütezeit: VII-VIII Samen: sehr leicht und sehr zahlreich Klonalität: gering	unklar, da Verbiss möglich, aber auch Vorteil aus Verbiss der umgebenden Vegetation	II, III, IV, V
Pinguicula vulgaris	Niederliegende Rosettenpflanze; Höhe < 5 cm	Blütezeit: VI Samen: sehr leicht und zahlreich Klonalität: stark	Vorteil auf Weide, da Rosette nicht verbissen wird, umgebende Vegetation schon	II, IV, V
Primula farinosa	Niederliegende Rosettenpflanze; Höhe < 5 cm	Blütezeit: V Samen: mittleres Gewicht, zahlreich Klonalität: gering	Vorteil auf Weide, da Rosette nicht verbissen wird, umgebende Vegetation schon	II, III, IV, V; Box
Serratula tinctoria	Hochwüchsig, ~ 60 cm	Blütezeit: VIII-IX Samen: schwer; relativ wenige Klonalität: gering	Nachteil auf Weide, da hochwüchsig und spätblühend	II, V; Box
Succisa pratensis	Hochwüchsig, ~ 60 cm	Blütezeit: VIII-IX Samen: schwer; relativ wenige Klonalität: gering	Nachteil auf Weide, da hochwüchsig und spätblühend	II, III, IV, V; Box
Tofieldia calyculata	Niedrigwüchsig, aber nicht niederliegend; Wuchshöhe ~ 10 cm	Blütezeit: VII-VIII Samen: leicht, zahlreich Klonalität: stark	unklar, da Verbiss möglich, aber auch Vorteil aus Verbiss der umgebenden Vegetation	II, III, IV, V

7 AUFBAU DER ARBEIT

Der Einfluss der Beweidung auf die Vegetation von Magerwiesen kalkreicher Niedermoore wird in dieser Arbeit mit zwei Methoden untersucht. Mit Hilfe eines beschreibenden Ansatzes sollen die Effekte langjähriger Beweidung auf die Vegetation im Vergleich zur Herbstmahd ermittelt werden. Durch den experimentellen Ansatz soll der Einfluss der Faktoren Tritt und Verbiss auf Individuen und auf einzelne Lebensstadien getrennt untersucht werden. Die Auswirkungen der Beweidung werden so auf der Ebene der Pflanzengemeinschaft, der Population der ausgewählten Arten und auf besonders kritische Lebensphasen (Keimung und Etablierung) mit denen der Herbstmahd und der Brache verglichen.

Im **Kapitel 2** wird die Vegetation langjähriger Weiden und Streuwiesen auf kalkreichen Niedermooren untersucht und die Unterschiede in der Artenzahl und der Artenzusammensetzung beschrieben. Dabei wird das Vorkommen von Artgruppen auf Streuwiesen oder Viehweiden mit Arteigenschaften wie Wuchsform oder Reproduktionseigenschaften in Beziehung gesetzt. Im **Kapitel 3** werden die

Unterschiede in der Populationsdichte und der Alters-Entwicklungsklassen-Struktur der ausgewählten Arten auf Weiden und Streuwiesen untersucht. So werden einerseits besonders gefährdete Lebensphasen der Arten auf der Weide, andererseits auch Lebensphasen, für die Beweidung von Vorteil ist, herausgearbeitet. **Kapitel 4** behandelt den Sonderstandort Trittstelle auf Viehweiden, weil offene Bodenstellen, in denen konkurrenzschwache Arten keimen können, als bedeutend für die Erhaltung der Artenvielfalt angesehen werden. Dabei wird die Besiedlung von Huftritten in Weiden und von künstlichen Lücken in Brachen durch Keimlinge und vegetative Sprosse untersucht. Schließlich wird in **Kapitel 5** die Lebensphase der Keimung und Etablierung, die für viele Arten limitierend ist, für die sechs ausgewählten Arten untersucht. Artspezifische Unterschiede in der Rekrutierung neuer Individuen werden dabei mit Hilfe zweier Aussaatexperimente in simulierter Weide, Streuwiese und Brache und unter Nutzung ermittelt. Als Ergänzung werden in einer **Box** die Ergebnisse eines Beweidungssimulations-Experiments zusammengefasst, bei dem der Einfluss unterschiedlicher, simulierter Verbissintensitäten und Verbisszeitpunkte auf ausgewählte Arten untersucht wurde. Dabei wird die Fähigkeit der einzelnen Arten, Biomasseverluste zu kompensieren, verglichen. Abschließend werden in **Kapitel 6** die Ergebnisse der Teilkapitel übergreifend diskutiert und mit Ergebnissen aus der Literatur verglichen. Daraus werden Empfehlungen für den praktischen Naturschutz abgeleitet.

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CHAPTER 2

ALTERNATIVE MANAGEMENT ON FENS: RESPONSE OF SPECIES COMPOSITION AND SPECIES TRAITS TO GRAZING OR MOWING

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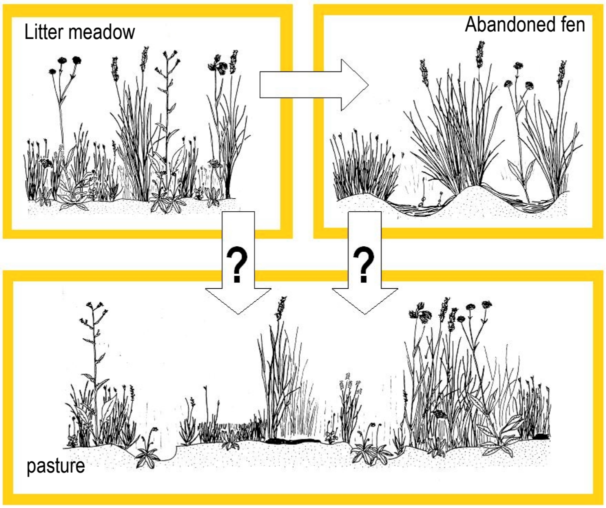

ALTERNATIVE MANAGEMENT ON FENS: RESPONSE OF SPECIES COMPOSITION AND SPECIES TRAITS TO GRAZING OR MOWING

ABSTRACT: The impact of cattle grazing on the vegetation of calcareous fens was compared to the effects of traditional autumn mowing in southern Germany. Vegetation composition was studied in 16 adjacent pairs of fen meadows and pastures with similar environmental conditions and biomass production. Vegetation data were analysed with respect to species richness, species composition and response of species traits to disturbance, including morphology, defence mechanisms, clonal growth form and generative reproduction. Species richness was significantly reduced by grazing, but the percentage of typical fen species or Red Data Book species was not affected by land use type. A detrended correspondence analysis indicated that species composition could best be explained using a land use gradient. Species traits showed a clear trend in their response to land use type. Grazing favoured grasses and small forbs. Only a few species with defence mechanisms against foraging were more frequent or abundant on pastures. Many other species with defence mechanisms, however, did not have an advantage on pastures. Flowering and seed dispersal traits did not respond significantly to grazing or mowing. Species with fast spreading stem-derived clonal organs were favoured on pastures, whereas all other clonal growth forms and especially non-clonal species were more abundant on meadows. More indicator species of wet soil conditions and species adapted to flooding were found on pastures. Grazing can be recommended as an alternative land use to mowing in contrast to abandonment, but a reduction in species richness and changes in species composition and species traits may occur.

NOMENCLATURE: Oberdorfer (1994) for vascular plants, Frahm & Frey (1992) for mosses.

KEYWORDS: cattle grazing, calcareous fen, pasture, fen meadow, plant functional type, clonal growth, growth form, reproduction

INTRODUCTION

Calcareous fens in the pre-alpine region of southern Germany have become rare due to drainage and land use intensification (Quinger et al. 1995, Güsewell et al. 1998). The common species-rich vegetation types of Molinion caeruleae and Caricion davallianae meadows are dominated by sedges and grasses and contain many prostrate and upright late flowering plants (Oberdorfer 1998). They have developed under traditional moderate land use such as late autumn mowing without fertilization: the low yield of the so-called litter meadows was not used as fodder but as bedding in cattle sheds. At present, land use changes generally lead to abandonment of low productive meadows on nutrient poor soils (Bakker & Berendse 1999). As a consequence, tall sedge species become more dominant, procumbent species decline and typical plant species of calcareous fens become rare or endangered (Diemer et al. 2001). Management for nature conservation in semi-natural grasslands should be aimed at reducing dominant species and promoting germination or vegetative spreading of target species which are often weak light competitors (e.g. Bakker 1989, Hald & Vinther 2000). Moderate grazing as the major management form in temperate grasslands (Bullock et al. 2001) is considered to maintain species diversity and is recommended as an alternative to traditional mowing regimes on semi-natural habitats (Bakker 1989, Pykälä 2000). Other studies suggest weak or even negative effects of grazing depending on grazing intensity and nutrient availability (Olff & Ritchie 1998, Proulx & Mazumder 1998). For calcareous fens, grazing is also discussed as a conservation management tool, particularly as it was the former land use before the development of litter meadows in the 19th Century (Radlmair et al. 1999).

Many studies exist which examine the influence of different stocking rates on vegetation composition (reviewed in Bullock et al. 2001) or on the comparison of grazing to abandonment or exclosures as a control (e.g. Vulnik et al. 2000, Diaz et al. 2001). However, only a handful of studies, most of them in dry habitats, directly compare moderate grazing and mowing. Gutser & Kuhn (1998) and Hansson & Fogelfors (2000) found no differences in species richness between meadows and pastures whereas Schläpfer et al. (1998) detected a higher species richness on grazed sites. For fen vegetation, investigations exist about the influence of land use considering different mowing times (Kapfer & Pfadenhauer 1986, Diemer & Pfadenhauer 1987) or abandonment (Diemer et al. 2001), but only Peintinger (1999) compared pastures and meadows on fens and found less species on pastures. As investigations concerning single species are very time consuming and generalizations are difficult, a considerable interest exists in the response of plant traits to grazing in order to predict vegetation dynamics (e.g. Lavorel et al. 1997, Bullock et al. 2001, Vesk & Westoby 2001): Moderate grazing offers an advantage for short-lived plants, grasses and flat rosettes and/or for species with high seed dispersal ability, but this has never been verified for fen vegetation. Furthermore, response of grazing related traits to mowing has not been investigated.

We analysed vegetation composition and species traits in order to compare the effects of grazing and autumn mowing on fen meadows. The aim of the study was to formulate recommendations as to whether grazing is suitable as an alternative form of land use in fens instead of the traditional mowing. The following questions were addressed: (1) Are there differences in the impact of grazing and mowing on vegetation composition, on species richness and on the occurrence of typical or endangered fen species? (2) Do differentiating species exist which are more favoured by grazing or mowing, respectively? (3) Can species groups based on traits of morphology, reproduction or defence mechanisms be identified, which are favoured or depressed by grazing? Are these response groups similar to general findings in other habitats?

METHODS

STUDY SITE

The study was carried out in 16 grazed and 16 mown fens in southern Germany in the pre-alpine region at an altitude between 630 and 870 m a.s.l. The geographical range varied between 10°40’ and 11°10’ E and 47°36’ and 47°42’N. The climate can be described as moist and cool with a mean annual temperature of 6 to 7 °C and a mean annual precipitation between 1200 and 1600 mm. A distinct rainfall maximum occurs during summer. Soils are nutrient poor as they were never fertilized intensively and consist of peat layers which have developed under high ground water tables above calcareous grounds. Two management types exist: late mowing in autumn and moderate cattle grazing. The meadows were mown not earlier than September when vegetation starts yellowing; the pastures were grazed moderately by less than 0.5 young cattle ha^{-1}. Most of the sites were grazed from May to October during the whole vegetation period; only a few were grazed for a couple of weeks in a higher intensity. Pastures on fens were always connected to areas on mineral soils with a higher fodder quality and a better nutrient availability. Vegetation is dominated by *Schoenus ferrugineus* and *Molinia caerulea*; *Carex* species are also abundant. Sites can be identified as Primulo-Schoenetum, Caricetum davallianae or Molinietum caeruleae in general (Oberdorfer 1998), but species composition is influenced by management and is therefore the object of the study.

FIELD METHODS

To reduce effects of other non-required factors, the study sites were selected in order to meet the following conditions: (1) the described vegetation types of nutrient poor calcerous fens has to be present; (2) actual land use of either grazing or mowing had to be continuous for at least 10 years; (3) paired study sites of mown and grazed fens had to be adjacent. To ensure the similarity of the abiotic conditions at the paired grazed and mown plots, ground water level and pH-value were measured once in each of the 32 sites. As a measure of productivity aboveground biomass was harvested at the time of maximum standing crop (August). At each of the 32 sites three biomass samples of 25 cm x 25 cm were clipped above soil level, dried to weight constancy and weighed. At each of the biomass sampling plots mean vegetation height was measured additionally as height, when a 0.25 m^2 styrofoam-quadrat (180 g) stopped falling. Vegetation plots of 5 m x 5 m had been established in summer 1994 by M. Brudi (unpublished report). The number of plots per site depended on the size of the fen. Overall, 109 plots were established on the 16 land-use pairs (51 on late mown fens, 58 on grazed ones). Cover of all species was recorded according to a modified Braun-Blanquet scale (Pfadenhauer et al. 1986).

DATA ANALYSIS

The factors groundwater level and pH-value and the factors biomass and vegetation height were analysed by a paired t-test. Between biomass and vegetation height a Pearson's correlation was calculated. For statistical analysis of the vegetation data, Braun-Blanquet-cover classes were transformed to mean percentage cover (class means). Species richness and evenness of all plots were determined. As evenness should be independent from species richness, the evenness index E1/D was calculated as recommended by Smith & Wilson (1996). The t-test or the Mann-Whitney U-test was used to compare species richness, species abundance and evenness of the two land use types. To compare adjacent sites the data of all plots per site and land use were summarized to one frequency data set. The frequency data were analysed by a paired t-test or the Wilcoxon-Test for non-parametric data. Plant species were defined as typical fen species when they belonged to the vegetation class Scheuchzerio-Caricetea nigrae or to the vegetation order Molinietalia (Ellenberg et al. 1992). For all plots the number of species listed in the Red Data Book (Korneck et al. 1996) was determined as they represent the target species of nature conservation. Plant species, which differed significantly in cover or frequency between grazed and mown sites, were defined as "differentiating species". A detrended correspondence analysis (DCA) was performed with the frequency data by PC-Ord 4 (McCune & Mefford 1999). Rare species appearing less than 3 times were excluded before the calculation. To compare the explained variance of the ordination with the real variance in the data set, an after-the-fact evaluation was calculated using the relative Euclidean distance as recommended by McCune & Mefford (1999). The after-the-fact evaluation is performed by calculating the coefficient of determination (r2) between distances in the ordination space and distances in the original space.

To analyse vegetation response to different management types, all vascular species were assigned to groups based on seven traits (Tab. 1). The selection of grouping variables considered response to grazing in particular. The percentage of the single groups was compared between land use types using the t-test or Mann-Whitney-U-test. For the traits "pollination", "dispersal" and "clonal growth form" species could be grouped to more than one class. The traits of the differentiating species were investigated separately. We looked for the impact of foraging and trampling using investigating factors including growth form, reproduction traits, clonal growth form and defence mechanism (for details see Tab. 1). Thereby the defence mechanisms were related to defence against domestic grazers like cattle or sheep and not against other herbivores like insects or snails. As grasses and forbs differ in their response to grazing, the analysis was performed for the whole dataset and for these two groups separately. Finally, the Pearson-Product-Moment correlation between the proportion of the different groups in the frequency data set and the site scores of the DCA and between the environmental factors and the site scores of the DCA was calculated.

Tab. 1: Species attributes for the identification of responses to grazing and mowing. All species were assigned to different groups of traits according to morphology, defence mechanism against herbivory, generative and vegetative reproduction. Grasses and forbs were further subdivided in subgroups. References and databases for each trait are listed in last column.

Trait	Group	Subgroup	Reference
Morphology	grasses forbs trees mosses	tillers, bulks rosettes, upright plants	Oberdorfer (1994)
Defence	chemical compounds mechanical defence without defence		Frohne & Jensen (1998), Stählin (1971) Klapp (1971)
Flowering time	early (starting May or earlier) middle late (starting August or later)		Oberdorfer (1994), Müller-Schneider (1986)
Flowering time span	short (1-2 month) middle (3-4 months) long (more than 4 months)		Oberdorfer (1994), Müller-Schneider (1986)
Pollination	insect self wind		Frank & Klotz (1988)
Dispersal	zoochoreous anemochoreous hydrochoreous		Müller-Schneider (1986)
Clonal growth form	non clonal root derived stem derived, fast spreader stem derived, slow spreader bulbs and tubers		Klimeš L. et al. (1997) and http://www.butbn.cas.cz/klimes/system.html

RESULTS

SITE CONDITIONS

Ground water level did not differ significantly between the two land use types mowing and grazing, but was slightly lower on the mown sites. The pH-value varied between 6.5 and 7.5, but was always similar for the paired sites, so no significant difference between grazed and mown sites could be found. Vegetation on mown sites was slightly higher (24.4 cm compared to 19.3 cm on pastures) and produced more aboveground biomass (1103 g m-2 compared to 954 g m-2 on pastures). But both differences were not significant. Additionally both parameters were positively correlated (r = 0.6; p < 0.001).

SPECIES RICHNESS

A total of 204 vascular plant species and 27 moss species were recorded on all plots. On the 51 mown plots, 180 vascular plants species and 26 moss species were found, compared to only 168 vascular plant species and 27 moss species on the 58 grazed plots. Sixty-nine species occurred on one land use type only, but only 14 (5 on pastures, 9 on meadows) of them were found in more then 4 plots. Management type had a significant effect on species richness concerning both number of species on the 25 m2 plots and number of species per study site (see Tab. 2). Evenness values E1/D were significantly higher on pastures than on meadows. The number of typical fen species and species listed in the Red Data Book was slightly higher on meadows than on pastures, but the proportion did not differ. On average 40 % of the species on a 25 m2 plot were typical fen species and 15 % were listed in the Red Data Book in both land use types. Total number of differentiating species (species which differed significantly (p < 0.05) between land use types concerning frequency and abundance) was higher on meadows (30) than on pastures (18) (see appendix 1). Most of the species differed in respect to frequency.

Tab. 2: Total number of species, species richness per 25 m^2 plot and per site, evenness $E_{1/D}$, number of typical fen species, Red Data Book species and number of differentiating species on pastures and meadows. The last column shows the significance levels of t-test (abbreviated: t), paired t-test (paired t) or U-test (U): n.s. not significant; * p < 0.05; ** p < 0.01; *** p < 0.001.

	Pasture	Meadow	Significance level	
Total number of species	195	206		
Average number of species per 25 m^2 plot (± standard deviation)	43.1 (± 9.8)	50.4 (± 9.0)	***	(t)
Average number of species per site (± standard deviation)	70.5 (± 19.4)	78.6 (± 21.0)	*	(paired t)
Evenness $E_{1/D}$ (± standard deviation)	0.30 (± 0.08)	0.23 (± 0.07)	*	(t)
Average number of typical fen species per 25 m^2 plot (± standard deviation)	17.5 (± 4.4)	19.4 (± 3.8)	*	(t)
Scheuchzerio-Caricetea nigrae (± standard deviation)	10.1 (± 3.3)	10.1 (± 2.5)	n.s	(U)
Molinietalia (± standard deviation)	7.4 (± 3.4)	9.3 (± 3.3)	**	(U)
Average number of Red Data Book species per 25 m^2 plot (± standard deviation)	6.4 (± 2.1)	7.4 (± 2.7)	*	(U)
Total number of differentiating species	18	30		
according to abundance	9	17		
according to frequency	16	26		
Total number of species, occurring only in one management type	25	36		
in more than 4 plots	5	9		

SPECIES COMPOSITION

The de-trended correspondence analysis of species frequency revealed a short gradient length of 1.6-standard deviation for the first axis, and of 1.2-standard deviation for axis 2 and 3. The after-the-fact evaluation of the ordination showed an r2 of 0.38 for axis 1, 0.09 for axis 2 and 0.01 for axis 3. The frequency of the following species showed a high correlation with axis 1: *Phyteuma orbiculare* (0.71), *Pimpinella major* (0.66), *Astrantia major* (0.64), *Primula elatior* (0.61), *Gentiana asclepiadea* (0.61), *Euphrasia rostkoviana* (0.59), *Trollius europaeus* (0.59), *Festuca ovina* (0.55), *Luzula multiflora* (0.54) and *Sanguisorba officinalis* (0.54) were more abundant on meadows, whereas *Juncus articulatus* (-0.80), *Mentha aquatica* (-0.72), *Valeriana dioica* (-0.59), *Trifolium repens* (-0.59) and *Mentha arvensis* (-0.50) occurred more frequently on pastures. The paired mown and grazed sites were separated very well by the DCA (Fig. 1). A paired t-test for the axis 1 scores showed significant differences between pastures and meadows (t = -7.1; p < 0.001). Some scores of pastures were close to the meadow group, but when the pairs of adjacent meadows and pastures were connected a clear trend in the direction of axis 1 was detected for all pairs.

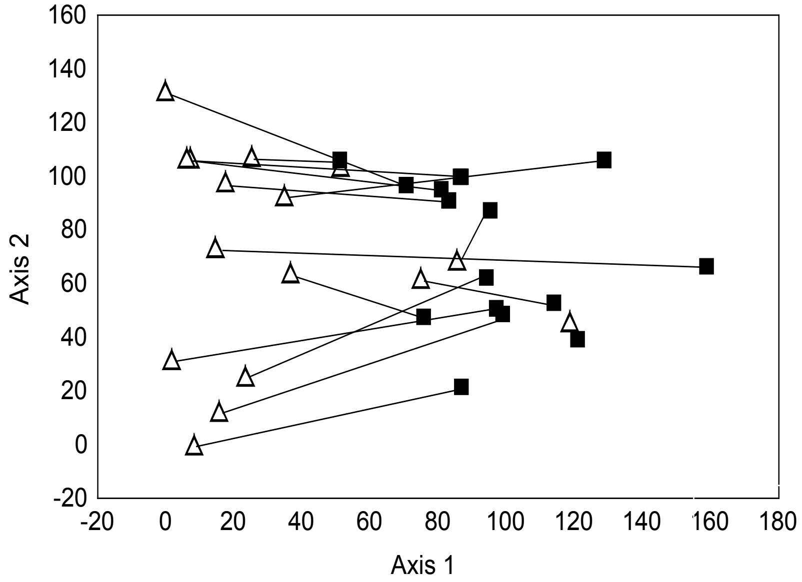

Fig. 1: Axis 1 and 2 of the de-trended correspondence analysis of the frequency data, scaled as raw scores. Each symbol marks a site. Lines connect the paired meadows (■) and pastures (Δ) of adjacent sites.

RESPONSE OF PLANT TRAITS

The analysis of plant traits indicated clear differences between pastures and meadows (Tab. 3). The percentage of grass species was significantly higher on pastures than on meadows where, in contrast, more forbs were found. For trees and mosses, no differences caused by management type were detected. On pastures, significantly more tiller forming grasses occurred, whereas on meadows the proportion of bulk grasses was higher. The forbs in the pasture were represented by relatively more rosettes and prostrate plants. In meadows, in contrast, more upright forb species were found (e.g. *Angelica sylvestris*, *Cirsium rivulare*, *Filipendula ulmaria*, *Gentiana asclepiadea*, *Laserpitium prutenicum*). The proportion of therophytes, which are generally uncommon in fen vegetation, did not differ between pastures and meadows (1-2 species per plot). The differentiating species showed similar trends: on meadows many herbs and especially upright plants were found. The species characterising pastures belonged to both the groups grasses and forbs.

Seventy percent of all recorded species demonstrated defence traits against cattle grazing (Tab. 3). Nevertheless, the proportion of species differed significantly between the two land use types. On litter meadows more plant species with chemical defence compounds were found, whereas relatively more species grew on pastures which had mechanical defence mechanisms. When the data were analysed for grasses and forbs separately, the differences were less pronounced as grasses possessed mainly mechanical defence mechanisms (66.7 %) whereas forbs used mainly chemical defence mechanism (64.6 %) for protection against cattle grazing. Most differentiating species on meadows did not have any defence mechanism, whereas on pastures 8 out of 21 species showed mechanical defence traits (e.g. Juncus sps., Cirsium palustre) or chemical compounds (e.g. *Mentha spp*., *Eupatorium cannabinum*).

The proportion of species with different clonal growth form traits was influenced by land use type. On pastures the proportion of species with fast spreading stolons was much higher than on meadows. Species with stem derived slow spreading or root derived clonal organs and species without any clonal growth form were significantly more abundant on meadows. Species with bulbs and tubers occurred only in low numbers and did not show significant differences. The differentiating species on pastures were often species with fast spreading organs, whereas on meadows the proportion of differentiating species with slow spreading clonal organs or no clonal growth was higher.

Most grasses (ca. 60 %) flowered early in the season and for a short time, whereas the flowering time of forbs lasted for 3 or 4 months and varied in time of year. On pastures, there were significantly more late flowering species, whereas on meadows more plants which start flowering mid summer (June, July) were found. For early flowering plants no significant differences could be observed. Management had no significant effect on the flowering time span except for a small number of long flowering forb species, which occurred to a higher proportion on pastures. The differentiating species did not reveal a clear pattern concerning flowering time or time span.

The three main types of pollination (insect, wind and self pollination) showed significant differences between land use types (Tab. 3). On meadows more insect- and self-pollinated species were found, whereas more wind pollinators were present on pastures. This difference resulted mainly from the grass/forb ratio of pastures and meadows as 98 % of all grasses were wind pollinated and 89 % of all forbs were insect pollinated and 40 % self-pollinated. When forbs were analysed separately, however, there were more insect pollinated species on pastures than on meadows. The pollination type of the differentiating species was not affected by land use.

Two dispersal types differed between meadows and pastures: on meadows the proportion of anemochorous species was higher whereas on pastures species with hydrochorous dispersal were more abundant. In contrast, the proportion of zoochoreous species was not affected by land use. The two classes forbs and grasses and the differentiating species responded in the same way.

CORRELATION OF THE TRAITS WITH ORDINATION AXIS

Neither groundwater level, pH-value nor aboveground biomass or vegetation height showed any correlation with the site scores of the DCA. But in many cases, the proportion of species belonging to different trait groups was correlated with axis 1 of the DCA which separated the two land use types (Tab. 3). Negative correlations with axis 1 were found for the proportions of species with the following traits indicating these traits are more abundant on pastures (in declining order): fast spreader, species with hydrochoreous dispersal, grasses (respectively tiller forming grasses), wind pollinated species, late flowering plants, species with mechanical defence and rosettes. The proportions of species with the following traits were positively correlated with axis 1 indicating that these traits were more abundant on meadows: slow spreader, species with chemical compounds, herbs, insect pollinated species, species with anemochoreous dispersal, mosses and non-clonal species.

Tab. 3: Mean percentage of species with different traits related to morphology, defence mechanism, clonal growth form and reproduction on 25 m^2 plots in pastures (n=58) and meadows (n=51) (for references concerning trait groups see Tab. 1). Data were analysed for all species and for grasses and forbs separately. Significance levels of the t-test (no labelling) or the U-test (U) are as follow: n.s. not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. The last column shows the Pearson-Product-Moment-correlation coefficient r between the first axis scores of the DCA and the proportion of the trait group.

	All species			Grasses			Forbs			**Correlation with axis 1**	
	Pasture	Meadows	Sign.	Pasture	Meadows	Sign.	Pasture	Meadows	Sign.	r	Sign.
Morphology											
Grasses	35.2	28.9	***							- 0.54	***
Tillers	18.6	13.2		49.5	42.7	***				- 0.77	***
Bulks	19.2	17.3		50.7	57.3	***				- 0.01	
Forbs	49.0	54.6	***							0.60	***
Rosettes	22.3	19.6					47.1	36.0	***	- 0.38	*
Stems	26.7	35.0					52.9	64.0	***	- 0.24	
Trees	1.8	1.5	n.s.							- 0.33	
Mosses	13.7	15.0	n.s.							0.48	**
Defence											
Without	26.4	25.2	n.s.	26.5	24.1	n.s.	27.3	26.1	n.s.	0.25	
chemical compounds	39.1	42.0	***	12.4	12.4	n.s.	64.8	66.1	n.s.	0.63	***
mechanical defence	35.1	32.2	*	70.5	71.7	n.s.	17.4	18.4	n.s.	- 0.46	**
Clonal growth											
non clonal	7.7	9.2	*	0	0	n.s. U	6.8	9.3	* U	0.40	*
root derived	8.3	10.4	* U	0	0	n.s. U	14.7	16.8	n.s.	0.15	
stem derived (fast)	44.9	34.5	***	67.4	59.8	***	31.5	22.9	***	- 0.92	***
stem derived (slow)	56.1	60.9	**	32.5	40.2	***	68.4	68.1	n.s.	0.68	***
bulbs and tubers	4.2	4.8	n.s. U	6.2	7.5	n.s. U	3.2	3.5	n.s. U	- 0.64	***
Flowering time											
early	42.6	41.4	n.s.	56.5	60.9	**	41,7	40.6	n.s.	- 0.00	
middle	33.2	35.9	* U	37.3	35.0	n.s.	37.1	43.8	***	0.43	*
late	12.4	9.5	***	6.2	4.2	* U	21.3	15.6	*** U	- 0.56	***
Flowering time span											
short	34.6	32.4	n.s.	62.6	64.5	n.s. U	19.0	19.7	n.s.	- 0.16	
middle	44.0	44.3	n.s.	34.5	33.2	n.s.	63.7	62.8	n.s.	0.03	
long	9.5	10.1	n.s. U	2.9	2.4	n.s. U	2.3	1.6	*** U	0.06	
Pollination											
insect	52.9	59.4	***	1.6	3.3	* U	93.8	90.7	*** U	0.57	***
self	25.8	28.4	*	0	0		34.6	37.0	n.s.	0.38	*
wind	44.2	35.4	***	93.3	93.1	n.s. U	4.9	5.1	n.s. U	- 0.53	**
Dispersal											
zoochorous	46.5	44.8	n.s.	49.3	46.9	n.s.	40.8	40.7	n.s.	- 0.15	
anemochoreous	70.6	73.9	**	78.9	79.6	n.s. U	58.4	63.6	**	0.54	***
hydrochoreous	21.6	14.5	*** U	31.1	26.7	**	15.9	8,3	*** U	- 0.77	***

DISCUSSION

EFFECTS ON SPECIES RICHNESS

In our study, species richness of both fen meadows and pastures was high (50 respectively 43 species per 25 m2) which showed that moderate land use offers good growing conditions for many species in this habitat. Abandonment, in contrast, reduces species richness (Diemer et al. 2001). Nevertheless, species richness on mown straw meadows was significantly higher (about 15 % more species) than on pastures, both for number of species per 25 m2 and for species richness per site. This difference can be attributed to the land use as the paired comparison of adjacent sites which were very similar concerning abiotic conditions reduced the variance caused by other environmental factors. In the only study which also compared fen meadows and pastures directly, species richness was also higher on meadows than on pastures (Peintinger 1999). Comparisons between annual mowing and grazing in other moderately used vegetation types are rare. Hansson & Fogelfors (2000) detected slightly more species on mown than on grazed semi-natural grasslands in Sweden. In moderately used so-called "bumpy meadows" (calcareous grasslands with wetter and drier parts) Gutser & Kuhn (1998) did not find a difference in species richness between mown and grazed plots. In contrast, Schläpfer et al. (1998) found significantly more species on grazed xeric calcareous grasslands than on mown sites. These contrasting results indicate differences in the impact of grazing depending on soil moisture conditions and not only on nutrient availability, as suggested by Olff & Ritchie (1998) and Proulx & Mazumder (1998). One explanation could be the different impact of trampling depending on soil moisture. The compaction of soft peat soil on fens caused by cattle hooves results in wetter soil conditions, or even in flooding of created gaps (Whinam & Chilcott 1999). This means that species on fen pastures have not only to cope with biomass destruction by trampling, but also with more anoxic soil conditions. Furthermore, straw meadows on fens differ markedly by the late cutting date from meadows in the other studies, where mowing took place earlier during the vegetation period (Gutser & Kuhn 1998, Schläpfer et al. 1998, Hansson & Fogelfors 2000). On fen meadows, litter is regularly removed, but living biomass is hardly affected. In contrast to grazing, late mowing in September provides a chance for species to allocate nutrients in belowground storage organs and protect them this way against nutrient loss. Especially on nutrient poor sites this strategy is of great importance (e.g. Ganzert & Pfadenhauer 1986, Diemer & Pfadenhauer 1987). Therefore, in our study the dominant species, which reduce species diversity in abandoned sites (Güsewell et al. 1998, Diemer et al. 2001), were repressed more strongly by grazing than by late mowing which resulted in higher evenness values on pastures.

Many species (164) occurred on both management types and only 48 were affected by land use. But apparently fewer species were supported by grazing than by mowing (18 differentiating species on pastures, 30 on meadows). In contrast, the proportions of typical fen species or species listed in the

Red Data Book as target species of nature conservation were the same for meadows and pastures, confirming observations of Peintinger (1999).

EFFECTS ON SPECIES COMPOSITION

The short gradient length of the DCA resulted from the narrow range of soil conditions and vegetation composition which was a prerequisite for site selection in order to focus on differences induced by management. This means that the variation in the whole data set was not very high. Other studies have shown that soil conditions can explain up to 40 % of the variance in the vegetation of fens (Olde Venterink et al. 2001). In the ordination of Peintinger's data (1999) the main gradient was related to altitude, but management type had no influence until the third axis. In our study the scores of the DCA axes did not show any correlation with the measured environmental factors. The two land use types, in contrast, were separated very well along the first axis with r2 of 0.38 for the correlation between distances in the ordination space and distances in the original space. The overall trend between pairs of grazed and mown plots was almost parallel to the first ordination axis. As the plots of pastures and meadows overlap in the ordination, the transition between the two land use types is smooth with no strict boundary. This is due to the fact that the impact of grazing is to a certain extent similar to that of mowing in terms of biomass loss and gap creation. Late mowing on fen meadows causes biomass loss for all species over the entire meadow at the end of the vegetation period, whereas moderate grazing causes small continuous disturbances by foraging and trampling. As grazing-related traits show high correlations with the DCA scores, grazing seems to restrict species occurrence more strongly to species traits like tiller forming grasses or fast spreaders. For single species, good correlations with the first axis were only found for the differentiating species. This result also indicates that land use was the main factor in the ordination. The second axis explained only a small amount of the variance and could not be related to any of the surveyed factors or traits.

EFFECTS ON SPECIES CHARACTERISTICS

In many studies, plant functional types concerning life history and morphology have been related to grazing. But Vesk & Westoby (2001) point out that there are limits concerning generalizations about species response to grazing. Our results support this statement, as on both management types species belonged to all groups of single traits and only 48 species (21 % of all) were significantly affected by land use. Nevertheless, we were able to find differences between grazing and mowing with respect to the impact on species traits, although in our study disturbance by mowing and grazing varied only in temporal and spatial aspects. We can confirm the common finding, that grasses, especially tiller forming grasses, were encouraged by grazing, as they can - in contrast to forbs - tolerate repeated biomass loss and compensate by re-growth even on nutrient poor soils like in fens (McNaughton 1982, Crawley 1997). Additionally, grasses have basal meristems and therefore a higher resistance to trampling (Peintinger 1999). Mowing in autumn affects hardly any living parts of plants. Therefore most plants do not have to cope with biomass loss which gives an advantage to upright forbs with poor compensatory growth. Small prostrate plants, which avoid being foraged by their adapted growth form, were found in higher proportions on pastures, which agrees with findings of Diaz et al. (2001) and Kahmen et al. (2002). Because of the highly significant differences in the grass/forb ratio between pastures and mown sites a hierarchical approach separating grasses and forbs for growth traits is necessary to reduce artefacts of significances (Lavorel et al. 1997, McIntyre et al. 1999).

Augustine & McNaughton (1998) found some cases of increase in biochemically unpalatable species under grazing, but others (Hadar et al. 1999, Diaz et al. 2001) did not find any change or even an increase of palatable species. In our dataset, only a quarter of all species had no defence mechanism. Most differences regarding mechanical or chemical defence mechanism have to be interpreted as an artefact of the grass/forb ratio. Therefore, classification of species traits as a defence mechanism against cattle grazing which had been developed for agricultural improved pastures has to be reconsidered for fen vegetation. Species pool of fen vegetation consists mainly of species less attractive for cows due to the high amount of fibres and tannins and the low nutrient content (Klapp 1971, Bakker et al. 1983, Gutser & Kuhn 1998). In southern Germany, fens were therefore mown in September to yield bedding material not fodder. Grazing was carried out, if adjacent areas on mineral soils were present which offered better forage quality. For the differentiating species, in contrast, defence mechanisms seemed to be more important: species indicating that pastures have defended themselves by mechanical means (e.g. *Juncus spp.*, *Cirsium palustre*, *Eriophorum angustifolium*) or chemical means (*Mentha spp.*, *Eupatorium cannabinum*) were apparent, whereas species indicating meadows without any defence mechanisms were suppressed on pastures. Thus, the finding of Bullock et al. (2001) that on pastures tolerance maybe a more successful strategy than avoidance cannot be confirmed for all species on fens.

Vegetative spreading, expressed as the clonal growth form, is of major importance to colonize new sites and to sustain species persistence. In our study, species with fast spreading stem-derived clonal organs like stolons were favoured by grazing (e.g. *Agrostis stolonifera*, *Carex hostiana*, *Valeriana dioica*, *Hieracium lactucella*), as they can effectively colonize gaps, e.g. hoof prints (Stöcklin 1992). All other groups, and especially the non-clonal species, were more frequent on meadows, which suggests the conclusion that grazing harms most species by trampling with the exception of fast spreading species. Although recruitment from seeds in perennial plant communities is rare (Crawley 1997, Eriksson & Eriksson 1997), trampling on pastures can support species diversity offering germination niches (Bullock et al. 2001, Isselstein et al. 2002). Schläpfer et al. (1998) traced species richness on pastures even back to seedling recruitment in hoof prints. In our study, the response of reproductive traits to land use was less pronounced than for all other traits, confirming the findings of Kahmen et al. (2002). In the investigated fen meadows therophytes which had to reproduce generatively and could quickly colonize gaps were rare in both land use types (only 4 % of all species). Pollination traits and the potential flowering time span did not vary between land use types. The assumed advantage of species on pastures which flower early in the season to avoid grazing or during a longer period to tolerate grazing by re-growth or delayed flowering (Lavorel et al. 1997) could not be confirmed. Not only flowering time, but also the time of ripening is obviously still very critical to loose reproductive organs. But grazing provided better conditions for late flowering species than mowing. During the late season, grazing intensity on fens declined strongly (pers. observations) due to a high amount of unattractive or unpalatable old vegetation with a higher fibre content (Crawley 1997). In contrast, on straw meadows mowing in September could still be too early for some species to finish their reproduction process (Dumontier 1996). Surprisingly, the amount of zoochoreous species was not higher on pastures than on meadows, demonstrating that cows acting as seed agents had no significant effect on species composition in fens.

CONCLUSIONS

Grazing is restricting species occurrence more strongly than mowing. This can mainly be explained by combinations of species traits. Species with fast spreading stem derived clonal organs, mostly tiller forming grasses, found good conditions on pastures. Forb species were favoured on pastures when they were prostrate, fast spreading rosette plants (e.g. *Trifolium repens*, *Valeriana dioica*, *Hieracium lactucella*) or upright forbs with defence mechanisms like chemical compounds (*Mentha spp.*, *Eupatorium cannabinum*, *Lycopus europaeus*) or thorns (*Cirsium palustre*). In contrast, upright herbs without defence mechanism were often harmed by grazing suffering from biomass loss by trampling or foraging, especially if they were only able to spread slowly like *Gentiana asclepiadea*, *Trollius europaeus* or *Sanguisorba officinalis* or did not possess any clonal organs like *Angelica sylvestris* or *Laserpitium prutenicum*. Bulk forming grass species like *Schoenus ferrugineus* or *Luzula multiflora* and grasses with below ground storage organs like *Molinia caerulea* or *Phragmites australis* were better supported by mowing as they were easily damaged by trampling in grazed areas.

Although mowing and grazing had different impacts on species richness, species composition and species traits on fens, vegetation of pastures and meadows was still quite similar. Pastures contained the same amount of typical fen species and Red Data Book species and grazing reduced the negative effects of abandonment (i.e. dominance of few species). Therefore, moderate grazing on fens can be recommended as an alternative conservation strategy to mowing. But optimal grazing conditions have to be developed to minimize the unwanted effects of foraging and trampling. In certain cases, e.g. when endangered species are involved, response of single species to grazing has to be investigated before decisions about grazing introduction can be made.

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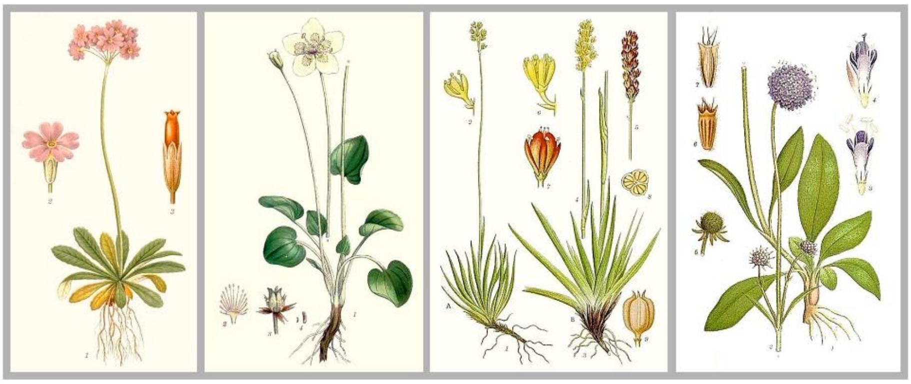
Appendix 1: Species differentiating between land use types according to abundance and/or frequency and their characteristics of the single traits. In bold print characteristics confirming response groups to land use. Typical species of calcareous fens (belonging to Scheuchzerio-Caricetea nigrae or to Molinietalia) were highlighted grey. Species marked in the first column occurred only on one management type, either mowing or grazing. Abbreviations: mech: mechanical; chem.: chemical; anem: anemochorous; zoo: zoochorous; hydro: hydrochorous

either meadow or pasture	**Differentiating Species**	**Species traits**								
		morphology		clonal growth	spreading velocity	defence	flowering time span	flowering time	dispersal	pollination
Pasture										
differentiated by abundance and frequency										
	Carex flacca	**gras**	tiller	**stem**	**fast** or slow	**-**	short	early	anem/zoo/hydro	wind
	Carex hostiana	**gras**	tiller/bulk	**stem**	**fast**	**-**	short	middle	anem/hydro	wind
	Juncus articulatus	**gras**	tiller	**stem**	**fast**	**mech**	middle	late	anem/zoo	wind
x	Juncus inflexus	**gras**	bulk	**stem**	**fast**	**mech**	middle	middle	anem	wind
	Mentha aquatica	forb	upright	**stem**	**fast**	**chem**	middle	late	hydro	insect
	Trifolium repens	forb	**prostrate**	**stem**	**fast**	**-**	middle	early	zoo	insect
	Valeriana dioica	forb	**prostrate**	**stem**	**fast** or slow	**-**	short	early	anem	insect
differentiated by abundance										
	Acrocladium cuspidatum	moss				-				
	Cirsium palustre	forb	upright	non clonal		**mech**	middle	late	anem/zoo/hydro	insect/self
differentiated by frequency										
	Agrostis stolonifera	**gras**	tiller	**stem**	**fast**	**-**	short	middle	anem/zoo	wind
	Carex flava	**gras**	bulk	**stem**	slow	**-**	long	early	hydro	wind
	Carex rostrata	**gras**	tiller	**stem**	**fast** or slow	**mech**	short	middle	anem/hydro	wind
	Epilobium parviflorum	forb	upright	**stem**	slow	**mech**	middle	middle	anem	insect/self
x	Eupatorium cannabinum	forb	upright	**stem**	**fast**	**chem**	middle	late	anem/zoo	insect/self
	Hieracium lactucella	forb	**prostrate**	**stem**	**fast** or slow	**-**	long	early	anem	insect/self
	Juncus effusus	**gras**	bulk	**stem**	**fast**	**mech**	middle	middle	anem/zoo	wind
	Mentha arvensis	forb	upright	**stem**	**fast**	**mech/chem**	middle	late		insect
	Trifolium pratense	forb	upright	**stem / root**	slow	**-**	middle	middle	zoo	insect
only on pastures but not differentiated by anything else										
x	Blysmus compressus	**gras**	tiller	**stem**	**fast**	**-**	middle	early	zoo	wind
x	Eriophorum angustifolium	**gras**	tiller	**stem**	**fast**	**mech**	short	early	anem	wind
x	Lycopus europaeus	forb	upright	tuber		**chem**	middle	late	zoo/hydro	insect
Meadow										
differentiated by abundance and frequency										
	Angelica sylvestris	**forb**	**upright**	**non clonal**		chem	middle	late	anem	insect/self
	Centaurea jacea	**forb**	**upright**	root / stem	fast	**-**	long	early	anem/zoo	insect/self
	Cirsium rivulare	**forb**	**upright**	stem	**slow**	**-**	middle	middle	anem	insect/self
	Euphrasia rostkoviana	**forb**	prostrate	**non clonal**		**-**	long	middle	anem	insect
	Filipendula ulmaria	**forb**	**upright**	stem	**slow**	**mech/chem**	middle	middle	anem/zoo	insect
	Galium boreale	**forb**	**upright**	stem	fast	**-**	short	middle	zoo	insect/self
	Gentiana asclepiadea	**forb**	**upright**	stem	**slow**	**-**	middle	late	anem	insect
	Phyteuma orbiculare	**forb**	**upright**	stem	**slow**	**-**	middle	early	anem/zoo	insect
	Primula elatior	**forb**	prostrate	stem	**slow**	**-**	short	early	anem/zoo	insect
	Ranunculus nemorosus	**forb**	**upright**	stem	**slow**	**-**	middle	early	zoo	insect/self
	Sanguisorba officinalis	**forb**	**upright**	stem	**slow**	chem	middle	middle	anem	insect
	Scabiosa lucida	**forb**	**upright**	stem	**slow**	**-**	long	middle	anem	insect
	Trollius europaeus	**forb**	**upright**	stem	**slow**	**-**	short	early	anem	insect/self
differentiated by abundance										
	Climacium dendroides	moss				-				
	Epipactis palustris	**forb**	**upright**	stem	fast	**-**	middle	middle	anem	insect/self
	Phragmites australis	gras	tiller	stem / tuber	fast	mech	middle	late	anem/zoo	wind
	Rhinanthus minor	**forb**	**upright**	**non clonal**		chem	middle	early	anem	insect/self
differentiated by frequency										
x	Allium carinatum	**forb**	**upright**	tuber		**-**	short	middle	anem	insect
x	Campanula patula	**forb**	**upright**	**non clonal**		**-**	middle	early	anem	insect
	Carex pulicaris	gras	tiller	stem	fast	**-**	short	early	zoo	wind
	Equisetum palustre		tiller	stem / tuber	fast	**mech/chem**	middle	early	anem	
x	Gymnadenia conopsea	**forb**	**upright**	root		**-**	short	middle	anem	insect
	Laserpitium prutenicum	**forb**	**upright**	**non clonal**		**-**	short	middle	anem	insect/self
x	Luzula multiflora	gras	**bulk**	stem	**slow**	mech	short	early	zoo	wind
	Molinia caerulea	gras	**bulk**	stem	**slow**	**-**	middle	late	anem/zoo	wind
	Parnassia palustris	**forb**	prostrate	stem	**slow**	**-**	middle	late	anem	insect
	Pimpinella major	**forb**	**upright**	stem	fast or **slow**	**-**	middle	middle		insect/self
	Schoenus ferrugineus	gras	**bulk**	stem	**slow**	**-**	short	early	anem	wind
	Thymus pulegioides	**forb**	prostrate	stem	fast	**-**	long	middle	anem/zoo	insect
x	Veratrum album	**forb**	**upright**	tuber		**-**	middle	middle	anem	
only on meadows but not differentiated by anything else										
x	Carex pallescens	gras	**bulk**	stem	**slow**	**-**	short	early	anem	wind
x	Gentiana clusii	**forb**	prostrate	stem	**slow**	**-**	middle	early	anem	
x	Lysimachia vulgaris	**forb**	**upright**	tuber		**-**	middle	middle	anem/zoo/hydro	insect/self
x	Platanthera bifolia	**forb**	**upright**	root		**-**	middle	early	anem	insect

Chapter 3

Effects of mowing and grazing on population density and age-state structure of four common fen species

with Kathrin Kiehl & Jörg Pfadenhauer



EFFECTS OF MOWING AND GRAZING ON POPULATION DENSITY AND AGE-STATE STRUCTURE OF FOUR COMMON FEN SPECIES

ABSTRACT: The effects of grazing and mowing on the population density and age-state structure of four common, habitat-specific species of calcareous fens were studied in southern Germany. On 13 pairs of adjacent late mown and cattle grazed fens the abundance, age-state structure (proportions of seedlings, non-flowering adults, flowering adults), seed number and seed weight of *Parnassia palustris*, *Primula farinosa*, *Succisa pratensis* and *Tofieldia calyculata* were determined. *Succisa* did not respond to land use type for any of the investigated parameter as the late-flowering species was harmed by late mowing as well as by grazing. All other species showed a significantly lower subpopulation density and abundance on pastures than on meadows. For *Parnassia* and *Tofieldia* grazing had a negative effect on the proportion of seedlings which was partly compensated by clonal growth (*Tofieldia*) or balanced by a high number of flowering individuals (*Parnassia*). For *Succisa*, *Parnassia* and *Tofieldia* seed number per individual did not differ between land use types. For *Primula*, the number of seedlings was the same in both land use types. The lower subpopulation density in pastures was probably due to a higher mortality rate of adult plants and a lower establishment rate. The lower number of flowering *Primula* plants on pastures compared to meadows was partly compensated by a higher number of seeds per individual. Although subpopulation density in old pastures was lower than in meadows it can be assumed to be stable. Therefore, grazing can be recommended for large fen areas in connection with meadows as an alternative land use. In small fens or for small populations, however, grazing will probably increase the risk for species decrease or extinction.

INTRODUCTION

Calcareous fens in the pre-alpine region of southern Germany contain species-rich vegetation types of Molinion caeruleae and Caricion davallianae dominated by sedges and grasses with many prostrate or upright, late-flowering plants (Braun 1968). They have developed under traditional moderate land use, which was mostly grazing, and since the middle of the 19th century autumn mowing without fertilization (Radlmair et al. 1999). Nowadays, mowing is the management form which is favoured by nature conservation. During the last decades, however, land use changes often led to abandonment of fen meadows as well as in other habitats on nutrient poor soils (Lavorel et al. 1998, Bakker & Berendse 1999). As a consequence, the dominance of a few sedge or grass species (e.g. *Molinia caerulea*, *Schoenus ferrugineus*) increased, whereas many typical plant species of calcareous fens became rare or endangered (Diemer et al. 2001). Moderate grazing is considered by a few authors as an alternative management tool to maintain species diversity by reducing dominant species (Bakker 1989, Hobbs & Huenneke 1992, Hald & Vinther 2000).

Plant species might respond differently to grazing and mowing concerning traits as growth form or flowering time (Lavorel et al. 1997, McIntyre et al. 1995). Peintinger (1999) and Stammel et al. (in press) also found differences in growth-form related species traits between mown and grazed fens, but not for the abundance of typical fen species determined as cover classes of vegetation relevès. As gradual changes may not be recognized when the whole community is studied, a population ecological approach may be more appropriate to predict species response (Hutchings 1991).

Investigations on population age-state structure can be used to differentiate the effects of land use on certain species by highlighting the most harmed stage on each land use type (Billeter & Diemer 2000). Age-state structure has often been studied to analyse the population viability and to predict future changes in population density when the type or the intensity of land use, or size of the fen has changed (Oostermeijer et al. 1994b, Hegland et al. 2001, Hooftman 2001). Up to now, population density or age-state structure have mostly been studied for rare or endangered species (e.g. Oostermeijer et al. 1994b, Colling et al. 2002, Willems & Ellers 1996). In contrast, the importance of common habitat-specific species for the functioning of ecosystems has been pointed out by Power et al. (1996) and Hooftman (2001). For example, Bühler & Schmid (2001) were able to predict changes in species composition by analysing changes in the demography of the common fen species *Succisa pratensis*. First investigations on common species of calcareous fens of Hooftman (2001) and Billeter (2001) showed an influence of habitat fragmentation or land use abandonment on population demography.

The aim of our study was to gain insight in general effects of different land use on population structure of common characteristic species of calcareous fens and to give recommendations about the suitability of grazing as an alternative management tool to autumn mowing. Therefore, we selected four common species (*Parnassia palustris*, *Primula farinosa*, *Succisa pratensis*, *Tofieldia calyculata*) which differed concerning growth form, flowering time and clonality. We analysed population density, age-state structure and reproductive output in order to evaluate the effects of grazing and autumn mowing on the population structure of four common habitat-specific species of calcareous fens. The focus of our study was to describe the effects of grazing and to analyse how species cope with the grazing related damage in different age states. Therefore we addressed the following questions: (1) Does land use influence population density and age-state structure of common fen species? (2) Do species with different growth forms respond to land use in different ways? (3) Are different age states and especially the reproduction of the investigated species affected by grazing in different ways? (4) Can grazing be recommended as an alternative land use to mowing on fens?

METHODS

STUDY SITE

The study was carried out in 13 grazed and 13 mown calcareous fens in southern Germany in the prealpine region at an altitude between 630 and 870 m above sea level (geographical coordinates: 10°40’ - 11°10’ E and 47°36’ - 47°42’N). The climate is moist and cool with a mean annual temperature of 6 to 7 °C and an average annual precipitation between 1200 and 1600 mm. Soils are nutrient poor and consist of peat layers which have developed under high ground water tables above calcareous grounds. In order to compare land use and to reduce effects of other non-required factors like abiotic conditions or microclimate, the study sites were selected in order to meet the following conditions: (1) actual land use of either grazing or mowing had to be continuous for at least 10 years and was established on most of the sites for a few decades; (2) paired study sites of mown and grazed fens had to be adjacent. Earlier investigations on the abiotic conditions of the sites had shown (Stammel et al. in press) that the paired sites did not differ significantly in groundwater level and pH-value. Plant standing crop in August as a measure of productivity was also similar on both land use types, when grazing was excluded on pastures. Where grazing was not excluded vegetation height and plant standing crop was lower on pastures than on meadows due to foraging.

The meadows were mown in September when vegetation started yellowing. The pastures were grazed moderately by less than 0.5 heifers ha^{-1} from May to October during the whole vegetation period. Pastures on fens were always connected to areas on mineral soils with a higher fodder quality. Vegetation was dominated by *Schoenus ferrugineus* and *Molinia caerulea*, *Carex* species were abundant. Vegetation types can be classified as Primulo-Schoenetum, Caricetum davallianeae or Molinietum caeruleae in general (Braun 1968) and have been described in relation to land use by Stammel et al. (in press).

STUDY SPECIES

The four investigated species are all subdominant perennial plant species which are habitat-characteristic and common species in wet calcareous fen meadows of the Caricon davallianae or Molinietum caerulea (Oberdorfer 1998). Their characterization follows Frank & Klotz (1988). *Parnassia palustris* is a prostrate species with upright growing leaves. It flowers in July/August; one to three stalks of 10-20 cm height bear one inflorescence with many (> 500) ovules. *Primula farinosa* is a procumbent rosette plant flowering as one of the first species in April/May. Plants consist of a mother rosette of 5-6 cm diameter, sometimes accompanied by daughter rosettes. The single inflorescence with 5-10 flowers which bear 80-90 ovules each reaches a height of about 10 cm. *Tofieldia calyculata* is a prostrate lilly, flowering in May/June. The upright leaves of the rosette form an appressed fan with the flowering stalk arising in the centre. The inflorescence with 10 - 30 flowers which produce many small seeds (> 500 per individual plant) is 15-20 cm long . The species, however, can also grow clonally by forming daughter rosettes. Plants can form large clones consisting of up to 20 fans; of these, only one or two ramets flower simultaneously (Billeter & Diemer 2000). *Succisa pratensis* is a tall, upright rosette plant, which flowers in August/September. It is generally aclonal, although daughter rosettes may sometimes be produced at the end of short stolons. The rosette produces one to four flowering shoots that can grow up to 80 cm. One shoot produces on average one to three inflorescences with 30-100 small single seeded flowers.

FIELD METHODS

In each of the 13 sites of adjacent pasture and meadow a transect of 73 m length was placed at a distance of 5 m on each side of the dividing fence between the two adjacent land use types mowing and grazing. 12 plots of 1m x 1m were installed every six meter along the transect in each site (312 plots in total). The number of individuals of the investigated species was counted in each plot of each land use type and determined as subpopulation density, as mown and grazes sites were adjacent and contain probably the same population. Individuals where counted separately for the age-state classes seedlings, non-flowering and flowering individuals. Individuals were considered as flowering individuals, even when the flower buds were bitten or destroyed as the age-state structure of the population was of interest. A further division into more age-state classes was not appropriate as for all species the same classes should be used. The stage “seedling” is the only ontogenetic stage which can be clearly determined in established plant populations in the field (Colling et al. 2002). We did not determine the stage “juvenile” as it cannot be clearly separated from the class non-flowering adults and seedlings and as for some of the investigated species a fast development from seedlings to flowering plants could be observed during one vegetation period in greenhouse experiments (unpublished results). For each species and each transect species frequency was determined as the proportion of plots where the species was present. As *Tofieldia* showed a strong clonal reproduction, the number of ramets was counted additionally. A group of ramets was considered as one individual when a connection between them could be ascertained. If no individual of one species was present at all in a plot, an additional plot of 1 m^2 was chosen randomly near the transect in order to provide the same number of replicates for the statistical analysis of density and age-state structure. In these additional plots the subpopulation density of the before-missed species was counted for all life stages in the same way as for the other plots.

To study fecundity, 20 flowering individuals of each species were randomly chosen within each site and land use type. For each individual, the number of inflorescences (flowers for *Parnassia*, *Primula* and *Tofieldia*; flower heads for *Succisa*) was counted and the ripe seeds were collected and brought in to the lab, where the weight of all seeds per individual was determined. For *Succisa* the number of all seeds per individual was counted as seeds were large. For the other species with smaller seeds, the weight of a certain number of seeds (Parnassia 250 seeds, Primula and Tofieldia 200) was determined three times and seed number per individual (weight of all seeds divided by weight per seeds) was calculated as counting of all seeds would have been too time consuming.

DATA ANALYSIS

Effects of site and land-use type on subpopulation density and age states were tested by a two-way ANOVA. Percentage data (proportion of flowering individuals and seedlings) were arcsin-transformed. As for each site the land use types were situated adjacent, we compared the mean frequency of each species (proportion of plots within the transect where the species was present) and the mean values of reproductive traits (number of flowers, seeds per individual, weight per seed) by the Wilcoxon-test for paired, non-parametric data. The data on mean subpopulation density of each species in each site and each land use type were log-transformed to calculate Pearson’s correlation between the density of different species.

RESULTS

SUBPOPULATION DENSITY AND AGE-STATE STRUCTURE

The frequency of *Succisa pratensis* did not depend on land use (0.68 on meadows, 0.58 on pastures) whereas for the other species frequency differed significantly between land use types. On pastures, the proportion of plots without any individuals of *Parnassia palustris*, *Primula farinosa* and *Tofieldia calyculata* was higher. *Parnassia* showed the highest frequency (0.93 on meadows, 0.78 on pastures; $p < 0.05$), whereas *Tofieldia* was the least abundant species. The difference between the two land use types was strongest for *Primula* (0.86 on meadows, 0.55 on pastures; $p < 0.01$) and *Tofieldia* (0.71 on meadows, 0.40 on pastures; $p < 0.05$).

Mean subpopulation density varied significantly between the different sites for all species (Tab. 1). For *Succisa* subpopulation density was lowest and did not differ between land use types (4.0 individuals m^{-2} on pastures, 4.1 on meadows). For all other species subpopulation density was significantly higher on meadows than on pastures (Fig. 1). *Primula* was present in the highest subpopulation density (22.2 on pastures, 39.6 on meadows), followed by *Parnassia* (14.4 on pastures, 17.4 on meadows) and *Tofieldia* (7.2 on pastures, 11.1 on meadows). Correlations between the subpopulation density of the different species were found for *Primula* and *Tofieldia* ($r = 0.89$; $p < 0.001$) and for *Primula* and *Parnassia* ($r = 0.57$; $p < 0.001$). The density of *Succisa* was not correlated to that of any other species.

Tab. 1: ANOVA table of the effects of land use (degrees of freedom: 1) and site (degrees of freedom: 12) on subpopulation density, percentage of flowering individuals and percentage of seedlings for each species. F: F-value, p: significance (n.s. not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

	Parnassia		*Primula*		*Succisa*		*Tofieldia*	
	F	p	F	p	F	p	F	p
subpopulation density								
land use	5.33	*	41.24	***	0.03	n.s.	20.21	***
site	13.11	***	10.72	***	4.08	***	8.98	***
percentage of flowering individuals								
land use	7.14	**	8.28	**	0.00	n.s.	0.03	n.s.
site	5.43	***	7.24	***	5.17	***	4.00	***
percentage of seedlings								
land use	4.87	*	7.39	**	0.50	n.s.	1.00	n.s.
site	0.84	n.s.	3.54	***	3.07	***	1.00	n.s.

The proportion of flowering individuals differed significantly between sites, but only for two species differences between land use types were significant (Tab. 1, Fig. 1). *Parnassia* showed a significantly higher percentage of flowering individuals on pastures (44.8 %) than on meadows (39.8 %), whereas for *Primula* more individuals flowered on meadows (50.7 %) than on pastures (46.0 %). For *Succisa* significantly more flowering individuals (in absolute numbers) were found on pastures. The number of seedlings was very low for all species and did not differ significantly between the land use types. For *Primula*, however, the percentage of seedlings in relation to the number of all individuals was significantly higher on pastures (17 %) than on meadows (12 %), whereas for *Parnassia* the percentage of seedlings was significantly higher on meadows (1.8 %) than on pastures (0.3 %).

REPRODUCTION

Parnassia and *Primula* produced more flowers on pastures than on meadows, but for *Parnassia* the difference was only slightly significant (Tab. 2). *Succisa* and T*ofieldia*, in contrast, showed more inflorescences on mown sites than on pastures (*Succisa* $p < 0.01$), but for *Tofieldia* the difference was only slightly significant. The number of seeds per individual was for *Primula* significantly higher on pastures than on meadows, but for the other species it did not differ between land use types. The seed weight also did not differ between land use types for any of the investigated species. *Tofieldia* and *Parnassia* produced most seeds and the weight per seed was lowest (*Tofieldia* 0.035 mg per seed, *Parnassia* 0.022 mg per seed). *Succisa* (3.4 mg per seed) had by far the heaviest seeds. Seeds of *Primula* weighed 0.046 mg per seed. *Tofieldia* was able to reproduce clonally. A significantly higher number of ramets per individual of *Tofieldia* was found on pastures (3.6) compared to mown sites (3.0).

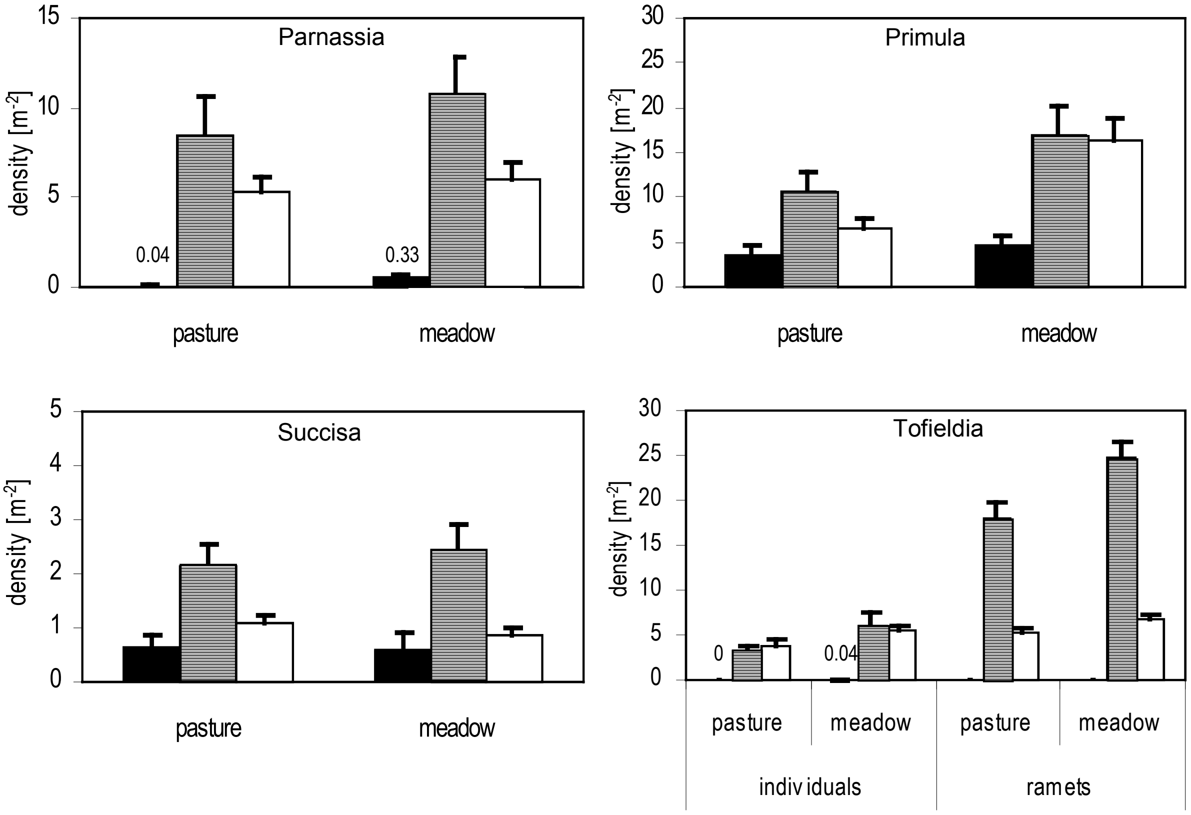


Fig. 1: Mean subpopulation density of different age states of the investigated species on pastures and meadows: mean number and standard error of seedlings (black), non-flowering individuals (grey) and flowering individuals (white) per square meter. For *Tofieldia*, the number of ramets is given separately. Consider the different scales.

Tab. 2: Mean number of inflorescences and seeds per individual, differentiated by land use. Significance was tested by Wilcoxon-test (n.s. p > 0.10, (*) p < 0.10; * p < 0.05; ** p < 0.01).

	inflorescences			seeds per individual		
	pasture	meadow	sign.	pasture	meadow	sign.
Parnassia	2.0	1.8	(*)	988.7	848.7	n.s.
Primula	9.2	8.0	*	302.0	143.5	**
Succisa	4.9	5.5	**	261.7	282.9	n.s.
Tofieldia	22.5	27.1	(*)	928.1	955.7	n.s.

DISCUSSION

EFFECTS OF LAND USE ON SUBPOPULATION DENSITY

In our study, subpopulation density and the proportions of age-states differed significantly between the investigated sites. This means that the selection of adjacent situated fen pastures and meadows was appropriate to compare land use types in order to minimize the effects of other factors differing between sites such as abiotic conditions or extent of population isolation. In spite of the differences between sites subpopulation density and reproductive traits of *Parnassia*, *Primula* and *Tofieldia* differed between land use types, whereas *Succisa* did not show any differences between meadows and pastures. This is in line with findings of Bühler & Schmid (2001) who also found no clear effects of mowing and grazing on the population density and the proportions of different age states of *Succisa*. In our study, grazing harmed *Parnassia*, *Primula* and *Tofieldia* which were less abundant and occurred in a lower subpopulation density in pastures than in meadows. Contrary to grazing, mowing in September was no severe disturbance for these species which had already set fruit and yellowed at this time. On pastures both plant frequency and mean subpopulation density of these species were generally lower than on meadows. The lower frequency was probably due to the higher heterogeneity of grazed sites where in some patches e.g. at trampled sites the investigated species were harmed severely or even excluded. In other habitats, e.g. in pastures on mineral soils heterogeneity created by grazing can have a positive effect on species abundance, because heavily grazed sites with good light conditions for seed germination or procumbent plants alternated with patches of taller vegetation (Bakker et al. 1983, Bokdam 2001). In contrast, in the here studied pastures neither higher densities on some plots in pastures nor higher variation in density could be observed due to a higher heterogeneity compared to meadows.

AGE-STATE STRUCTURE AND CRITICAL AGE STAGES ON PASTURES

Single plant individuals can respond to grazing induced biomass loss by compensatory growth, some species react to the loss of flower buds with a creation of sometimes even more buds (Belsky 1986, Diemer & Pfadenhauer 1987, Hawkes & Sullivan 2001). For our investigated species the production of new flowers after flower loss could only be observed for *Succisa* and for a few individuals for *Parnassia* (unpubl. results). On the other hand species can avoid biomass loss by grazing or mowing by their growth form and growing time (e.g. Lavorel et al. 1997). Nevertheless the late flowering, upright species *Succisa* was harmed on both land use types, in our study. On pastures, adult plants of *Succisa* were harmed by foraging or trampling, but due to the late flowering date the species can also be harmed by mowing in September when the species had not finished its growth and fruit set (Billeter 2001). The damage by mowing, however, can easily be prevented by a later mowing date as it was common when litter meadows were traditionally used, whereas nowadays the meadows were mown as soon as possible after the 1st of September due to the policy of public subsidies. The number of *Succisa* seedlings was the same under both land use types in our study, which supports findings of Kotorova & Lepš (1999), Hooftman (2001) and Isselstein et al. (2002) that *Succisa* germinates almost independently of microsites. In total, no differences concerning the effects of land use could be found for any age-state of *Succisa*. Seed number per individual did not vary between pasture and meadow, because the higher number of flowers per individual on meadows was equalized by a higher number of seeds per flower head on pastures.

The other investigated species were not damaged on meadows due to their early flowering and growth period. On pastures, in contrast, they occurred in lower numbers, although for *Primula* and *Parnassia* the prostrate growth form of the rosette plants was considered as avoidance against grazing or even as competitive advantage on pastures as they were not bitten by cows in contrast to taller species (McIntyre et al. 1995, Stammel et al. in press). As land use was continuous on the investigated sites since decades, we assume that population densities on pastures were not declining and 'regressive' (sensu Oostermeijer 1994b) but stable, although the number of seedlings of *Parnassia* and *Tofieldia* was lower and the proportion of flowering plants was higher than on meadows. To evaluate populations viability and interpret age-state structure, longevity of single individuals and duration in single age-states should be considered, which could differ between different types of land use (Oostermeijer 1994b). But in our one-year study on plant species with a life span of probably at least 10 years we were not able to determine the age of individual plants in the two land use types. Tolvanen et al. (2001) found a lower longevity of tillers of sedges under grazing in contrast to ungrazed plots, which could also be of importance for the population density of the investigated fen species. Such effects are probably not only due to biomass loss by foraging but also due to the lethal effects of trampling (Stammel & Kiehl in press).

Hardly any seedlings of *Tofieldia* were found in our study areas which is confirm to findings of Billeter & Diemer (2000) in abandoned and mown fens and to Maas (1987) who studied germination in soil filled pots. On pastures no germination at all could be observed in our study, whereas on meadows few seedlings were found, which might be a reason for a lower population density on pastures. But *Tofieldia* was able to reproduce successful vegetatively and the higher number of ramets per individual on pastures might compensate for the lower individual and seedling numbers. The number of flowering *Tofieldia* plants and the number of seeds per individual, however, did not differ between pastures and meadows, in contrast to results of Billeter & Diemer (2000) who found a trade-off between flowering individuals and daughter tillers on abandoned fens. Our results were more in line with findings of Stöcklin (1999) who found a higher clonality of *Epilobium spp.* in stressful environments without reduced seed production. He proposed a higher dependence of long-term survival of populations on clonal spreading, and only the need of germination for colonisation of new sites. The importance of clonal reproduction and a low ability to colonize unoccupied sites for *Tofieldia* in contrast to the other species was consistent with the most clumped distribution of all investigated species (lowest frequency) regardless of land use.

Seedling recruitment of *Parnassia* took hardly place on both land use types in our investigation, although large numbers of seeds were produced. Maas (1989), too, found a generally low germination capacity for *Parnassia* seeds tested in the germination chamber. On meadows, seedling number in our study was higher than on pastures, although the number of produced seeds was similar on both land use types. This is probably one reason for the higher population density on meadows: *Parnassia* is not able to balance the lower seedling recruitment on pastures by a stronger clonal spreading as *Tofieldia* did. Additionally, the lower number of adult plants on pastures indicates that established individuals suffer from a higher mortality risk. Surviving *Parnassia* individuals, however, flowered to a larger amount on pastures and probably took advantage of the better light conditions.

Primula, in contrast, showed a lower amount of flowering individuals on pastures. Those individuals, however, which flowered on pastures, bore more capsules with more seeds, and were able to compensate for the lower amount of flowering plants. It seems possible, that only vigorous adult individuals in pastures were able to flower and to reproduce successfully. The similar seedling number on both land use types indicates that germination conditions were similar for *Primula* seedlings on pastures and meadows. Maas (1988), in contrast, found a higher germination rate of *Primula* in plots were vegetation was kept low, comparable to pastures. Considerably fewer adult *Primula* plants occurred on pastures than on meadows, so additionally, grazing harmed the establishment of seedlings and the survival of adult plants most.

CONSEQUENCES FOR CONSERVATION MANAGEMENT

In spite of the similar abundance and cover of common fen species on fen meadows and pastures studied by vegetation relevès (Stammel et al. in press, Peintinger 1999), subpopulation density of the investigated species varied with land use. This means that these species can serve as indicator species as recommended by Bühler & Schmid (2001). Further evidence that common fen species are useful as indicator species is given by the fact that *Primula*, the species with the highest density, showed positive correlations with the two other prostrate fen species *Tofieldia* and *Parnassia*. So, we can probably extend our results of population density dependence on land use to other, less abundant prostrate species. In the same way it can be assumed that tall, late-flowering species as *Succisa* respond similar to grazing and mowing, since their reproduction is interrupted both by foraging flowers and by late mowing. In spite of the similarities of differences in density between pasture and meadows all prostrate species responded differently to the hazards of grazing concerning their age-state structure. So, further research is needed about the response of single species in single age-states in order to clarify which traits in relation to grazing are most important and to be able to give more detailed recommendations for management.

As land use was continuous since more than 10 years in our study sites (mostly several decades) we can assume, that subpopulation density of the species is more or less balanced and not further declining due to grazing. Nevertheless, smaller populations on pastures compared to those on meadows may probably face a higher risk of extinction. For small and isolated populations environmental stochasticity can be a major threat, but also the lower attraction to pollinators (Agren 1996, Vergeer et al. 2003). Additionally, the lower genetic variation and increased inbreeding may reduce fecundity and offspring performance in small populations (Oostermeijer et al. 1994a, Fischer & Matthies 1998, Kery et al. 2000). In our investigation, however, we did not compare isolated populations in pastures and meadows as the paired sites were adjacent and plants belong to one population only split by the fence. But when isolated fens would be grazed, populations of all investigated species except for *Succisa* would suffer probably from a higher risk of decline or extinction in contrast to mowing. Especially for small and isolated fens, grazing cannot be recommended as an alternative management tool in nature conservation. But for ample fens or for sites in connection with fen meadows grazing can be recommended as it enhances also the diversity of age-state structure in the subpopulations by a higher diversity of land-use types.

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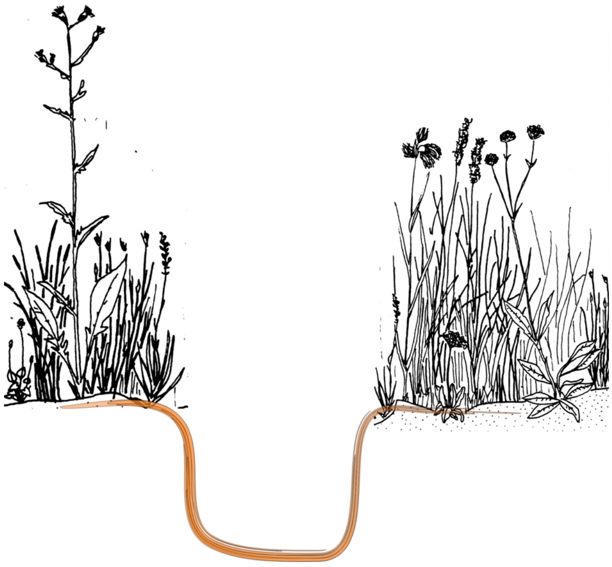
CHAPTER 4

DO HOOF PRINTS ACTUALLY SERVE AS A REGENERATION NICHE FOR PLANT SPECIES IN FENS?

with Kathrin Kiehl

accepted for publication in Phytocoenologia



DO HOOF PRINTS ACTUALLY SERVE AS A REGENERATION NICHE FOR PLANT SPECIES IN FENS?

ABSTRACT: Plant species revegetation of hoof prints in a calcareous fen pasture and of artificially created hoof-print like gaps in an abandoned fen was investigated over two years and compared with the surrounding vegetation. The investigation of abiotic conditions showed that two hoof-print zones had to be distinguished: the steep, drained edge with good light conditions and the flat, dark, but wet bottom. Vegetative spreading and seedling recruitment were examined separately. After two years, hoof prints were not recolonized reasonably, indicating that both hoof-print zones did not offer good conditions for recolonization. Occurrence of frequent species and species numbers were similar in hoof prints, in the surrounding vegetation and in the seed bank. For many fen species germination from the seed bank was better in water-logged pots than in regularly-watered pots. Most species recolonized hoof prints both generatively and vegetatively. In the bottom zone more species germinated than spread vegetatively, but many seedlings died. At the edge, vegetative spreaders finally dominated in spite of high germination rates, because seedling mortality was also high. Overall, recolonization on the edges was more successful than on the bottom, probably because of better light conditions. Only few new species occurred inside hoof prints and only few species were frequent in hoof prints, but not in the surrounding vegetation. Those species were exclusively prostrate species germinating on the edges. The number of recolonizing species did not differ between pasture and abandoned site. Germination, however, was more severely limited in the abandoned fen due to low light availability, litter accumulation and competition by mosses. Altogether, our results show that the presumed importance of hoof prints for species recruitment has to be reconsidered for fen vegetation. On wet peat soil negative effects of soil compaction and changed water and light availability probably prevail over positive effects such as the promotion of subordinate species.

KEYWORDS: cattle grazing, calcareous fen, abandoned fen, gap, vegetative spreading, seedling recruitment, germination, trampling

INTRODUCTION

In semi-natural grasslands species richness mostly depends on continuous disturbances like mowing or grazing (Bakker 1989, Pickett & White 1985) which provide suitable habitat conditions for seedling establishment, the most critical step in the plant life cycle (Harper 1977, Grubb 1977). Several studies have shown that seedling recruitment can be enhanced by grazing of domestic life stock (e.g. Oesterheld & Sala 1990, Eriksson & Eriksson 1997). Watt & Gibson (1988) and Schläpfer et al. (1998) suggested that germination and seedling establishment is higher in gaps created by trampling than in the surrounding vegetation. For fen vegetation a positive effect of gaps on germination has been demonstrated for many species (e.g. Kotorova & Lepš 1999, Krenova & Lepš 1996, Isselstein et al. 2002). Olff & Ritchie (1998), however, pointed out that gaps created by trampling can also have negative effects on the local colonization process, as detrimental soil disturbances which are only tolerated by a few plant species can reduce species diversity. Especially soft peat soils in fens can be substantially damaged by trampling through compaction and development of anoxic conditions (Arnesen 1999, Touzard et al. 2002). Therefore, abiotic conditions in gaps can differ considerably from those in the surrounding vegetation as has also been shown for other habitats (Hillier 1990, Ryser 1993, Suding 2001).

Not only the existence of microsites for germination, but also the availability of seeds is of major importance for the recruitment of new individuals (Turnbull et al. 2000, Zobel et al. 2000, Coulson et al. 2001). Seeds can originate from the seed bank or from the recent seed rain. In pastures, creation of gaps might activate the seed bank (Kalamees & Zobel 2002, Kratochwil et al. 2002). Especially on abandoned sites reestablishment of declined species is only possible by germination of seeds from the seed bank or from seed rain from adjacent sites (Bakker & Berendse 1999). As the vegetation of abandoned fens and grasslands is often dominated by tall-growing species, recolonization might be only possible in gaps (Burke & Grime 1996). Colonization of gaps can also happen by vegetative spreading of plants with the consequence of competition between seedlings and vegetative in-growth in the gaps (Bullock et al. 1994). In semi-natural grasslands, small gaps are mostly dominated by clonal spreading (Arnthorsdottir 1994, Edwards & Crawley 1999, Kalamees & Zobel 2002). Watt & Gibson (1988) pointed out the importance of gaps for subordinate species both for vegetative spreading and for germination.

To date, revegetation of real hoof prints has only been observed in mesic grasslands (Bullock et al. 1994), but not in fens where the impact of trampling is different due to the soft soil and the low nutrient availability. We investigated seedling recruitment and vegetative revegetation in natural hoof prints on a fen pasture and in artificially created hoof-print like gaps in an abandoned fen over a period of two years focussing on the following questions: (1) Which species are able to recolonize hoof prints by seedling recruitment or by vegetative spreading? (2) Does colonization success differ between different zones of a hoof print? (3) Do hoof prints and their surrounding vegetation differ in species composition? (4) Are there differences in gap revegetation between abandoned sites and pastures? (5) Can hoof prints enhance species richness in formerly abandoned sites?

STUDY AREA

The study was conducted in a calcareous fen near Füssen in the prealpine region of southern Germany (800 m above sea level). Annual mean temperature in this area varies between 6 and 7 °C. Mean annual precipitation is 1500 mm yr^{-1}. Soils are nutrient-poor and consist of peat layers which have developed under high groundwater tables above calcareous grounds. The groundwater level fluctuates between 0 and 20 cm below soil surface during the vegetation period. Since 1998 one part of the fen has been moderately grazed from May to September by 20 heifers on 1.5 ha of peat soil and on adjacent 4 ha of mineral soil. Before grazing was introduced, the fen meadow was regularly mown in September. Another part of the fen was abandoned approximately 10 years ago. Nutrient availability in all parts of the fen is very low, hence aboveground standing crop reaches around 120 g m^{-1}. Vegetation of the study site can be classified as Caricion davallianae (Oberdorfer 1998). Dominant species are small sedges *(Carex davalliana, C. panicea, C. hostiana*) and the grass *Molinia caerulea*, but small rosette plants (e.g. *Primula farinosa*) and late flowering herbs (e.g. *Succisa pratensis*) are present as well. On the pasture, the cover of *Carex elata* is high, whereas at the abandoned site a transition of Caricion davallianae to moss-rich (*Sphagnum species*) Rhynchosporion and to Primulo-Schoenetum is taking place.

METHODS

FIELD METHODS

Sixty hoof prints were selected and marked along two transects in the pasture in autumn 2000. At the abandoned site 60 hoof prints were artificially created using a cow hoof fixed to a wooden pole and pressed into the peat soil by applying three blows with a heavy hammer. In this way the size and depth of the artificially created hoof prints was the same as that of the real hoof prints in the pasture: around 10 cm in diameter and 10 cm deep. The revegetation of the gaps was monitored monthly during the vegetation periods of 2001 and 2002. Nomenclature follows Oberdorfer (1994). At the last census total vegetation cover and moss cover were estimated for the revegetated hoof prints and the surrounding vegetation. Two zones of the hoof prints were defined and distinguished in the census: the flat bottom of the hoof print and the steep edge. Separation was clear, due to a hard borderline between the zones. All species were recorded separately as seedlings and as vegetative spreaders. Revegetation was separated into recolonization of new ramets or individuals on the bottom zone and into leaf extension of existing species from the edge without colonizing the gap itself. Regrowth of already existing individuals which had been harmed by trampling could not be separated clearly from the vegetative recolonization of new individuals as most species spread clonally below ground. If recorded species were not found at the next census they were classified as not survived. Few seedlings could not be identified to species, as it was not possible to mark them properly on the pasture for easier identification at the next census. They were counted separately. It was not possible to determine the survival of individual seedlings as their markings were destroyed by cows. The vegetation surrounding the hoof prints was investigated within a circle of 20 cm in diameter around the gap.

Data of abiotic conditions in the two hoof-print zones were collected in summer 2002, namely soil temperature, soil water content and percentage of photosynthetic active radiation (PAR) reaching the soil. Temperature was measured both on a sunny and a cloudy day, from sunrise to sun-set. Soil-water content was measured by taking soil samples from additional hoof prints 10 days after the last rainfall when the water level did not reach the bottom of the hoof print. Samples of approximately 50 cm^3 were collected, kept cool in plastic bags and taken quickly to the lab. Soil-water content (percentage of wet soil) was determined gravimetrically after the soil was dried at 105 °C to constant weight.

An attempt was made to measure seed rain by trapping seeds within soil-filled plastic pots placed on the soil surface, but most of the pots were destroyed by cows. Seed bank was investigated using a soil core with a diameter of 10 cm and a depth of 10 cm (3142 cm^3), which corresponds to the size of a hoof print. The soil was spread in a thin layer over sterilized soil in styrofoam pots and exposed to natural weather conditions in the experimental garden in Freising. Thirty out of 60 samples were kept in a water-logged basin (water level at soil surface), the other 30 samples were watered regularly. Seedlings emerging from the seed bank samples were identified, counted and removed every two weeks. Seedlings that could not be identified were left in the pot or transferred to single pots once they had achieved a reasonable size and were then allowed to grow until identification was possible.

DATA ANALYSIS

Differences between two different groups (e.g. bottom and edge, pasture and abandonment) were tested for statistical significance employing the Mann-Whitney U-test. For both land use types, frequency data of species found inside all hoof prints were summarized in individual data sets - separately for each of the zones and each form of colonization as well as for the surrounding vegetation and the seed bank. A hierarchical, agglomerative cluster analysis was conducted for the frequency data applying the Sørensen similarity index as the distance measure and the group average as the linkage method, using the software package PC-Ord (McCune & Mefford 1999). The cluster analysis of the vegetation inside the hoof prints and the surrounding areas as well as that of the species in the seed bank were performed for both land use types together. To analyse the preference of single species for different hoof-print zones, the frequent species, which occurred in more than 10 % of all hoof prints, were considered.

RESULTS

ABIOTIC CONDITIONS

Physical conditions differed between the two hoof-print zones 'edge' and 'bottom' (Tab. 1). Soil water content was significantly higher in the bottom zone than in the edge zone for both management types. At some of the census dates the bottom zones were even flooded. The percentage of photosynthetic active radiation (PAR) in the bottom zone was significantly lower than at the edge of a hoof print. In artificially created hoof prints at the abandoned site the proportion of PAR was much lower than in the pasture, in both zones. The difference in temperature between the two hoof print zones varied depending on the weather and the time of the day. On a cloudy day, the temperature at the bottom was only slightly lower than at the edge. On a sunny day, however, the difference increased from morning until midday and then decreased again until evening. At the south-exposed side of the hoof print the temperature was higher than at the north-exposed slope; at noon the difference was 9.8° C on average.

Tab. 1: Mean abiotic conditions (percentage of soil-water content, percentage of photosynthetic active radiation (PAR), temperature) for bottom zone and edge zone of hoof prints in the pasture and at the abandoned site; differences between bottom and edge zone were tested by U-test; significance levels: *** p < 0.001; ** p < 0.01; n.s. not significant.

		Pasture			**Abandonment**		
		bottom	edge	p	bottom	edge	p
Water content [%]		89.3	81.4	**	89.9	81.5	***
PAR [%]		27.1	73.6	***	9.9	25.2	***
Temperature [°C]							
cloudy day -	morning	12.8	12.5	n.s.	12.1	11.8	n.s.
	midday	15.9	16.1	n.s.	15.2	15.5	n.s.
	evening	14.8	14.9	n.s.	14.2	14.4	n.s.
sunny day -	morning	13.6	10.5	***	13.1	11.4	**
	midday	15.7	23.0	***	14,7	19.4	***
	evening	14.8	17.7	***	13.9	16.1	**

VEGETATION COVER

Mean cover of the surrounding vegetation in the grazed fen was significantly lower than in the abandoned fen (Tab. 2). For both management types the moss cover amounted to ca. 20 %. After two years of observation, the cover of revegetating plants inside hoof prints was significantly lower than the cover of the surrounding vegetation ($p < 0.001$) reaching only 12.2 % in pastures and 29.6 % in abandonment. At the abandoned site the moss cover in hoof prints was high with a mean of 25 %, but with a high standard deviation of 27.5, as some gaps became overgrown by mosses whereas others remained without any moss.

Tab. 2: Means of total vegetation cover and moss cover in hoof prints after 2 years compared to the surrounding vegetation, in the pasture and at the abandoned site. Differences were tested by U-test for total cover and moss cover separately. Equal letters indicate no significant differences ($p < 0.01$).

	Pasture	**Abandonment**
total cover [%]		
hoof print	12.2 a	29.6 b
surrounding vegetation	65.6 c	77.8 d
moss cover [%]		
hoof print	4.9 a	24.8 b
surrounding vegetation	19.1 b	23.6 b

TOTAL SPECIES RICHNESS

In total, 52 species were found in all hoof prints on the pasture compared to 51 species at the abandoned site (Tab. 3). The surrounding vegetation contained the same number of species on the pasture, but fewer species were present at the abandoned site. The seed bank contained slightly more species than had germinated in the hoof prints (Tab. 3). Forty-one species colonized gaps vegetatively, which was similar to the number of species recruited by seedlings. Twelve species on pastures and 9 species at the abandoned site grew into the hoof prints from the edge only extending their leaf area and not creating new ramets. Only 89 % of all germinated species on pastures and 78 % at the abandoned site were able to establish. When the total number of species was considered, the proportion of surviving recolonizers was between 96 % at abandoned sites and 98 % on pastures since the vegetative spreaders hardly ever disappeared again. Most species recolonized the gaps in both ways, i.e. vegetatively and generatively. Only eight species on the pasture and ten at the abandoned site spread only vegetatively, and nine, respectively eight, species occurred only as seedlings. On the pasture, five new species occurred as compared to the surrounding vegetation, three of which established (*Frangula alnus, Cirsium palustre, Lycopus europaeus*), whereas at the abandoned site four new species occurred and two of them established (*Cardamine pratensis, Frangula alnus*). In total, more species revegetated at the hoof-print edge on the pasture, which resulted in 48 surviving species at the edge compared to 33 surviving species on the bottom. At the abandoned site fewer differences could be observed between the two zones as more vegetative spreaders grew in from the edge, but more seedlings germinated in the bottom zone. The number of surviving species, however, was higher at the edge.

The cluster analysis of the summarized species frequency data revealed a high similarity between the surrounding vegetation and the hoof prints in both land-use types (Fig. 1). In contrast, species composition in the seed bank was very similar in both land use types, but differed considerably in comparison to the surrounding vegetation and the recolonization in hoof prints.

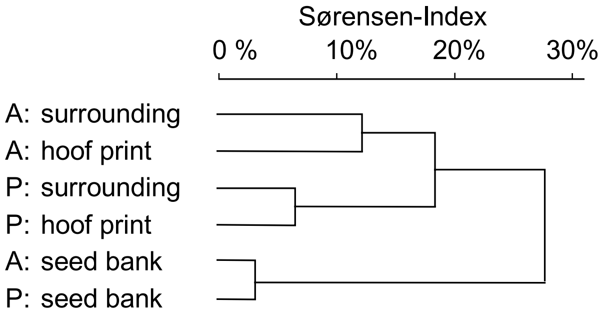


Fig. 1: Dendrogram representing results of the cluster analysis of species frequency in hoof prints, in the surrounding vegetation and in the seed bank for both land use types (P: pasture, A: abandonment). Distance measure: Sørensen-dissimilarity index; linkage method: average of the group.

Tab. 3: Number of species occurring and surviving in hoof prints, in the surrounding vegetation and in the seed bank, shown separately for the edge and bottom zone, and for different colonization types (vegetative colonizers or seedlings).

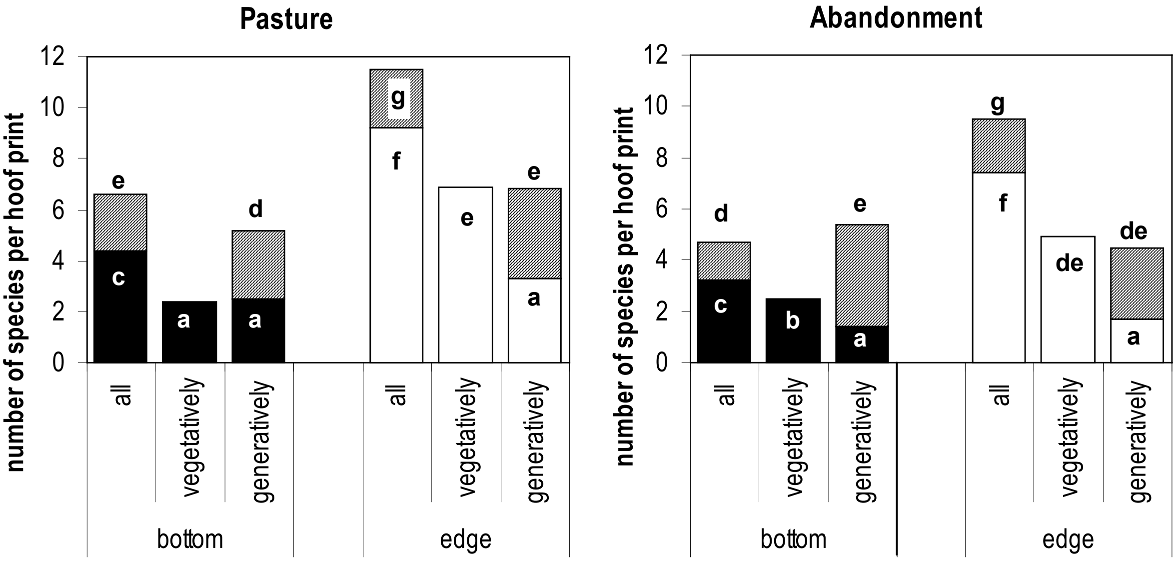
	Pasture		**Abandonment**	
	all	**survived**	**all**	**survived**
Hoof prints				
All species				
total	52	51	51	49
bottom	40	33	47	38
edge	49	48	47	42
Vegetative colonizers				
total	41	41	41	41
bottom	23	23	31	31
edge	39	39	35	35
Seedlings				
total	44	39	41	32
bottom	37	27	37	21
edge	39	31	30	28
Species, extending leaf area	12	12	9	9
Surrounding vegetation	52		47	
Seed bank	47		44	

NUMBER OF SPECIES IN DIFFERENT HOOF-PRINT ZONES

Significantly more species per hoof print were found on the pasture with a mean of 14.2 (11.4 established) compared to the abandoned site with 12.4 species per hoof print (9.5 established). The surrounding vegetation of a hoof print contained fewer species (10.4 on pasture, 8.3 on abandonment). At the abandoned site, the number of species differed significantly between hoof prints and the surrounding vegetation, but the difference disappeared when only surviving species were compared to the surrounding vegetation. Only few species grew in the bottom-zone (Fig. 2). On average 2.5 species recolonized the bottom zone vegetatively or regrowth in both land use types with twice as many species germinating there. The number of revegetating species in the edge zone was nearly twice as high as in the bottom zone. More species spread vegetatively at the edge as compared to the bottom.

Additionally, few procumbent rosette plants like *Primula farinosa* or *Leontodon hispidus* were able to take advantage of the gap creation by enlarging their leaves along the edge (0.9 on pastures, 1.1 on abandonment). The number of germinating species was similar at the bottom and the edge. In the pasture, 52 % of the germinated species per hoof print established in both hoof-print zones, whereas at the abandoned site only 38 % of the seedlings survived at the edge and 26 % at the bottom. Hence, species which established in hoof prints mainly originated from vegetative spreading in the edge zone, and only to a small extent from seedling establishment or vegetative spreading at the bottom.

Fig. 2: Number of recolonizing species per hoof print in the pasture and at the abandoned site shown separately for bottom (black) and edge (white) zone, for vegetative spreaders and seedlings and for the number of died species (grey) and surviving species after two years. Equal letters indicate no significant difference, to be read for each land use type separately.



SPECIES COMPOSITION IN DIFFERENT HOOF-PRINT ZONES

Frequent species in hoof prints (frequency > 10 %) were similar to frequent species in the surrounding vegetation. At the abandoned site only two out of 18 frequent species in the surrounding vegetation did not occur frequently in the hoof prints (*Trichophorum alpinum* and *Eriophorum latifolium*). Only four species out of 20, which were frequent in the artificially created hoof prints, were less abundant in the surrounding vegetation(*Polygala vulgaris*, *Linum catharticum*, *Galium uliginosum*, *Agrostis stolonifera*). On the pasture, seven frequent species out of 21 of the surrounding vegetation (*Carex pulicaris*, *C. flava*, *Schoenus ferrugineus*, *Eriophorum latifolium*, *Tofieldia calyculata*, *Briza media*, *Holcus lanatus*) were found only rarely in hoof prints and five out of 24 species were frequent in the hoof prints, but not in the vegetation (*Linum catharticum*, *Galium uliginosum*, *Viola palustris*, *Mentha arvensis*, *Parnassia palustris*).

Tab. 4: Frequent species recolonizing hoof prints in the different land use types, differentiated into groups: ‘Matrix species’: frequent in both zones by both colonization types; ‘edge colonizers’: frequent on hoof-print edges by both colonization types; no species group recolonizing the bottom zone could be found; ‘Germinating species’: recolonization by germination on the edge only; ‘vegetative spreaders’: revegetation by vegetative spreading only;

	Species with both recolonization types		Germinating species	Vegetative spreader
	Matrix species	Edge colonizers		
Both land use types	*Molinia caerulea* *Carex davalliana* *Juncus articulatus*	*Leontodon hispidus* *Potentilla erecta*	*Linum catharticum* *Galium uliginosum*	*Vaccinium oxycoccus*
Pasture	*Carex echinata* *Carex elata* *Carex panicea* *Carex hostiana*	*Primula farinosa* *Menyanthes trifoliata*	*Cardamine pratensis* *Drosera rotundifolia* *Parnassia palustris* *Viola palustris* *Mentha arvensis*	*Hieracium lactucella* *Tofieldia calyculata*
Abandonment	*Potentilla erecta* *Schoenus ferrugineus*	*Viola palustris* *Drosera rotundifolia*	*Agrostis canina*	*Carex echinata* *Carex elata* *Carex panicea* *Carex hostiana*

The most common species, mainly grasses and sedges, frequently occurred in both zones and in both spreading forms (Tab. 4: matrix species). None of the frequent species was restricted to the bottom zone neither by vegetative spreading nor by germination. A few species, however, grew mainly on the edge (Tab. 4: edge colonizers). These species revegetated gaps both generatively and vegetatively or additionally by extending the leaf area. Some species were restricted to germination on the edge and were frequent in the hoof print but not in the surrounding vegetation (Tab. 4: germinating species). Only vegetative spreading from the edge of hoof prints was found for *Vaccinium oxycoccus*. At the pasture, the edge of hoof prints were additionally colonized by *Hieracium lactucella* and *Tofieldia calyculata*, whereas at the abandoned site sedge species recolonized the hoof prints vegetatively, but were not able to germinate there in contrast to their ability in hoof prints in pastures (Tab. 4: vegetative spreaders).

SEED BANK

The seed bank contained a total of 47 species in pastures and 44 species at the abandoned site. In the pots, which were only watered and not water-logged, fewer species germinated (43 on pasture, 33 at the abandoned site). Species which did not germinate under drier conditions were mostly species indicating wet conditions (e.g. *Carex canescens, Eriophorum angustifolium*, *Lycopus europaeus*, *Menyanthes trifoliata*, *Phragmites australis*, *Drosera rotundifolia*, *Pinguicula vulgaris*). By contrast, some species did not germinate under water-logged conditions (e.g. *Polygala vulgaris*, *Lotus uliginosus*). Generally, fewer individuals and species germinated in regularly watered soil (32 individuals of 4.9 species on pastures, 42 individuals of 5.9 species at the abandoned site) than in water-logged soil (93 individuals of 8.6 species on pastures, 84 individuals of 9.9 species at the abandoned site). In both sites, the seed bank was dominated by *Juncus articulatus* and *Carex elata*. High seedling numbers were also found for *Potentilla erecta*, *Molinia caerulea*, *Carex davalliana*, *Linum catharticum*, *Drosera rotundifolia* and *Primula farinosa*. Four species present at the abandoned site (*Carex flava*, *Myosotis palustris*, *Vaccinium oxycoccus*, *Valeriana dioica*) and two species of the pasture (*Hypericum tetrapterum*, *Vaccinium oxycoccus*) were not found in the seed bank, although seedlings had been detected in hoof prints. Fifteen species at the abandoned site and 11 species on the pasture were found in the seed bank, but did not germinate in the hoof prints. These species were mainly present in the surrounding vegetation. Only six species at the abandoned site and three species on the pasture were found in the seed bank that were not present at all in the actual vegetation of the fen.

DISCUSSION

REVEGETATION OF HOOF PRINTS

Number and frequency of species revegetating hoof prints did not differ much from the surrounding vegetation in both land use types, which confirms results from pastures on acid grassland (Bullock et al. 1994, Bullock et al. 1995, Edwards & Crawley 1999) and on semi-natural grasslands in Sweden (Eriksson & Eriksson 1997). By contrast, Losvik (1999) found many new species in created gaps in abandoned hay meadows in Norway. In our study, only few new species were able to establish or became more frequent in the hoof prints than in the surrounding vegetation. On the other hand, only few species of the surrounding vegetation were not found in the hoof print, indicating that most species are able to grow in hoof prints. An important finding was that the cover of revegetating plants in gaps created by hoof prints was still low after two years although germination and vegetative spreading had taken place. The sparse colonization supports assumptions by Hillier (1990), Pakeman et al. (1998) and Verkaar & Londo (1993) that gaps in low productive ecosystems remain open for a long time due to the slow growth rate of seedlings and vegetative spreaders. In contrast, gaps in more nutrient-rich pastures were revegetated after 50 weeks or even sooner (Bullock et al. 1995, Arnthorsdottir 1994). Apart from the low nutrient availability, plant species recolonization was also restricted by the abiotic conditions in the investigated gaps, which differed strongly from the surrounding vegetation due to the severe disturbance of the soft peat soil.

RECRUITMENT DEPENDING ON RECOLONIZATION TYPE AND HOOF-PRINT ZONE

Germination is necessary for the introduction of new species and can occur more frequently in gaps (Burke & Grime 1996). In our study, however, only few new species occurred in the hoof prints, and germination rate in total was low. This could be attributed either to limited seed availability or to limited safe site availability (Zobel et al. 2000, Turnbull et al. 2000). It can be assumed that enough seeds were provided by the seed bank and additionally by seed rain. Only few species which germinated in the hoof print were not present in the seed bank and must therefore have originated from the seed rain, whereas many species occurring in the seed bank did not germinate in the hoof print at all. Several studies have shown that gaps in fens, where only vegetation was removed, offer more suitable safe sites for germination than undisturbed vegetation (Kotorova & Lepš 1999, Krenova & Lepš 1996, Isselstein et al. 2002). In hoof prints, however, which are gaps with severe soil disturbance, germination and establishment were restricted in both zones, by at least one factor, as shown in our investigation. At the edges, the dormancy breaking effect of better light conditions and strongly fluctuating temperatures was probably counterbalanced by the negative effects of soil drainage. The results of our seed bank analysis revealed that most fen species germinated better in water-logged soils than under drier conditions. Patzelt et al. (2001), Jutila (2001) and Isselstein et al. (2002) also found a high dependence of germination on wet soil conditions. This means that water conditions in the bottom zone of a hoof print are suitable for germination. Light availability, however, was probably too low there and anoxic conditions might have had negative effects on seedling establishment.

More than half of all germinated species per hoof print disappeared during the two years of observation confirming results of Hillier (1990) and Ryser (1993) in calcareous grasslands. Maas (1988), in contrary, found establishment rates of more than 50 % considering single seedlings and not only species. In both hoof-print zones the factors repressing germination were also limiting seedling establishment. Although the number of germinating species was the same in both zones, establishment rate was much lower in the bottom zone. This means that light availability was probably more restricting for successful seedling survival than water availability in fens. Furthermore, seedling mortality in the pasture was high due to trampling damage whereas at the abandoned sites snail feeding probably had a strong negative influence on seedling survival (pers. observation) as was also found by Wilby & Brown (2001) and Hanley et al. (1996).

In our investigation both germination and vegetative spreading were still taking place after two years as gaps were not revegetated then. On average more species germinated in a hoof print than spread clonally or grew in from the edge, which is in line with findings of Kalamees & Zobel (2002) in dry grasslands. But more than half of all species that emerged as seedlings died during the observation period, whereas vegetative spreaders seldom disappeared. Therefore, regarding the origin of species present after two years, most species spread vegetatively thus confirming results of Hillier (1990), Arnthorsdottir (1994), Edwards & Crawley (1999) from drier habitats. Consequently, species composition in hoof prints and the surrounding vegetation was similar. Vegetative spreading from the surrounding vegetation cannot introduce new species, but can change species proportions. Not only dominant sedge species but also procumbent rosette species grew vegetatively into the edge zones of the hoof prints. Some of the procumbent species, however, did not spread clonally by building new ramets, but grew in from the edge by extending only their leaves in vertical dimension along the steep edge. In the bottom zone, in contrast, the very low number of only 2.5 vegetative recolonizing species per hoof print originated mainly from species which were able to compensate for trampling damage (i.e. sedges and grasses) by regrowth, which could not be separated clearly from vegetative spreading. Species from the surrounding vegetation hardly spread into the bottom zone by crossing the edge zone due to the lack of fast spreading organs and to the changing abiotic conditions.

In total, two thirds of all species revegetate hoof prints both by seedling recruitment and vegetative growth. But only a few species (the ‘matrix-group’) were able to colonize hoof prints in both zones and in both ways. These species were exclusively matrix species of fen vegetation like grasses, sedges or rushes which are generally favoured on pastures (Peintinger 1999). But none of the species grew only on the bottom, elucidating that the bottom zone restricts species occurrence. New species requiring wetter conditions which might invade there were not found in our investigation. In contrast, some species were restricted in their recolonization ability to the edge. Only few of these species possessed fast spreading organs (the speader group) and were able to spread over larger distances (e.g. *Vaccinium oxycoccus*, *Hieracium lactucella*, *Agrostis canina*). But also slow spreaders and even rosette species were able to grow into the edge zone vegetatively. The only group of species for which creation of hoof prints seems to be really beneficial is the group of ‘germinating species’ (Tab. 4), only germinating on the edge (e.g. *Linum catharticum*, *Galium uliginosum* and *G. palustre*, *Drosera rotundifolia*, *Primula farinosa*). They were the only species that were frequent in the hoof prints, but not in the surrounding vegetation. The promotion of such subordinate plants in the edge zone is probably the reason for the maintenance of species richness by gap creation as was suggested by Suding (2001).

DIFFERENCES IN REVEGETATION BETWEEN PASTURE AND ABANDONED FEN

In our study, the surrounding vegetation and seed bank of the pasture and the abandoned site did not differ much. This is in line with findings of Jensen (1998) for early successional stages of abandoned sites as our study site. The different recolonization pattern in the two land use types was therefore probably due to differences in vegetation structure and treatment and not in vegetation composition. The number of vegetative spreaders per hoof print did not differ between pasture and abandonment. However, when all species occurring at the abandoned site are considered, more species were able to compensate for trampling damage on the bottom of a hoof print. This might be due to the simulated trampling which probably did not harm the species as severe as real trampling by cows. Germination rate, however, differed strongly between the two land use types. Subordinate species often depend on germination and therefore decline after abandonment of land use (Jensen & Schrautzer 1999, Diemer et al. 2001). In our study, creation of hoof prints did not lead to recruitment of new species which had not been present in the surrounding vegetation. In the bottom zone with low light availability, growth conditions did not differ much between pasture and abandoned site. But on hoof print edges, germination and establishment rates were lower at the abandoned site than on the pasture. Some frequent species which germinated in hoof prints on pastures spread only vegetatively on abandoned sites (e.g.

Carex panicea, *Carex echinata*). At abandoned sites even in gaps germination is restricted due to shading by the surrounding vegetation and the litter accumulation (Diemer et al. 2001, Facelli & Pickett 1991). Furthermore, germination in fens can be hindered by a thick moss cover (Špackova et al. 1998). This was probably also the case in our study, where mosses regenerated quickly after gap creation at the abandoned site. In contrast, moss growth in the pasture was probably impeded by new trampling in the surrounding which means that germination, and seedling establishment at the edges was further indirectly supported by grazing.

CONCLUSION

Our results indicate that the importance of hoof prints for species recruitment has to be reconsidered for fen vegetation. In our study, species frequency in hoof prints was similar to the surrounding vegetation, indicating that – in the long run – gaps may contribute to the maintenance of species composition in fens, but do not enhance species richness. Vegetation cover in hoof prints, however, was still very low after two years and especially in the bottom zone of hoof prints growth conditions for most fen species were unfavourable. Vegetative recolonization occurs only randomly as the number of fast spreading species is low in low-productive fens. It is only possible for species which are - by chance - present in the surrounding vegetation at the edge of a hoof print. Successful recruitment of seedlings, and in particular of new species, did hardly occur. This means that gap creation by trampling is probably not a suitable conservation management tool on abandoned fens to increase the occurrence of formerly declined species since seeds of these species are hardly available and suitable microsites lacking. The positive effect of grazing in general on seedling recruitment in fens in contrast to abandonment is probably more due to the reduction of the litter layer by foraging (Facelli & Pickett 1991, Špackova et al. 1998) than to gap creation by trampling. Zobel et al. (2000) and Watt & Gibson (1988) also pointed out that in nutrient poor grasslands, such as low-productive fens, germination is often not gap dependent owing to the fact that vegetation per se is not very dense. The aim of an appropriate grazing regime on fens should therefore not be to create gaps but to reduce soil disturbance. Our study, however, only considered single hoof prints rather than an accumulation of many hoof prints, where no clear division between bottom and edge can be made anymore. There, the abiotic conditions may be different again and the very wet parts might get enough light offering a new habitat for species requiring wetter conditions. Trampling damage to recolonizers, however, will be even more severe at such sites.

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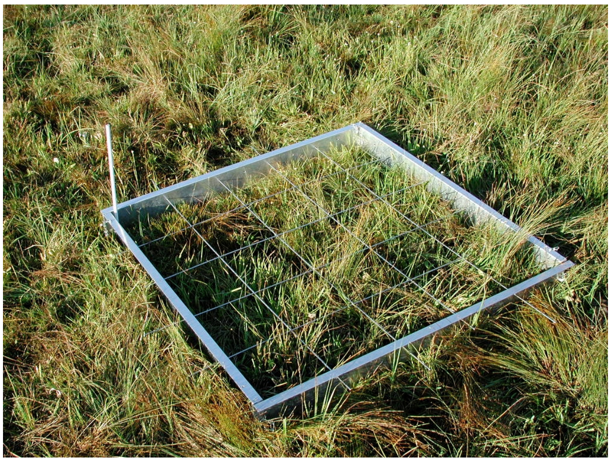
CHAPTER 5

EFFECTS OF REAL AND SIMULATED LAND USE ON GERMINATION AND ESTABLISHMENT OF SIX FEN SPECIES

with Kathrin Kiehl & Jörg Pfadenhauer

submitted to Basic and Applied Ecology



EFFECTS OF REAL AND SIMULATED LAND USE ON GERMINATION AND ESTABLISHMENT OF SIX FEN SPECIES

ABSTRACT: The effects of land use on germination and establishment of six fen species were investigated in a land-use simulation experiment with changed vegetation structure and under real land use in a calcareous fen. The investigated species differed in seed weight and growth form of the adult plants. In the land-use simulation experiment, seeds of all six species were sown in plots with different treatments: simulated grazing and mowing with or without litter removal, grazing + trampling and abandonment. Under real land use, the impact of mowing, grazing, trampling and abandonment on emergence and survival of experimentally sown seeds was investigated.

On abandoned plots and plots without litter removal, germination rates of all species were low as germination was negatively affected by litter and moss cover. The effects of simulated grazing and mowing were very similar. Gap creation by trampling did not increase germination rate. Trampling, in contrast, had a severe negative effect on seedlings survival. Species differed in their germination ability tested in the germination chamber and in their response to land use. These differences could be related to seed size and hence to regeneration strategies. *Succisa pratensis* with the heaviest seeds germinated well in the chamber and in the field more or less regardless of land use and was strongly seed limited. *Parnassia palustris,* a species with low germination rates both in the germination chamber and in the field, showed a seed limitation, but also a dependence on microsite. *Serratula tinctoria* and *Primula farinosa* were microsite limited as their seeds germinated well in the germination chamber, but seedlings were repressed by litter or moss cover. Microsite limitation was even stronger for *Tofieldia calyculata* and *Pinguicula vulgaris* which did hardly germinate at all under natural conditions, in spite of a high amount of germinable seeds in the germination chamber. For these two species clonal reproduction seems to be more successful.

ZUSAMMENFASSUNG: In zwei Aussaatexperimenten in Kalkflachmooren wurde der Einfluss unterschiedlicher Landnutzung auf die Keimung und Etablierung von sechs Niedermoorarten untersucht. Diese unterschieden sich hinsichtlich ihres Samengewichts und der Wuchsform der adulten Pflanzen. Im ersten Experiment wurden verschiedene Landnutzungsvarianten durch die Veränderung der Vegetationstruktur simuliert (Beweidung und Mahd mit oder ohne Entfernung der Streuschicht, Tritt und Brache). Das zweite Aussaatexperiment wurde in unterschiedlich genutzten Kalkflachmooren durchgeführt (Varianten: Weide, Weide mit intensiver Trittbelastung, Herbstmahd und Brache).

Für alle Arten wurde unter Brachebedingungen und in Varianten ohne Entfernung der Streuauflage eine geringe Keimrate aufgrund der dichten Streu- und Moosschicht beobachtet. Die Keimungs- und Etablierungsraten auf genutzten Flächen war dagegen höher; sie waren auf der Weide und der gemähten Streuwiese sehr ähnlich. Die Schaffung von offenen Trittstellen konnte die Keimrate nicht erhöhen. Starke Trittbelastung wirkte sich negativ auf das Überleben der Keimlinge aus.

Die untersuchten Arten unterschieden sich sowohl hinsichtlich ihrer Keimfähigkeit, die im Keimschrank getestet wurde, als auch hinsichtlich der Intensität ihrer Reaktion auf die Landnutzung. Die Samen von *Succisa pratensis* waren am schwersten und keimten sowohl im Keimschrank als auch im Freiland gut. Keimung und Etablierung wurden durch die Nutzung kaum beeinflusst. Die Keimung war im Freiland hauptsächlich durch die Samenverfügbarkeit limitiert. Die Samen von *Parnassia palustris* wiesen im Keimschrank nur geringe Keimraten auf, diese waren im Freiland jedoch genauso hoch. Diese Art war vor allem durch die Verfügbarkeit keimfähiger Samen limitiert, dennoch konnte ein Einfluss der unterschiedlichen Nutzungen festgestellt werden. Die Keimung von *Serratula tinctoria* und *Primula farinosa* war in hohem Maße durch die Verfügbarkeit von Keimnischen eingeschränkt. Beide keimten im Keimschrank gut, im Freiland wurde die Keimung jedoch in Anwesenheit einer dichten Moos- und Streuschicht unterdrückt. *Tofieldia calyculata* und *Pinguicula vulgaris*, die beiden Arten mit den leichtesten Samen, keimten im Freiland kaum, obwohl ihre Samen eine hohe Keimfähigkeit im Keimschrank aufwiesen. Sie benötigen spezielle Keimbedingungen, die nur in wenigen Keimnischen gegeben sind. Die klonale Ausbreitung ist für diese Arten offenbar erfolgreicher.

KEYWORDS: pasture, litter meadow, abandonment, calcareous fen, cattle grazing, seedling recruitment, seed weight, trampling

INTRODUCTION

Although semi-natural grasslands and calcareous fens are dominated by perennial plants, maintenance of species richness is limited by seedling recruitment, a critical life phase of plants (Grubb 1977, Harper 1977). Land use as regular mowing plays a primary role in determining the diversity of grassland communities by generating suitable safe sites for germination (Pickett & White 1985, Jutila & Grace 2002). Abandonment, in contrast, leads to species decline due to dominance of competitive species and litter accumulation (Facelli & Pickett 1991, Xiong & Nilsson 1999) which has also been proven for fen vegetation (Diemer et al. 2001). In an abandoned meadow, adult plants which are less affected by litter can persist for a long time, but germination of seeds is often inhibited by an increased litter layer (Krenova & Lepš 1996, Kotorova & Lepš 1999).

Due to the overall trend of abandonment of traditional land use in low productive meadows, grazing is discussed as a tool for conservation management as it reduces litter accumulation in a similar way as mowing (Bakker 1989). In comparison to traditional autumn mowing in fens, biomass loss due to grazing takes place more constantly during the whole vegetation period and additionally, trampling by grazing animals creates gaps in the vegetation cover. As a consequence, species composition varies between pastures and meadows which is often related to growth form of adult plants (Lavorel et al. 1997).

The effect of grazing on germination and seedling establishment is not known for fen species. In contrast to mowing, grazing resulted in higher germination rates for some species in a salt-marsh (Bakker & de Vries 1992), but not for species in mesotrophic grassland (Coulson et al. 2001). Compared to abandonment, grazing enhanced seedling recruitment in Pampa-grassland (Oesterheld & Sala 1990) and in semi-natural Swedish grassland (Eriksson & Eriksson 1997). Up to now, seedling recruitment of fen species has only been studied in relation to vegetation structure. Germination rate of fen species is negatively affected by vegetation height (Maas 1988), whereas for the moss layer both negative and positive effects on species recruitment have been reported (Špackova et al. 1998, Overbeck et al. 2003). Although seeds and seedlings may require different conditions (Schupp 1995), many studies showed similar effects of vegetation structure on germination and seedling establishment (Kotorova & Lepš 1999, Kupferschmid et al. 2000, Stampfli & Zeiter 1999). On pastures, cow hooves can create gaps which are often regarded as regeneration niches (Isselstein et al. 2002, Krenova & Lepš 1996, Kotorova & Lepš 1999), but obviously trampling can also increase seedling mortality compared to mowing or abandonment (Crawley 1997).

Germination requirements of species are known to differ strongly in respect to seed size or weight due to abiotic conditions which might be influenced by land use (e.g. Stockey & Hunt 1994, Eriksson & Eriksson 1997). Further, recruitment success may not only be limited by suitable microsites, but also by availability of germinable seeds (Turnbull 2000). Therefore, we carried out two sowing experiments in different land use variants under natural conditions with six plant species typical for calcareous fens in Central Europe that differed in growth form and seed size. We addressed the following questions: (1) What is the effect of different variants of real and simulated land use on germination and seedling establishment of selected species? (2) Can this effects be related to differences in land use induced vegetation structure? (3) Are the selected species mainly limited by seed availability or by microsite availability? (4) Is it possible to identify species strategies regarding both seedling response and traits of adult plants?

METHODS

STUDY SITE

The study was carried out in a calcareous fen near Füssen in the prealpine region of southern Germany (800 m above sea level). Annual mean temperature varies between 6 and 7 °C, mean annual precipitation is 1500 mm yr^{-1}. The water level changes between 0 and 20 cm below surface during the vegetation period. Under traditional land use, the fen had been mown in autumn (September); the harvested biomass served as bedding in cow stables. Land use was abandoned in one part of the fen approximately 10 years ago. In another part, mowing was ceased and grazing was introduced in 1998 in connection with a pasture on mineral soils. Grazing intensity was low with ca. 20 heifers grazing from May until September on 4 ha of mineral soil and 1.5 ha of peat soil. Adjacent to the pasture an unfertilised litter meadow was still traditionally mown in September. Nutrient availability in all parts of the fen was low, aboveground standing crop reached only around 120 g m^{-1}. Vegetation of the study site can be classified as Caricion davallianae (Oberdorfer 1998) dominated by small sedges (*Carex davalliana*, *C. panicea*, *C. hostiana*) and the grass *Molinia caerulea*. On the pasture, the cover of *Carex elata* was higher, whereas at the abandoned site *Schoenus ferrugineus*, *Rhynchospora alba* and *Sphagnum* species had higher cover values.

SPECIES CHARACTERIZATION

For the sowing experiment, six common fen species characteristic for the vegetation of the study area were selected. All species were perennial herbs. According to Maas (1989), the seeds of all six species show primary dormancy, which can be broken by cold-wet stratification, chemical treatments and temperature fluctuation. All species build up a short-term persistent seed bank, but they differ in growth form, ability of clonal spreading and seed weight. *Serratula tinctoria* and *Succisa pratensis* are tall, late flowering herbs. Their relatively big seeds weighed 1.2 mg, respectively 3.6 mg and did not ripen before September. *Primula farinosa* and *Parnassia palustris* are small rosette plants, flowering in spring or summer. Their mean seed weight was much lower with 0.06 mg (*Primula*) and 0.02 mg (*Parnassia*). *Tofieldia calyculata* and *Pinguicula vulgaris* are small rosette plants able to reproduce clonally. Both species flower in spring and early summer. Seeds of *Tofieldia* weighed on average 0.04 mg, seeds of *Pinguicula* 0.002 mg.

SOWING EXPERIMENTS

To observe the impact of simulated land use on vegetation and seedling recruitment, a sowing experiment was started in autumn 2000. Seeds of the six fen species were collected on adjacent fens and mixed for each species. The seeds were sown out immediately after collection to prevent induced dormancy. Due to different ripening times sowing dates varied between 5th July (*Pinguicula*), 1st August (*Primula*, *Tofieldia*, *Parnassia*) and 18th September (*Succisa*, *Serratula*). The land use simulation experiment was conducted at the abandoned site with different treatments as listed in Table 1. For the treatment 'trampling' gaps of the size of a hoof print and a depth of approximately 10 cm were created by a hoof dummy pressed in the soft peat soil by a hammer. The earlier mowing date in July was to simulate biomass loss on pastures during the grazing season in contrast to traditional mowing in September. Litter removal was to simulate a continuous land use where no litter accumulation had taken place.

Tab. 1: Treatments in the land-use simulation experiment, regarding mowing time, litter removal and initial trampling. The abbreviations are used in the following.

	Abbreviation	mowing	litter removal	trampling
Abandonment	A			
Mowing	M	September	x	
Grazing	G	July	x	
Trampling	GT	July	x	x
Mowing without litter removal	M –L	September		
Grazing without litter removal	G –L	July		

In July and September 2000, treatments were applied on plots of 1 m^2 in a completely randomised block design with 10 replicates. Mowing was repeated in July or September 2001, respectively. Seeds were sown out on 25 x 25 cm in the middle of each 1 m^2 plot to avoid edge effects. For species with bigger seeds (*Succisa* and *Serratula*) 25 seeds each were placed along a grid pattern in order to relocate seed position later. 50 seeds of each smaller seeded species were sown out as equally as possible into a wooden frame. To estimate seed rain and recruitment of the seed bank of the investigated species on the site, control plots without any sowing were established. Only for *Primula* a negligible amount of seedlings (5 in total) could be found in the control. Therefore all emerging seedlings in the experiment were considered to have originated from sown seeds. Seedling emergence and survival were monitored once in October 2000, and in two-week intervals from beginning of April to July

2001. In August and September 2001 seedlings were counted monthly. A last counting took place in April 2002 to check mortality over winter and second-year germination. Seedlings were marked by coloured toothpicks and grid position was annotated in order to identify them exactly.

In autumn 2001, a second sowing experiment was started in differently managed fens in order to study the effects of real land use on seedling recruitment and to validate the results of the land-use simulation experiment. Four fen sites with different land use were selected: ‘abandonment’ (A), ‘litter meadow’ (M), ‘grazing’ (G) and ‘trampling’ (GT). The latter represented the part of the pasture with intense trampling pressure and therefore a high amount of bare soil (more then 70 %). In each of the sites ten plots of 25 cm x 25 cm were established in September 2001. The number of seeds was doubled compared to the number in the land-use simulation experiment because some species had shown low germination rates. Sowing and monitoring of germination and seedling survival was carried out in the same way as in the land-use simulation experiment until September 2002.

For the characterization of the habitat conditions vegetation structure was studied in July. Vegetation height was measured as height when a 0.25 m^2 Styrofoam plate stopped falling. Total vegetation cover, litter cover and moss cover were estimated separately. As mosses reached generally high cover values in the land-use simulation experiment the thickness of the moss layer was measured additionally.

Germination ability of the seeds was tested for seeds of both years in a germination chamber at conditions proven to be suitable for the investigated species (Maas 1989). In eight replicates, 50 seeds of each species were put on moist blotting paper in petri dishes and watered with distilled water if necessary. Swollen seeds were stratified for six weeks at 3 °C and exposed to a fluctuating regime of 14 light hours at 22 °C and 10 dark hours at 12 °C. Seedlings were counted and removed twice a week. Observation ended two weeks after the last germination had occurred.

DATA ANALYSIS

As not all seeds were able to germinate, the percentage of germinated seeds in the germination chamber was defined as “percentage of germinable seeds”. Germination rate was calculated as percentage of seeds germinated in the field to sown seeds, multiplied with the percentage of germinable seeds. The same computation was conducted for the establishment rate. Survival rate represents the percentage of established seedlings in relation to emerged seedlings.

Original data were logtransformed ($x' = \log(x+1)$) if necessary to fulfil test requirements. All percentage data were transformed by arc-sin function. Differences between treatments or land use for each experiment were evaluated by a one-way ANOVA. For the land-use simulation experiment, the block effect was determined in order to reduce the amount of variance not explained. Significant differences between single treatments were tested post-hoc by Tukey-test. Correlations between vegetation structure and the number of emerged seedlings or survival rate data were analysed by calculating Pearson's correlation or by a Spearman-rank correlation. For data of the sowing experiment under real land use, the trampled sites were excluded from this correlation analysis because trampling effects prevailed over the impact of vegetation structure.

RESULTS

VEGETATION STRUCTURE

In both experiments, vegetation structure differed significantly between land use types for all measured parameters (Tab. 2). Under real land use, the vegetation was highest and densest at the abandoned site with a dense moss layer and a thick litter layer. Trampling by cattle led to low vegetation cover and height with no moss or litter layer at all. Vegetation structure on the pasture and on the litter meadow was intermediate between these two extremes concerning all measured parameters. On the pasture, vegetation was lower and denser than on the meadow and moss cover was higher, whereas litter cover did not differ between grazed and mown sites.

Tab. 2: ANOVA results (F-values, df: degrees of freedom) of the two sowing experiments for treatment and block effect and mean values of vegetation structure data for the single treatments (A: abandoned site, M: mowing; G: grazing; GT: trampling; M -L: mowing without litter removal; G -L: grazing without litter removal). Significance levels of the ANOVA: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Equal letters next to mean values indicate no significant differences according to Tukey-test ($p > 0.05$). Letters have to be read for each experiment and each parameter separately.

	treatment		**block**		**mean values**					
	df	**F-value**	**df**	**F-value**	**A**	**M**	**G**	**GT**	**M -L**	**G -L**
land-use simulation experiment										
vegetation height [cm]	5	4.1 **	9	24.9 ***	33.2 b	31.8 b	29.5 a	29.1 a	32.1 b	30.4 a
vegetation cover [%]	5	3.3 *	9	37.7 ***	63.7 b	58.7 b	58.3 b	49.2 a	62.5 b	61.3 b
moss cover [%]	5	2.9 *	9	85.5 ***	40.7 b	37.2 ab	37.4 ab	32.0 a	41.2 b	43.4 b
moss thickness [cm]	5	11.6 ***	9	13.5 ***	4.2 a	1.7 bc	1.8 bc	1.0 c	2.6 ab	2.7 ab
litter cover [%]	5	19.3 ***	9	8.3 ***	35.9 a	10.8 cd	10.7 cd	7.0 d	15.8 c	18.6 b
real land use										
vegetation height [cm]	3	112.3 ***			27.7 a	17.4 b	11.8 c	6.7 d		
vegetation cover [%]	3	204.2 ***			90.8 a	61.0 b	79.0 a	8.0 c		
moss cover [%]	3	54.2 ***			72.5 a	33.0 c	40.0 b	0.0 d		
litter cover [%]	3	38.7 ***			29.2 a	2.4 b	2.0 b	0.0 b		

The land-use simulation experiment showed similar results as the sowing experiment in real land use, but differences between treatments were less pronounced because a large proportion of the variance was explained by the block effect. Vegetation was higher on both mown plots and abandoned plots compared to all three 'grazed' plots (G, GT, G -L). Vegetation cover was significantly lower in the trampling treatment (GT) compared to the other treatments. Moss cover was low on mown and on grazed plots where litter of former years had been removed, and even lower on trampled plots. Thickness of the moss layer was highest on abandoned plots declining on mown or grazed plots without litter removal, but lowest values could be found for mown and grazed plots with litter removal as well as for the trampling treatment. Litter cover reached 36 % on abandoned plots, followed by 16 % on mown and 19 % on grazed plots without litter removal.

GERMINATION UNDER CONTROLLED CONDITIONS

The mean germination rate in the germination chamber after cold-wet stratification varied in 2000 (land-use simulation experiment) between 11.6 % for *Parnassia* and 96.8 % for *Pinguicula*, in 2001 (experiment under real land use) between 1.6 % for *Serratula* and 74.4 % for *Tofieldia* (Tab. 3). The low germination rate of *Parnassia* did not differ between years. Germination rates of the other species differed significantly both between species and between years for the single species.

GERMINATION IN THE FIELD

Germination rates in the field differed significantly between species (Tab. 3). In the land-use simulation experiment, ca. 80 % of the germinable seeds of *Succisa* and *Parnassia* germinated, compared to 18 % of the *Primula* and 29 % of the *Serratula* seeds. For *Pinguicula* and *Tofieldia* only a very small number of seedlings was observed. Under real land use, two thirds of the germinable seeds of *Serratula* germinated, but, due to a very low overall germination rate in 2001, this was only 1 seedling per plot in absolute numbers. Almost half of all *Succisa* seeds germinated but the absolute number of seedlings was high due to high germination ability. For *Primula* and *Parnassia* less than one third of all possible seedlings occurred, for *Pinguicula* and *Tofieldia* only very few seedlings were found.

In both experiments, treatments had significant effects on germination rates of most of the investigated species (Fig. 1). *Pinguicula* seedlings, however, occurred with low numbers in three treatments only (mowing, grazing, trampling) in the land-use simulation experiment. *Succisa*, in contrast, showed relatively high germination rates in all plots. For all species, a clear trend could be observed: on abandoned plots germination rate was lowest (below 10 % for all species except *Succisa*), followed by a low germination rate on plots without litter removal. For the other treatments of the land-use simulation experiment no consistent trend could be found. Artificially created gaps in the treatment "trampling" offered best conditions for *Parnassia*, even better than in the germination chamber, whereas for the other species the treatments “mowing” (*Tofieldia*, *Primula*) or “grazing” (*Succisa*, *Serratula*) showed the highest germination rates. No significant differences were found for any of the species either between “mowing” and “grazing” or between “mowing without litter removal” and “grazing without litter removal”.

Response of most species to real land use was in general similar as in the land-use experiment (Fig. 1). For *Tofieldia, Pinguicula* and *Serratula*, however, seedling emergence did not differ significantly between land use types due to the overall low germination rate. Some seedlings of these species emerged on mown sites and only few on trampled or grazed plots, but none on the abandoned site. The lowest germination rates for *Primula* and *Parnassia* were observed at the abandoned site. No *Parnassia* seedlings were found on mown sites, whereas the germination rate of *Primula* did not differ significantly between meadow, pasture or trampled site. For *Succisa,* germination rates were lowest on mown sites and on abandoned sites and highest on trampled and grazed sites.

Tab. 3: Effects of real and simulated land use on germination rates of six fen species: Germination rates in the germination chamber are given as percentage of all seeds; germination rate in the field as percentage of germinable seeds related to germination chamber results and as mean, maximum and minimum of absolute number per 25 cm x 25 cm plot, letters in brackets indicate the land use type (A: abandoned site, M: mowing; G: grazing; GT: trampling; M-L: mowing without litter removal; G-L: grazing without litter removal); survival rate is calculated as rate of established seedlings in relation to germinated seedlings in the field.

	germination chamber	**seedling number**				**survival rate**
	mean [%]	mean [%]	mean	max	min	mean [%]
land-use simulation experiment						
Parnassia	11.6	81.6	4.7	8.3 (GT)	0.5 (A)	77.3
Primula	94.8	18.4	8.7	14.1 (M)	1.2 (A)	66.9
Serratula	57.6	29.1	4.2	7.1 (G)	1.2 (A)	73.0
Succisa	49.6	79.3	9.8	12.8 (G)	7.6 (A)	78.3
Pinguicula	96.8	0.6	0.3	1.0 (G)	0.0 (A, G-L, M-L)	58.9
Tofieldia	59.6	6.8	2.0	4.3 (M)	0.0 (A)	59.0
real land use						
Parnassia	23.2	28.1	6.5	18.5 (M)	1.0 (A)	44.3
Primula	58.4	26.5	15.5	22.6 (M)	4.2 (A)	39.4
Serratula	1.6	64.2	1.0	1.5 (GT)	0.0 (A)	43.3
Succisa	73.6	44.1	16.8	22.4 (G)	9.6 (M)	52.7
Pinguicula	62.7	1.9	1.2	2.7 (M)	0.0 (A)	48.2
Tofieldia	74.4	2.5	1.9	3.2 (GT)	0.0 (A)	40.6

SURVIVAL RATE – MORTALITY AND ESTABLISHMENT

Survival rate in the land-use simulation experiment ranged between 59 % for *Pinguicula* and *Tofieldia* and 78 % for *Succisa*, but did not differ significantly between treatments (Tab. 3). However, a trend from highest survival rates at the abandoned site to lowest on trampled sites could be observed for all species. Seedling mortality was highest during the summer whereas in winter almost no seedlings died. Effects of simulated land use on established seedlings (Fig. 1) were very similar to the effects on germination. For *Succisa*, no significant effects of the different treatments were found anymore, for the other species differences between treatments became smaller.

Real land use had a significant effect on seedling survival. Highest mortality was found at the trampled sites where no seedlings of *Serratula* and *Parnassia*, only 9 % of the *Succisa* seedlings and 19 % of the *Primula* seedlings were able to survive until autumn. At the abandoned sites survival rate was highest with 100 % for *Parnassia* and 87 % for *Succisa*. *Primula*, in contrast, showed the highest survival rate on mown sites (72 %) compared to only 44 % of the seedlings surviving until autumn at the abandoned site. Establishment rate on trampled sites therefore was as low as on abandoned sites (*Parnassia*, *Primula*, *Serratula*) or even lower (*Succisa*). For *Parnassia*, *Serratula* and *Succisa* survival rates did not differ between mown and grazed sites. *Pinguicula* seedlings established only on mown sites. For *Tofieldia* seedling survival rate was higher on mown sites (1.9 of 2.7 germinated seedlings) than on pastures (0.2 of 0.8 germinated seedlings).

CORRELATIONS BETWEEN SEEDLING RECRUITMENT AND VEGETATION STRUCTURE

The effect of vegetation structure on germination and survival rates differed between species (Tab. 4). *Succisa* showed the same response in both experiments: germination rate was negatively correlated with vegetation height, whereas survival was positively related to litter cover. For *Serratula*, survival in the land-use simulation experiment was positively correlated with litter cover and negatively with vegetation cover, moss cover and moss layer thickness. Germination rates of both *Parnassia* and *Primula* under real land use were negatively correlated with vegetation cover and moss cover (*Primula* also with moss layer thickness), whereas survival rate of *Primula* was negatively related with vegetation cover but positively to vegetation height. For *Parnassia,* germination rate was negatively correlated with litter cover in the land-use simulation experiment, but survival rate at real land use showed a positive relation to litter cover.

Tab. 4: Significant correlations between vegetation structure data (cover, height) and germination rate and survival rate for land-use simulation experiment and real land use. Only significant correlation coefficients are listed, tested by Spearman-rank correlation: * p < 0.05; ** p < 0.01; *** p < 0.001.

Germination rate	*Parnassia*	*Primula*	*Serratula*	*Succisa*	*Pinguicula*	*Tofieldia*
land-use simulation						
Vegetation cover					-0.30 *	
moss cover					-0.31 **	
litter cover	-0.41 **					-0.49 ***
Vegetation height	-0.35 **			-0.40 **		
moss layer thickness		-0.43 ***	-0.29 *		-0.35 **	-0.33 *
real land use						
Vegetation cover	-0.78 ***	-0.75 ***			-0.59 **	-0.46 *
moss cover	-0.66 **	-0.77 ***			-0.65 ***	
litter cover			-0.50 **			
Vegetation height				-0.44 **		
Survival rate	*Parnassia*	*Primula*	*Serratula*	*Succisa*	*Pinguicula*	*Tofieldia*
land-use simulation						
Vegetation cover		-0.29 *	-0.40 **			
moss cover			-0.38 **			
litter cover			0.31 *	0.44 ***		
Vegetation height						
moss layer thickness			-0.42 ***			
real land use						
Vegetation cover		-0.44 *				
moss cover						
litter cover	0.48 *			0.46 *		
Vegetation height		0.42 *			0.67 *	

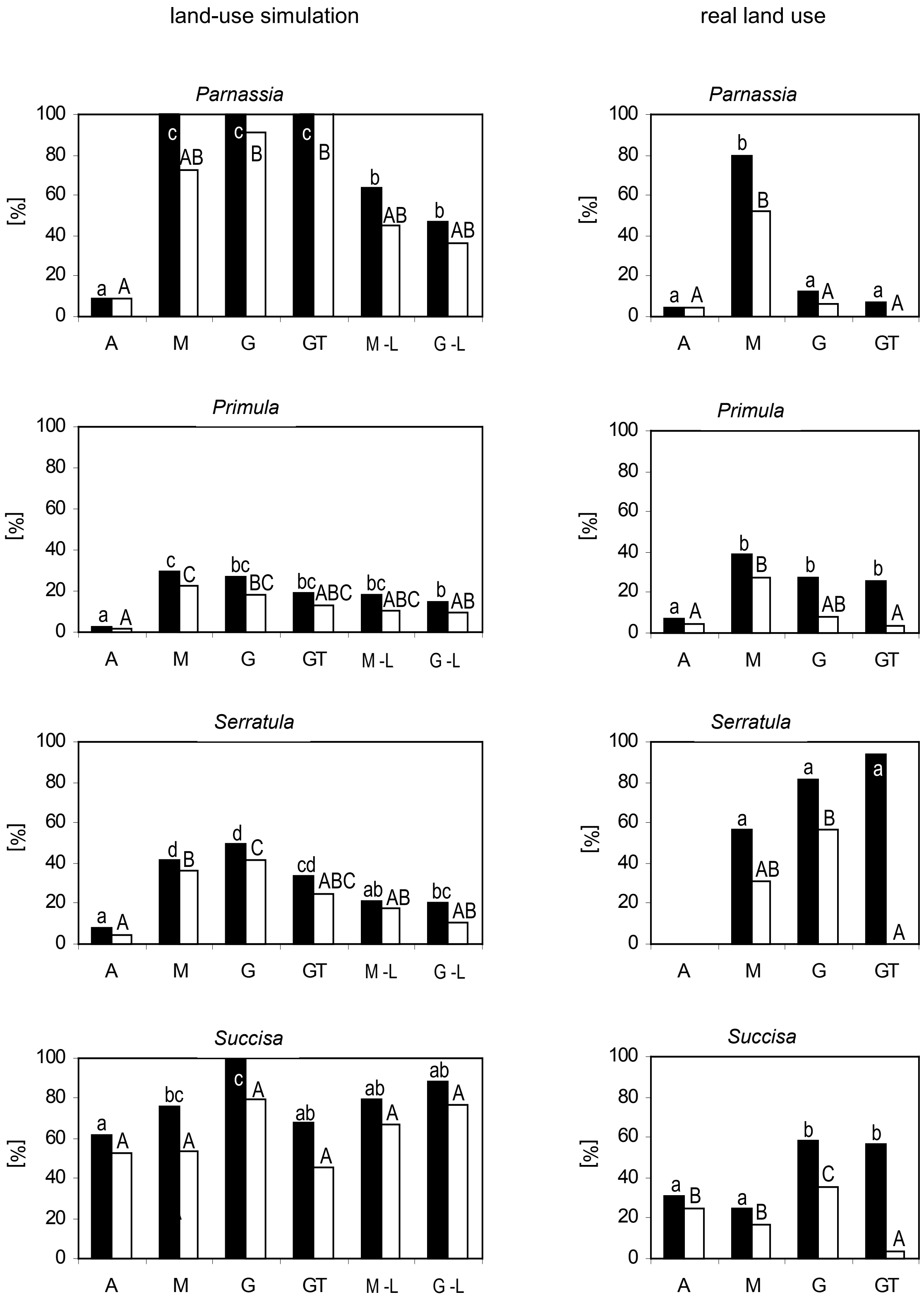


Fig. 1: Effect of simulated land use (left column) and real land use (right column) on germination rate (black) and establishment rate (white) as rate of germinable seeds (germination chamber) for species with a mean germination rate higher than 10 % (for *Pinguicula* and *Tofieldia* see text). Equal letters above bars indicate no significant differences ($p < 0.05$) between treatments for germination rate (lower case letters) respectively establishment rate (upper case letters). Treatment abbreviation: A: abandonment; M: mowing; G: grazing; GT: grazing and trampling; M-L: mowing without litter removal; G-L: grazing without litter removal

DISCUSSION

GENERAL RESPONSE OF SPECIES TO LAND USE

In our study, germination rates differed considerably between the investigated species. Nevertheless some similarities between species could be found which will be discussed first to elucidate the overall effect of land use on germination of fen species. Germination of all species was promoted by any form of treatment and land use in contrast to abandonment. The most obvious difference between abandoned sites and other plots was the presence of a dense litter cover. Many studies have shown that litter accumulation reduces germination rates of plant species due to changed light and temperature conditions in fens (Krenova & Lepš 1996, Kotorova & Lepš 1999) as well as in other habitats (Xiong & Nilsson 1999, Facelli & Pickett 1991). In our study, negative correlations between germination rate and litter cover were found for most of the species in at least one of the experiments. Presence of mosses also had a negative effect on germination of most of the species. Reduced germination rates with increasing moss cover were also found by Špackova et al. (1998), Oostermeijer et al. (1994) and Kotorova & Lepš (1999) in fens. Van Tooren (1990) stated that the moss layer can have negative effects on germination because of changing quantity and quality (red/far red ratio) of light, prevention of seeds from reaching the soil and allelopathic effects on germination. Positive effects of the moss layer on germination and seedling establishment by providing suitable water supply, as was found by Overbeck et al. (2003) in a fen with fluctuating groundwater levels or by Ryser (1993) in calcareous grasslands, did not occur in our study, probably because the investigated plots did not dry out.

A further similarity in the response of single species was the missing difference between simulated grazing and mowing which demonstrated that biomass removal only is not sufficient to simulate grazing. The earlier cutting date of the simulated "grazing" resulted only in a lower vegetation height compared to the mown sites, which had no influence on germination of the investigated species except for *Succisa* which is discussed later. As vegetation was not very dense, the amount of light reaching the soil surface was hardly reduced by increasing vegetation height, whereas the horizontal alignment of litter was restricting light availability much stronger. Maas (1988) also found no negative effects of vegetation height on germination rates in nutrient poor calcareous fen meadows, but in nutrient enriched fens with a denser vegetation germination rates decreased with increasing vegetation height .

Many studies have shown that dense vegetation hindered germination and that gaps in fens therefore had positive effects on germination (e.g. Isselstein et al. 2002, Krenova & Lepš 1996, Kotorova & Lepš 1999). In our experiment, however, both the artificially created gaps and the open sites of "trampling" favoured germination only in contrast to abandonment, but not in contrast to mowing or grazing without trampling. In our study, gaps created by cow hooves mean not only vegetation removal, but also soil disturbance with dramatically changed environmental conditions: deep holes arised with a steep, drained edge and a dark bottom which was sometimes flooded. Here, seedling recruitment was probably inhibited by drainage of the hoof-print edge leading to desiccation or by inundation of the bottom zone leading to annoxia (Isselstein et al. 2002, Patzelt & Pfadenhauer 1998). Therefore, seeds in hoof prints of fens cannot take advantage of the more suitable light conditions, in contrast to drier habitats where soil disturbance by trampling is less severe (Hillier 1990, Bullock et al. 1994, Jutila & Grace 2002).

It has been shown that seedling survival is affected by competition, by soil conditions and microclimate or by herbivores like slugs (Ryser 1993, Patzelt & Pfadenhauer 1998, Hanley et al. 1996). In the land-use simulation experiment, these factors were obviously not influenced by the treatments as survival rates did not differ significantly. Although vegetation structure was significantly changed by simulated grazing or mowing it had hardly any effect on seedling establishment indicating that light availability was probably more limiting germination than establishment. Different types of real land use, in contrast, had a highly significant effect on survival rate as not only modifications of vegetation structure occurred, but continuous trampling in different intensities. Foraging did probably not affect seedling survival rates as cows are not able to bite in such a low height, but trampling harmed seedlings to a large extent. In those parts of the pasture where trampling occurred in lower intensity, mortality rate of seedlings was also slightly reduced compared to mowing or abandonment. This is in contrast to the low seedling mortality rate in grazed arid grasslands found by Fowler (1988) or to the similar survival rates in mown and grazed salt marshes (Bakker & de Vries 1992) and mesic grassland (Coulson et al. 2001) where trampling effects were less severe due to the drier mineral soils.

DIFFERENCES IN SPECIES RESPONSE TO LAND USE

In spite of the above mentioned general trend of germination response to vegetation structure, differences between species occurred which can be related to seed size and weight. The denser vegetation of the pasture in comparison to the traditionally mown meadow led to lower germination rates of the small seeded *Parnassia palustris*, *Primula farinosa*, *Tofieldia calyculata* and *Pinguicula vulgaris*. In contrast, *Succisa pratensis*, was favoured by grazing as germination was correlated with vegetation height and not with vegetation cover. *Succisa* also showed a slightly higher survival rate than the other species which indicates that heavy seeds with big reserves have a positive effect on establishment rates (Stockey & Hunt 1994). Germination of *Succisa pratensis* and *Serratula tinctoria* were less affected by a higher vegetation and moss cover than the other species as their big seeds might remain on top of the procumbent vegetation layer and due to their large reserves seedling roots were still able to reach the soil surface. Smaller seeds of the other species, in contrast, probably sank down to the soil surface where shading hindered their germination. If small seeds, however, remain on top of the procumbent vegetation, their seedlings probably die by desiccation due to their smaller reserves and therefore smaller roots. For *Succisa*, even a dense litter layer had a positive effect on the survival rate, indicating that litter can protect seedlings in the same way as surrounding vegetation (Ryser 1993) as seedlings are big enough to penetrate the litter layer.

All investigated species were seed limited in both experiments as the control plots without seed addition showed almost no germination at all. Seed availability, however, may also be affected by land use because both on pastures and on meadows, seeds may be destroyed by grazing or mowing prior to ripening and dispersal (Dumontier et al. 1996, Coulson et al. 2001). The differences in the germination chamber indicate differences in the germination ability of the sown seeds, whereas the differences in germination rates between treatments indicate differences in microsite limitation for the investigated species. *Succisa*, *Primula* and *Serratula* (only in the first year) germinated well both under controlled conditions and in the field. *Succisa* with the highest germination rate of all tested species in the field and only a weak response to treatments seemed to be most seed limited of all species tested, which is typical for dominant species (Turnbull et al. 2000). It was hardly suppressed by litter or by cover of surrounding plants and mosses which is in agreement with the findings of Patzelt & Pfadenhauer (1998) and Isselstein et al. (2002). *Primula*, in contrast, was more strongly affected by land use. Although germination took place to a reasonable amount, *Primula* was mainly microsite limited, whereas *Parnassia* showed a different response: a very low germination rate under "optimal" conditions in the germination chamber, but almost the same amount of seedlings in the field. This species was seed limited to a high extent, as not enough germinable seeds could be provided. Nevertheless, the differences between land use indicate that germination of *Parnassia* still depended on microsites. Further, it has to be taken into account that probably not the "optimal" conditions could be simulated in the germination chamber. Maas (1989) found for *Parnassia* a high dependence on chemical dormancy breaking mechanism which have not been performed in our study in order to treat all species in the same way. Therefore, dormancy breaking conditions were probably better in the field which resulted in calculated germination rates of sometimes more than 100 % in relation to the amount of "germinable" seeds. The low germination rate in the chamber for *Serratula* in the second year, in contrast, was probably due to an unfavourable fruiting season. *Pinguicula* and *Tofieldia* with the smallest seeds of all investigated species, in contrast, showed a high germination rate in the germination chamber, but did hardly germinate in the field. Maas (1989) also found very low germination rates for these species in soil filled pots compared to the germination chamber. These species were strongly microsite limited as they did not germinate at all without litter removal in our experiment. So the known relation between seed size and gap dependence due to large reserves (e.g. Burke & Grime 1996, Eriksson & Eriksson 1997) can be extended explicitly to dependence on absence of litter. Additionally, *Pinguicula* seedlings are very tiny and can be identified well on filter paper, but may be overlooked easily on soil (Svensson et al. 1993). A quick mortality which is also typical for small seeded species could be another reason that no germination of *Pinguicula* and also of *Tofieldia* could be observed.

PERSPECTIVES FOR SPECIES PERSISTENCE UNDER DIFFERENT LAND USE

In our study, seedling recruitment varied between land use types and the response of single species differed to a large extent depending on seed weight. Only, the detrimental effects of trampling on the soft peat soil were the same for all species independent of seed weight. Therefore, both growth form of adult plants (Lavorel et al. 1997) and reproductive traits have to be considered to predict population development of species under different land use types. Our results can probably be extrapolated to other fen species with similar traits regarding growth form, clonality, seed weight, seed number and germination capacity of seeds. *Succisa* as a large seeded, tall and late flowering forb is a competitive species, not only as an adult plant (Billeter et al. 2003), but also regarding germination. It is very successful in its recruitment by seeds and only slightly affected by land use type. *Primula farinosa* and *Parnassia palustris,* in contrast, are small rosette plants which are less competitive when land use is abandoned both regarding adult plants (Bosshard et al. 1988, Thorn 2000, Diemer et al. 2001) and seedlings. In our study, abandonment or a high vegetation cover on the pasture hindered seed germination of these two species. For adult plants, in contrast, better conditions can be assumed on pastures than on meadows because of the lower vegetation height (Peintinger 1999). *Serratula* is situated between these two groups as an upright, late flowering herb with seeds of intermediate size, which are negatively affected by abandonment concerning germination. Adult plants of *Tofieldia* and *Pinguicula* as subordinate small rosette plants react similar to land use as *Primula* or *Parnassia*. But they show a different pattern in their reproduction, as they are able to reproduce clonally. Although their seeds were highly germinable, seedling recruitment of *Tofieldia* and *Pinguicula* was lacking on abandoned sites and occurred hardly on managed sites. For these species, seed germination seems to be possible only under very special conditions, which were hardly found on our sites. In contrast, clonal reproduction is frequent, although plenty of seeds are produced (Billeter & Diemer 2000, Worley & Harder 1996). For both species the selection to more and lighter seeds for large distance dispersal to find suitable safe sites by chance seems to be true (see Stöcklin 1999 for Epilobium spp.).

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Box

Effects of experimental clipping at different times and in different intensities on fen species in the experimental garden and under natural conditions

EFFECTS OF TIMING AND INTENSITY OF EXPERIMENTAL CLIPPING ON FEN SPECIES: EXPERIMENTS IN THE EXPERIMENTAL GARDEN AND IN THE FIELD

INTRODUCTION

The vegetation of calcareous fens in the prealpine region of southern Germany is adapted to autumn mowing. Typical plant species, such as upright, late-flowering forbs are not directly harmed by late mowing, as they have already finished their growing season. Procumbent rosette species can be favoured by mowing, as litter accumulation which is limiting their abundance on abandoned sites is inhibited. During the last years grazing has been considered as an alternative management tool to autumn mowing. On pastures, however, the potential biomass loss due to foraging occurs during the whole vegetation period. The ability of species to compensate or to avoid biomass loss can vary strongly and is often related to species growth form (Lavorel et al. 1997). Some species may be harmed by foraging, whereas others may be favoured as they can compensate for biomass loss faster than other plant species in the surrounding vegetation or when they are avoided by the grazing animals (McNaughton 1983, Belsky 1986).

We hypothesized that grasslike species would be able to compensate biomass loss by regrowth, whereas upright herbs would be harmed severely due to the loss of meristems. For procumbent herbs we assume even an advantage in contrast to non-grazed sites, as their leaves cannot be bitten due to their growth form, but they might be favoured by the increased light availability on pastures.

EXPERIMENTAL DESIGN

Species of three growth form types were selected for the investigation: the grass-like sedge species *Carex davalliana*, the procumbent rosette plant species *Primula farinosa*, and two upright, late flowering plant species, namely *Serratula tinctoria* and *Succisa pratensis*. Individuals were grown from seeds collected in a calcareous mown fen near Pfefferbichl (see map in chapter 1, description in chapter 4 and 5) in autumn 2000. During the first half year, the plants were grown in a greenhouse in Freising. In May 2001, individuals were transplanted either to pots (8 cm x 8 cm) in the experimental garden (*Carex davalliana*, *Primula farinosa*, *Serratula tinctoria)* or to an abandoned calcareous fen near Pfefferbichl (*Carex davalliana*, *Primula farinosa*, *Succisa pratensis*). Treatments were repeated 12 times in the field experiment and for *Primula* and *Serratula* in the garden experiment. For *Carex* in the garden experiment we had 20 replicates to differentiate into 10 male plants and 10 female plants. Plants were clipped at a height of 7 cm (observed foraging height of cows) at different times of the year and in different intensities to simulate different land use types. In the field experiment, the individuals were planted in a randomized block design. The whole plots with the planted individuals were clipped in the same way in 2001 and 2002: twice in June/August (similar to heavy grazing), once in July (light grazing), once in October (mowing) or never as a control (abandonment). In the garden experiment, all individuals were clipped in autumn 2001, when plants had already yellowed. In 2002, they were clipped at different times to investigate the ability to compensate for repeated biomass loss: once (in May or July), twice (May/July or June/August), four times (May/June/July/August; abbreviated in the following as 4x) or never as a control. Clipped biomass of both experiments was dried at 65 °C to weight constancy and weighed by a precision scale. In both experiments, the number of leaves or tillers of all individuals were counted in the beginning of October 2002. Subsequently, all aboveground biomass of the individuals was harvested (in the following named biomass at the end of the experiment), and the weight of dried biomass was determined as described above. Differences between treatments were statistically analysed by an one-way ANOVA, for the field experiment the block effect was considered. The Tukey-test as a post-hoc test was used to test for differences between treatments.

RESULTS AND THEIR INTERPRETATION

EXPERIMENTAL GARDEN

Clipping of *Primula farinosa* affected only the flowers, but not the leaves. As ripe seeds were shed in July, later clipping did not affect the individuals anymore. Individuals which lost flowers or unripe seeds due to early clipping (May, June) were not able to compensate for the loss by producing new flowers. Clipping had no effect on the amount of harvested biomass in October at the end of the experiment.

For *Carex davalliana* the biomass of the control plants at the end of the experiment differed significantly ($p < 0.001$) from that of the other treatments (Fig. 1). Plants were less affected by the biomass loss, when they were clipped early in the season and only once. But except from the individuals clipped in May, all plants were able to compensate for the biomass loss. They tended to produce even more biomass in total (biomass at the end + clipped biomass) than the unclipped control, but the differences were not significant. For the number of tillers no significant differences could be observed. The highest number was found in the treatment May/June (221), followed by the control (204), July (201), 4x (198), May (190) and June/August (180).

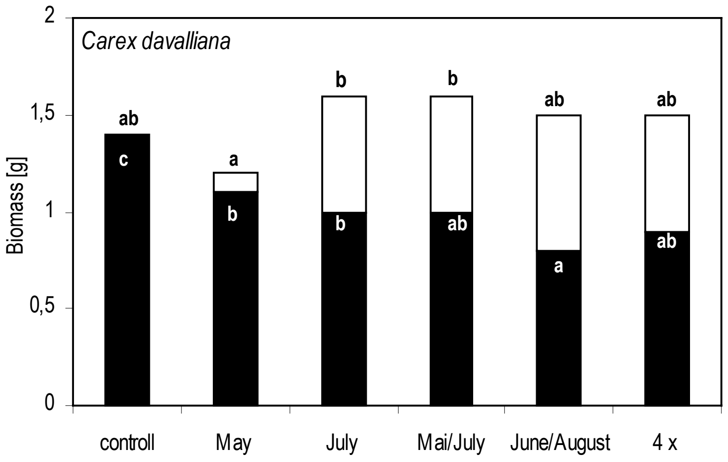

Fig. 1: Biomass at the end of the experiment (black) and clipped biomass (white) of *Carex davalliana* in 2002 for different clipping dates and intensities in the garden experiment. Equal letters indicate no significant differences between treatments for the harvested biomass (white letters) and for total biomass, i.e. sum of clipped and harvested biomass (black letters).

For *Serratula tinctoria* the biomass at the end of the experiment differed also significantly ($p < 0.001$) between treatments (Fig. 2), in the control the individuals had the highest amount of biomass at this time. When plants were clipped in May, plants lost only few biomass. Biomass at the end of the experiment did not differ significantly from the control plants. Plants clipped in May were still able to flower. But later in the season plants lost more biomass by clipping and *Serratula* was obviously not able to compensate for the loss by regrowth. Total biomass produced over the year (biomass at the end of the experiment + clipped biomass) did not differ between all treatments.

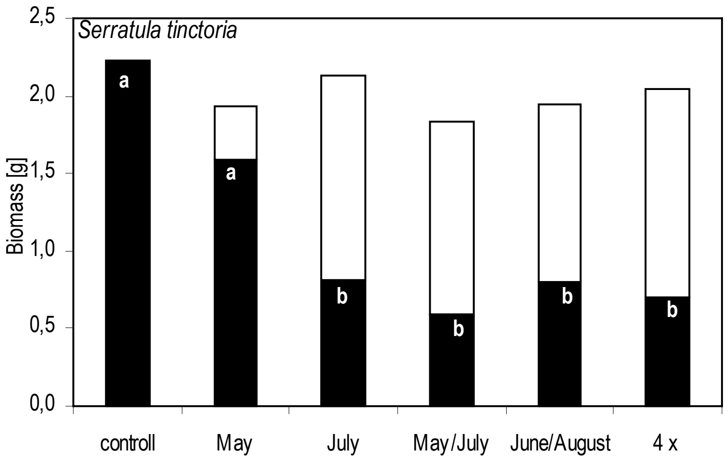

Fig. 2: Biomass at the end of the experiment (black) and clipped biomass (white) of *Serratula tinctoria* in 2002 for different clipping dates and intensities in the garden experiment. Equal letters indicate no significant differences between treatments for the harvested biomass. Differences between the total biomass (black and white) were not significant.

The number of leaves per plant varied between the treatments in the same way as the biomass at the end: the control plants had most leaves (23.7), followed by plants clipped in May (22.6). The plants in the other clipping treatments had significantly ($p < 0.001$) less leaves: July (11.2), May/July (9.5), June/August (16.7) and 4x (13.2).

FIELD EXPERIMENT

Leaves of *Primula farinosa* were hardly affected by the clipping treatments, flowers and unripe seeds were only clipped in the June/August treatment. The biomass of the plants at the end of the experiment did not vary between the treatments. So the plants were not able to take advantage of the reduced light competition by the clipped neighbouring vegetation and the increased light.

Under field conditions, the biomass of *Carex davalliana* at the end of the experiment differed only slightly ($p < 0.10$) between treatments (Fig. 3 A). The highest biomass values were found for the plants clipped in October (comparable to litter meadows). Plants clipped in July or never clipped at all in both years did not differ, whereas for the plants clipped two times biomass was lower at the end of the experiment. In both treatments clipped during the vegetation period, however, total biomass (biomass at the end of the experiment + clipped biomass) tended to be higher, indicating that *Carex davalliana* was able to compensate for biomass loss to a certain extent also under natural conditions. This was also indicated by the fact that individuals on the clipped sites produced slightly significant ($p < 0.10$) more tillers (July: 74, June/August: 63), than the non-clipped treatments (Ocotber: 57, Abandonment: 49).

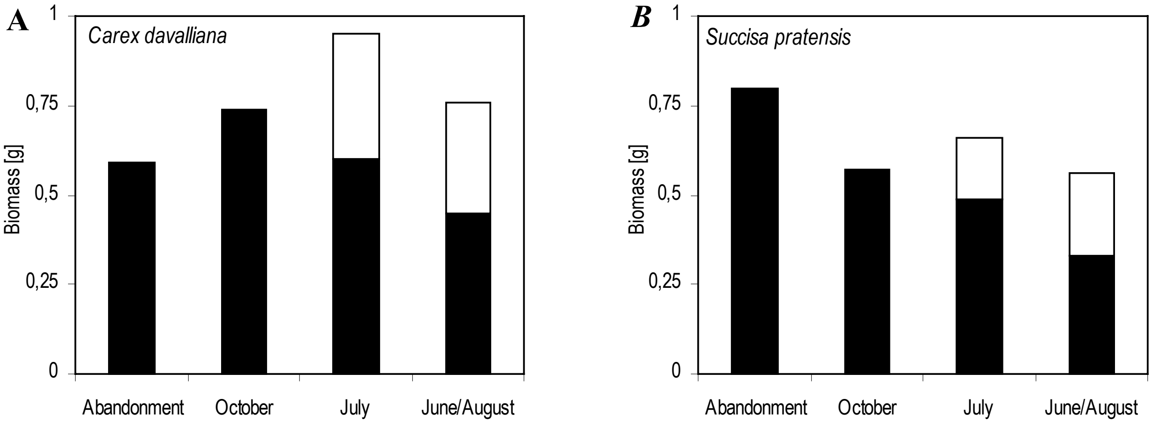

Fig. 3: Biomass at the end of the experiment (black) and clipped biomass (white) of *Carex davalliana* (A) and *Succisa pratensis* (B) in 2002 for different clipping dates and intensities in the field experiment. Anova showed only slight differences between treatments ($p < 0.10$).

For *Succisa pratensis*, the differences between biomass values of the clipping treatments at the end of the experiment were also only slightly ($p < 0.10$) significant (Fig. 3 B). At the abandoned site the biomass was highest, whereas the plants clipped two times had the lowest biomass at the end of the experiment. For the number of leaves per plant, in contrast, no differences could be observed (between 13 and 18), as often only parts of the leaves of the rosette plant and mostly the stems had been clipped. *Succisa* was not able to compensate for the biomass loss by regrowth, but was able to compensate for lower light conditions due to litter accumulation by a higher biomass production.

CONCLUSIONS

Vegetative parts of procumbent rosette plants as *Primula farinosa* were not affected by foraging. But when reproductive organs were clipped the species was not able to produce new flowers. On the other hand, the species was not able to take advantage of the reduction of the neighbouring plants by enlarging its size. The sedge species *Carex davalliana* was more able to compensate for biomass loss during the vegetation period (e.g. on pastures) by producing more tillers or by regrowing from the basal meristems. No differences were found between the simulation of light grazing (clipping in July) and abandonment, which obviously suppressed *Carex* in contrast to autumn mowing. Clipping more than one time, however, harmed the plants significantly, as compensation ability is limited under nutrient poor conditions (c.f. Hawkes & Sullivan 2001). Upright, late-flowering species as *Serratula tinctoria* and *Succisa pratensis* were not able to compensate for severe biomass loss during the vegetation period. Especially, lost flowers can hardly be replaced by new flowers. But simulated grazing early in the year (May or June) damaged the species only little as they were still very small and leaves were hardly affected. In abandoned fens, in contrast, they produced more biomass to compensate for the lower light availability. So only the grass-like sedge species seem to be able to regrow after biomass loss during the vegetation period and may be favoured on pastures. On nutrient poor soils, however, this ability is limited.

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CHAPTER 6

BEWEIDUNG VON KALKREICHEN NIEDERMOOREN (KLEINSEGGENRIEDER UND PFEIFENGRASWIESEN) - EINE ALTERNATIVNUTZUNG ZUR STREUMAHD?

EINE SYNTHESE

BEWEIDUNG VON KALKREICHEN NIEDERMOOREN (KLEINSEGGENRIEDER UND KALK-PFEIFENGRASWIESEN) - EINE ALTERNATIVNUTZUNG ZUR STREUMAHD?

EINE SYNTHESE

In halbnatürlichen Lebensräumen Mitteleuropas stellen geringe Nährstoffverfügbarkeit und regelmäßige Störung die Grundlage für die Erhaltung der Artenvielfalt dar (u.a. Grace 1999, White & Jentsch 2001). Auch sekundäre Kleinseggenrieder und Kalkpfeifengraswiesen müssen durch eine extensive Nutzung mit regelmäßiger Störung und Erhaltung des geringen Nährstoffangebots bewahrt werden. Fallen sie dagegen brach, so bildet sich eine dichte Streuschicht, Grasartige werden dominant und verdrängen konkurrenzschwache Arten, die oftmals Zielarten des Naturschutzes sind (Jensen & Schrautzer 1999, Diemer et al. 2001). Aufgrund des Rückgangs des Streubedarfs durch Veränderungen in der modernen Landwirtschaft wird die traditionelle Herbstmahd oftmals nur noch als Pflege, nicht aber aus Nutzungsinteresse durchgeführt. Seit einigen Jahren wir deshalb zunehmend diskutiert, ob Beweidung eine angemessene, aber kostengünstigere Nutzungsalternative zur Streumahd ist (Quinger et al. 1995, Radlmair et al. 1999). Im Vergleich zur Brache verhindert Beweidung ebenfalls die Bildung einer Streuschicht, doch treten die “Störungen” der Weide nicht im Herbst auf wie in Streuwiesen, sondern während der gesamten Vegetationsperiode in Form von Tritt, Verbiss und Kotablagerungen (Mulder 1999). Um zu beurteilen, ob die Beweidung aus der Sicht des Naturschutzes tatsächlich eine geeignete Alternative zur Pflegemahd ist, wurden sowohl die Auswirkungen auf die gesamte Pflanzengemeinschaft, als auch auf Zielarten des Naturschutzes berücksichtigt (Kap. 2 bis 5). Abschließend werden hier die Ergebnisse übergreifend diskutiert. Unter Berücksichtigung des Einflusses der Beweidung auf einzelne Lebensphasen der Arten, auf die Populationen und auf die gesamte Artenzusammensetzung der Vegetation kalkreicher Niedermoore werden abschließend Empfehlungen für den Naturschutz formuliert.

1 AUSWIRKUNGEN DER BEWEIDUNG AUF INDIVIDUEN DER UNTERSUCHTEN ARTEN IN VERSCHIEDENEN LEBENSPHASEN

EINFLUSS DER BEWEIDUNG AUF KEIMUNG UND ETABLIERUNG

Die Etablierung neuer Individuen durch Keimung ist eine kritische Phase im Lebenszyklus von Pflanzen (Harper 1977, Fenner 1985) und ist daher sowohl für die Erhaltung einzelner Arten als auch für die Artenvielfalt von Pflanzengemeinschaften von großer Bedeutung (Grubb 1977, Cornelius 1991). Dies gilt insbesondere in den untersuchten kalkreichen Niedermooren, wo im allgemeinen nur wenige Keimlinge zu finden sind (Kap. 3). Die Aussaat von Samen (Kap. 5) erbrachte eine deutlich erhöhte Anzahl an Keimlingen im Vergleich zu den Kontrollquadraten ohne Samenausbringung. Die Keimung in kalkreichen Niedermooren war demnach durch die Verfügbarkeit der Samen limitiert, auch wenn große Mengen an Samen produziert wurden (s. Tab. 1) Die Verfügbarkeit keimfähiger Samen kann durch eine Ausbreitung nur in der Nähe der Mutterpflanze oder aufgrund von Verlusten durch Prädation oder Pilzinfektion eingeschränkt sein (Bonn & Poschlod 1998).

In den beiden Aussaatexperimenten (Kap. 5) konnten deutliche Unterschiede zwischen den einzelnen Arten hinsichtlich der Keimfähigkeit der Samen und der Abhängigkeit von “microsites” als Keimnischen gefunden werden. Die Keimfähigkeit unter adäquaten Bedingungen im Keimschrank war artspezifisch und konnte nicht in Beziehung zu anderen Sameneigenschaften gesetzt werden. *Parnassia palustris* zeigte nur eine geringe Keimfähigkeit, für *Serratula tinctoria* konnten starke Schwankungen zwischen den Jahren festgestellt werden, während die übrigen Arten in beiden Jahren gut keimten. Die Abhängigkeit von Keimnischen dagegen war umso größer, je kleiner und leichter die Samen waren. Arten mit kleinen Samen wurden besonders durch eine dichte Vegetations- oder Streudecke in ihrer Keimung gehindert. Auf Brachen war die Keimung vieler Arten daher eingeschränkt oder nahezu ganz unterdrückt, lediglich die großsamige Art *Succisa pratensis* wies dort hohe Keimraten auf. Zwischen den gegenüber der Brache höheren Keimraten auf Weiden und Streuwiesen gab es für alle Arten kaum Unterschiede. Eine gegenüber der Herbstmahd geringere Vegetationshöhe durch Beweidung hatte keinen fördernden Einfluss auf die Keimrate der Arten. Die lückige Vegetationsdecke genutzter, aber nicht gedüngter kalkreicher Niedermoore bietet also offenbar genügend Nischen für die erfolgreiche Keimung der untersuchten Arten; lediglich *Pinguicula vulgaris* und *Tofieldia calyculata* mit den leichtesten Samen keimten sowohl in Streuwiesen als auch in Weiden schlecht. Die durch Huftritte geschaffenen Offenstellen fungieren nicht als Keimnischen (Kap. 4 und 5). Auf dem weichen Moorboden sanken selbst Jungkühe zentimetertief ein, wodurch sich Trittstellen mit zwei Zonen herausbildeten, die beide trotz der Beseitigung der Konkurrenz kaum geeignete Bedingungen für eine Keimung der Zielarten liefern: der verdichtete und vernässte, teilweise überflutete Boden des Hufabdrucks ist zu dunkel für Lichtkeimer; der hellere und wärmere Rand ist zwar besser geeignet, jedoch verhindert die durch den Dräneffekt hervorgerufene Bodentrockenheit die Keimung.

Keimfähige Samen, die keine geeigneten Keimbedingungen vorfinden, können in die Samenbank übergehen. Die meisten krautigen Pflanzenarten (so auch die untersuchten Arten) bilden nur eine kurz- bis mittelfristig persistente Diasporenbank aus, während Gräser und Seggen-Arten häufiger eine persistente Samenbank in Niedermooren aufweisen (Maas 1989, Jensen 1998). Insbesondere in Trittstellen auf der Weide könnte eine Rekrutierung von Keimlingen aus der Samenbank angeregt werden. Eine Keimung ist allerdings auch dort nur im Frühjahr wahrscheinlich, da die Samen der meisten Arten einer Kälte-Stratifikation zur Brechung der Dormanz bedürfen (vgl. Maas 1989). Der Einfluss der Samenbank bei der Besiedlung von Trittstellen (Kap. 4) war damit nicht groß.

Für die Entwicklung von Keimlingen zu adulten Pflanzen stellt die Beweidung sogar ein großes Hindernis dar. Während auf der Streuwiese und der Streuwiesenbrache ein Großteil der Keimlinge das erste Jahr überlebte, wurde auf der Weide die höchste Sterberate festgestellt (Kap. 5). Der Verbiss spielte dabei kaum eine Rolle, da die kleinen Keimlinge nicht von der Zunge des Weideviehs erfasst werden können. Gefährdend ist der Tritt, insbesondere in den stärker begangenen Bereichen der Weide. In den untersuchten einzelnen Trittstellen (Kap. 4) war das Überleben der Keimlinge auch ohne weiteren Tritt kaum möglich, da sie in der hellen Randzone unter Austrocknung litten, am Boden des Huftritts dagegen unter Dunkelheit und Staunässe.

EINFLUSS DER BEWEIDUNG AUF ADULTE PFLANZEN

Die Reaktion von Keimlingen und adulten Pflanzen auf Nutzungsformen kann unterschiedlich sein (Urbanska 1992). Die Eigenschaften der adulten Pflanzen sind neben denen der Keimlinge ebenfalls für das Vorkommen der Art und die Artzusammensetzung von Pflanzengemeinschaften wichtig, da die adulte Lebensphase in der Regel den Hauptteil des Lebenszyklus perennierender Pflanzen darstellt. Daher wird häufig die Wuchsform der adulten Pflanzen betrachtet, um zu ermitteln, ob Pflanzenarten durch Beweidung Vor- oder Nachteile haben (McIntyre et al. 1999, Lavorel et al. 1997). Auf Weiden haben Arten Vorteile, die Verbiss entweder vermeiden oder tolerieren können (Bullock et al. 2001). Pflanzenarten können Verbiss tolerieren, indem sie den Biomasseverlust schneller als andere Arten kompensieren. Dieses Verhalten ist typisch für viele Gräser und Seggen, die aufgrund der basalen Lage ihrer Meristeme durch erneutes Wachstum auf den Verlust reagieren können (Crawley 1997). In der vorliegenden Arbeit zeigte *Carex davalliana* jedoch keine ausgeprägte Fähigkeit zur Kompensation. Diese Art konnte bereits bei zweimaligem Biomasseverlust in einem Jahr den Verlust nicht mehr ausgleichen (s. Box), vermutlich aufgrund der geringen Nährstoffversorgung (Hawkes & Sullivan 2001). *Succisa pratensis* bildete dagegen nach simuliertem Verbiss überhaupt keine neuen Blätter oder Stengel (Box) und war damit nicht in der Lage, den Biomasseverlust zu kompensieren.

Eine zweite Strategie ist die Vermeidung des Verbisses z.B. durch niedrigen Wuchs. Niedrigwüchsige Pflanzen haben aus diesem Grund im Allgemeinen einen Konkurrenzvorteil auf Weiden (Kap. 2). Kleine Rosettenpflanzen, die ihre Blätter bodennah ausbilden, wie beispielsweise *Primula farinosa* und *Pinguicula vulgaris* werden nicht durch Verbiss geschädigt, da die Zunge der Rinder nicht so tief reicht. In der vorliegenden Arbeit zeigten *Primula farinosa*-Individuen jedoch keinen Biomassezuwachs, wenn konkurrierende Arten verbissen wurde (s. Box). Dagegen produzierte *Primula* auf nährstoffreichen Böden nach Entfernung von konkurrierenden Arten mehr Biomasse (Pauli 1998). Eine weitere Strategie zur Vermeidung des Verbisses ist die Bildung chemischer Inhaltsstoffe oder mechanische Abwehrorgane (z.B. Dornen). Die Einordnung der Abwehrmechanismen hinsichtlich ihrer Wirksamkeit gegen Beweidung mit Kühen wurde allerdings für Futterwiesen entwickelt (Stählin 1971) und ist nur schwer auf die Arten der Kleinseggenrieder und Pfeifengraswiesen zu übertragen. Da drei Viertel der Arten der untersuchten kalkreichen Niedermoore sogenannte chemische oder mechanische “Abwehrmittel” besitzen, ist es für die Kühe nicht möglich nur die schmackhaften Arten ohne „Abwehrmittel“ auszuwählen, so dass auch Arten mit „Abwehrmitteln“ gefressen werden. Nur wenige Arten besitzen jedoch tatsächlich chemische oder mechanische Abwehrmittel, die auch auf kalkreichen Niedermooren wirksam sind (z.B. *Mentha spp.*, *Juncus spp.*); sie werden auf Weiden gefördert, da sie nicht gefressen werden (Kap. 2).

Im Gegensatz zum Verbiss können Pflanzen die Trittbelastung nicht durch spezielle Strategien oder Wuchsformen vermeiden, sie kann nur toleriert werden. Geringe Trittbelastung wirkt sich auf Pflanzen ähnlich aus wie der Verlust von Biomasse durch Verbiss, allerdings sind auch niedrigwüchsige Arten davon betroffen. Somit sind auch hier die Grasartigen mit ihrer Fähigkeit, Biomasseverluste schnell zu kompensieren, im Vorteil. Wie die Untersuchung der Trittstellen ergab, konnten sich am trittbelasteten Grund der Huftritte fast ausschließlich Seggen und Binsen wieder erholen und ausbreiten (Kap. 4). Krautige Arten dagegen, die vor dem Trittereignis ebenfalls dort wuchsen, konnten sich nur selten wieder regenerieren. Die Schaffung von Offenstellen durch Tritt kann aber andererseits eine indirekte Förderung für Arten am Rand der Huftritte darstellen, die nicht selbst betroffen sind. Dort können auch niedrigwüchsige Rosetten-Arten den entstehenden Raum durch Vergrößerung ihrer Blattfläche nutzen (Kap. 4). Nur wenige Arten auf Streuwiesen besitzen dagegen die Fähigkeit, Trittstellen schnell und zielgerichtet neu zu besiedeln und so die Offenstellen schneller als Individuen anderer Arten zu erreichen, sei es durch ein schnelles Keimen, wie es für Therophyten (z.B. *Linum catharthicum*, *Euphrasia rostkoviana*) charakteristisch ist, oder durch schnelle vegetative Vermehrung (z.B.“Guerilla”-Strategen wie *Agrostis canina*). Die Offenstellen bleiben daher lange nur spärlich besiedelt. Die vegetative Vermehrung ist bei krautigen Arten in Niedermooren generell selten. Von den untersuchten Arten war lediglich *Tofieldia* in der Lage sich in größerem Umfang vegetativ zu vermehren. Diese Art wurde auf Weiden gefördert, da ihre Individuen dort eine höhere Anzahl an Rameten aufwiesen als auf Streuwiesen.

EINFLUSS DER BEWEIDUNG AUF DIE GENERATIVE REPRODUKTION

Beweidung schädigt die Reproduktion von Pflanzen direkt durch den Verbiss oder Tritt der Infloreszenz. Beim Entfernen von Blütenstengeln sowohl im Knospenstadium als auch bei der Blüte konnte bei Individuen von *Primula*, *Succisa*, *Serratula* und *Carex davalliana* kein Wiederaustrieb einer zweiten Blüte im selben Jahr beobachtet werden (s. Box). Im Gelände konnte kein selektives Fressverhalten der Rinder bezüglich der Blüten der untersuchten Pflanzenarten festgestellt werden, was bei anderen Weidetieren teilweise zu beobachten ist (vgl. Mulder 1999). Wie stark die Beweidung die Reproduktion einzelner Pflanzenarten stört, also zu welchem Anteil blühende Individuen verbissen werden, wurde in dieser Arbeit nicht untersucht, kann aber anhand des Blühzeitraums abgeschätzt werden. Die generativen Organe frühblühender und frühfruchtender Arten sind einer kürzeren Zeit der Beweidung und damit einem geringeren Verbissrisiko ausgesetzt, da sie bereits bei Weidebeginn blühen. Persönliche Geländebeobachtungen zeigten, dass der Weidedruck in den Bereichen auf Niedermoor höher wird, wenn der erste Aufwuchs auf den benachbarten mineralischen Flächen abgegrast ist, also erst ab Juni/Juli. Pflanzenarten, die bis dahin reife Samen gebildet haben, sind wenig gefährdet. Der Weidedruck nimmt dann gegen August wieder ab, wenn die Niedermoorflächen ebenfalls abgeweidet sind. Die Blüten spätblühender Arten (ab August) haben damit ebenfalls ein geringeres Verbissrisiko und eine höhere Chance einer erfolgreichen generativen Reproduktion als Arten, die bereits im Juni oder Juli blühen.

Durch Verbiss der vegetativen Teile von Pflanzen kann die Reproduktion indirekt beeinflusst werden, da verbissene Individuen in ihrer Entwicklung gehemmt werden und somit weniger Ressourcen für eine erfolgreiche Reproduktion zur Verfügung stehen (Mulder 1999). Eine vermehrte Reproduktion als Folge von Verbiss (vgl. Paige & Whitham 1987) konnte für die untersuchten Arten nicht festgestellt werden (Box). Durch Biomasseverluste (Tritt, Verbiss) verbleiben die Individuen der untersuchten Pflanzenarten dagegen vermutlich länger unterhalb des “Schwellenwertes” an Biomasse, der zum Eintritt in die reproduktive Phase notwendig ist (vgl. Abs 1994). Nur die kräftigsten Individuen bilden dann Blüten aus, können aber mehr Samen produzieren. So wurden in der vorliegenden Arbeit auf Weiden proportional weniger blühende *Primula*-Individuen gefunden, diese produzierten aber mehr Samen (Kap. 3). Für die anderen Arten wurden dagegen keine signifikanten Unterschiede im Anteil der blühenden Individuen auf Weide und Streuwiese beobachtet. Auf Brachen ermittelte Billeter (2001) für *Succisa* einen höheren Anteil an blühenden Pflanzen als auf Streuwiesen, während für *Tofieldia* auch dort keine Verschiebung zu erkennen war. Für die vorliegende Arbeit muss jedoch beachtet werden, dass nur Daten von einem Jahr vorliegen, der Anteil der Blühenden aber von Jahr zu Jahr stark variieren kann (Schopp-Guth 1993, Cornelius 1991). Bezüglich des Samengewichts wurde bei den untersuchten Arten kein Einfluss der Nutzungsformen Weide und Mahd ermittelt (Kap. 3). Schopp-Guth (1993) fand hinsichtlich der Abhängigkeit von der Nutzungsform ebenfalls eine deutlich geringere Schwankung der reproduktiven Merkmale im Vergleich zu den vegetativen.

2 AUSWIRKUNGEN DER BEWEIDUNG AUF DIE POPULATIONEN DER UNTERSUCHTEN ARTEN

Neben der Fähigkeit der Individuen einzelner Arten, mit Beweidung, Mahd oder Brache in den verschiedenen Lebensphasen zurecht zu kommen, können auch nutzungsabhängige Veränderungen in der Lebensdauer oder der Alters-Entwicklungs-Klassen-Struktur das Vorkommen und die Dichte einer Art beeinflussen (Urbanska 1992). Die Tatsache, dass Individuen unter veränderten Bedingungen unterschiedliche Lebensdauer aufweisen, wurde für andere Habitate festgestellt: so wurden für Rosettenpflanzen höhere Lebenserwartungen in offenen Rasen als in Waldbeständen (Abs 1994, Tamm 1972), für Arten der Trespen-Halbtrockenrasen längere Halbwerts-Lebenszeiten auf ungedüngten als auf gedüngten Wiesen ermittelt (Marti 1994). Da Pflanzen in allen Lebensphasen durch Tritt stark und oft auch letal geschädigt werden, ist generell von einer höheren Mortalität auf Weiden im Vergleich zu Streuwiesen, und damit von einer kürzeren Lebensdauer auszugehen.

Eine höhere Mortalitätsrate auf Weiden kann durch die Rekrutierung neuer Individuen durch höhere Keimraten oder größere Samenproduktion ausgeglichen werden. Die Alters-Entwicklungsklassen-Struktur kann daher die besonders kritischen Phasen, aber auch Vorteile einzelner Lebensphasen auf

Weiden und Brachen im Vergleich zu Streuwiesen deutlich machen (Abb. 1). Auf Brachen ist durch die starke Unterdrückung der Keimung auf lange Sicht eine Überalterung der Population und eine Reduzierung der Dichte zu erwarten. Nur großsamige Arten wie *Succisa* können auf Brachen sogar bessere Keimbedingungen und höhere Samenmengen vorfinden (Billeter et al. 2003). Die Art konnte aber auch auf Weiden die geringere Lebensdauer durch höhere Keimraten ausgleichen, so dass die Populationsdichte von *Succisa* auf Weide und Streuwiese gleich war. Die Samenzahl pro Fläche ist auf Weide und Streuwiese ebenfalls gleich (Tab. 1); sowohl der Tritt, als auch die frühe Mahd können die Samenbildung der Art gefährden. Die übrigen Arten dagegen konnten die höhere Mortalität auf Weiden nicht durch eine erhöhte Keimrate ausgleichen und wuchsen dort in geringerer Dichte. *Primula* produzierte auf der Weide zwar mehr Samen pro Individuum. Da die Individuendichte auf der Weide jedoch deutlich geringer war, stand dennoch eine geringere Samenmenge pro Fläche zur Verfügung (Tab. 1). Zusätzlich wurden die Populationen durch die Etablierung der Keimlinge dort stark beeinträchtigt (Abb. 1). Für *Parnassia* war die verfügbare Samenmenge dagegen auf der Weide höher als auf der Streuwiese. Dennoch wurden auf Weiden weniger Keimlinge gefunden, allerdings bei generell sehr geringen Keimlingszahlen (Abb. 1). *Tofieldia* keimte sowohl in Streuwiesen als auch in Weiden schlecht, obwohl auf der Streuwiese deutlich mehr Samen zur Verfügung standen als auf der Weide. Diese Art kann die höhere Mortalität auf Weiden durch die Bildung einer größeren Zahl von Rameten pro Individuum ausgleichen (Abb. 1). Allerdings sterben damit beim Absterben eines Individuum auch mehr Rameten gleichzeitig ab. Daher sind die Populationsdichte und Frequenz von *Tofieldia* auf Weiden besonders niedrig.

Tab. 1: Mittlere Samenmenge pro Quadratmeter auf Streuwiesen und Weiden, errechnet aus der Dichte der Blühenden und der Samenanzahl pro blühendem Individuum (Kap. 3) für vier untersuchte Zielarten.

	Samenmenge / m^2	
	Streuwiese	Weide
Parnassia palustris	5.000	5.500
Primula farinosa	2.600	1.700
Succisa pratensis	200	200
Tofieldia calyculata	4.000	1.600

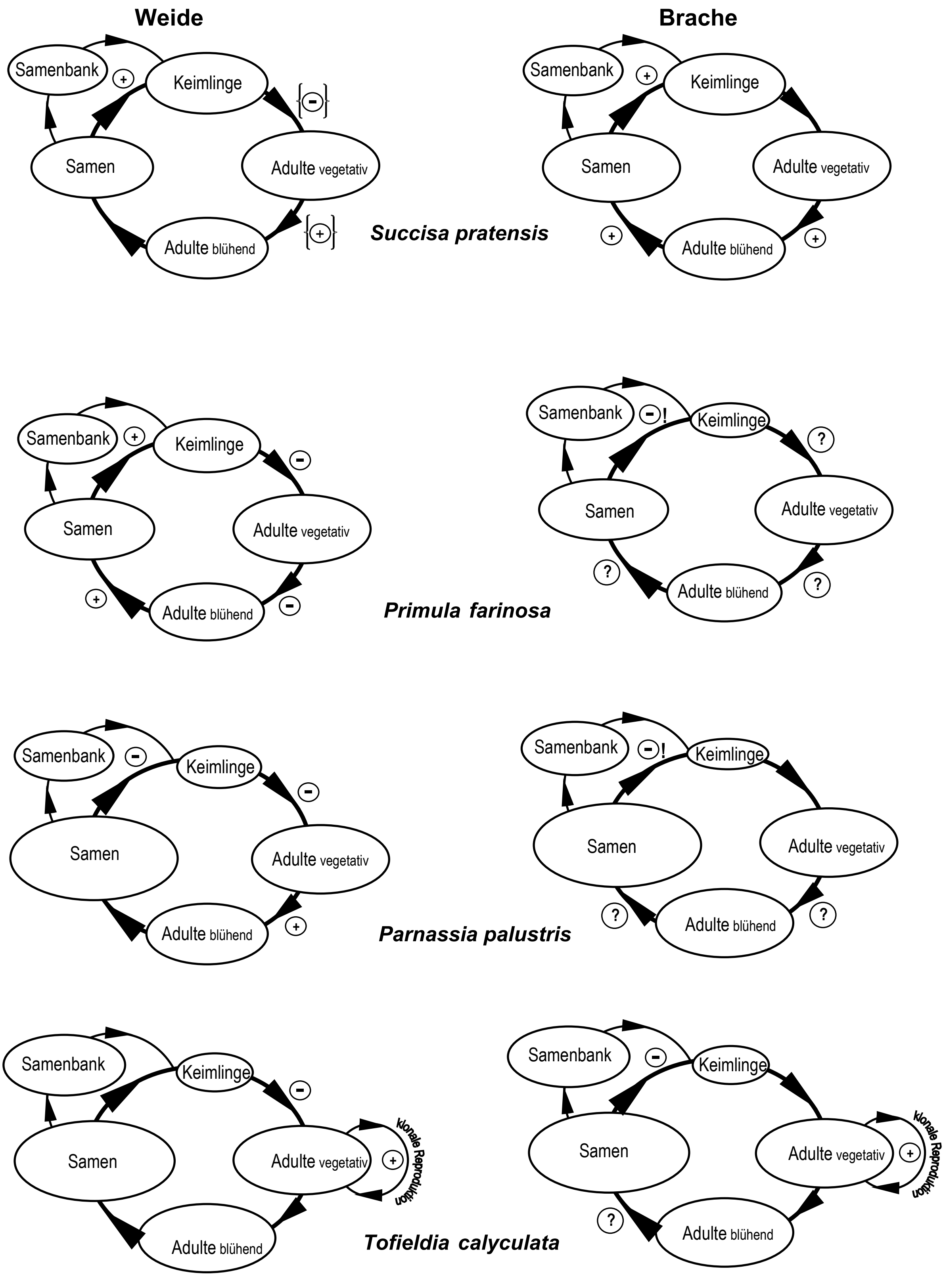

Abb. 1: Schematischer Lebenslauf der untersuchten Arten auf Weide und Brache (vgl. Billeter 2001) im Vergleich zu den Verhältnissen auf Streuwiesen; Auswirkungen auf die verschiedenen Lebensphasen der Individuen: ⊕ positiv, ⊖ negativ (kritische Phase), ⊖! stark negativ (sehr kritische Phase), (?) Auswirkungen nicht bekannt; { } Auswirkungen nur schwach ausgeprägt. Die Größenverhältnisse der Ellipsen zeigen schematisch das Verhältnis der einzelnen Alters-Entwicklungsklassen zueinander.

Da die untersuchten Weiden schon seit Jahrzehnten beweidet werden, ist trotz der geringeren Individuendichte im Vergleich zur Streuwiese von stabilen Populationsgrößen auszugehen. Durch die kürzere Lebensdauer der Individuen kann man im Allgemeinen mit weniger Reproduktionszyklen und damit wahrscheinlich mit einer geringeren Fitness der Individuen rechnen. Zusammen mit der geringeren Populationsgröße sind damit die Risiken für das Aussterben der Population durch genetische Verluste, durch Zufallsereignisse und durch Effekte, die bei kleineren Populationen auftreten (z.B. geringere Bestäubung, geringere Fitness) erhöht (u.a. Fischer & Matthies 1998, Kery et al. 2000, Oostermeijer et al. 1994).

3 AUSWIRKUNGEN DER BEWEIDUNG AUF DIE PFLANZENGEMEINSCHAFT

Die Beweidung reduziert die mittlere Artenzahl der Kleinseggenrieder und Kalk-Pfeifengraswiesen im Vergleich zur Herbstmahd (Kap. 2). Dennoch sind nur wenige Pflanzenarten an eine der beiden Nutzungsformen gebunden; die meisten Arten kommen in beiden Nutzungstypen vor. Da sekundäre Kleinseggenrieder sich vermutlich meist durch Beweidung aus Erlenbruch- oder Erlen-Eschenwäldern entwickelt haben (Pfadenhauer 1989), können die meisten Arten eine extensive Beweidung tolerieren. Auf Weiden werden im Vergleich zu Streuwiesen vor allem Grasartige (Seggen, Gräser) gefördert, während krautige Arten Biomasseverluste kaum kompensieren können und auf Weiden in reduzierter Anzahl vorkommen. Lediglich manche krautige Arten können den Verbiss durch mechanische Abwehrorgane, chemische Abwehrstoffe oder durch eine kleine Wuchsform vermeiden. Insbesondere höherwüchsige Krautarten können auf Weiden nur erfolgreich sein, wenn sie die höhere Mortalität durch ebenfalls höhere Reproduktions- oder Keimraten ausgleichen können. Nur wenige Arten des Artenpools der Kleinseggenrieder und Kalk-Pfeifengraswiesen sind in der Lage, Offenstellen, die auf der Weide vermehrt durch den Tritt auftreten, schnell zu besiedeln (r-Strategen sensu Grime 2001). Daher können langfristig auch weniger expansive Arten die lange offenbleibenden Trittstellen besiedeln. Für die meisten Arten gilt aber, dass die höhere lokale Extinktionsrate auf Weiden in kalkreichen Niedermooren nicht durch eine schnellere Wiederbesiedlung kompensiert werden kann (Kap. 4, vgl. Marti 1994). Dadurch kommt es zur Reduzierung der Artenzahl, bei der insbesondere auch der Zufall einen Einfluss hat, ob eine Art verschwindet oder nicht (vgl. van der Maarel & Sykes 1993).

Weitere Aspekte tragen zusätzlich zur Besonderheit der Beweidung auf Niedermoor im Vergleich zu anderen Nutzungstypen bei. Es kann durch die Beweidung zu Veränderungen der abiotischen Bedingungen kommen (vgl. Mulder 1999), die für die typischen Arten der Streuwiesen nicht optimal sind. So gibt es einige Arten, die sogar an die Beweidung von Feuchtstandorten gebunden sind, wie beispielsweise *Apium repens*, *Sagina nodosa* oder *Sedum villosum* (Barth et al. 2000). Wie die Untersuchung der Trittstellen zeigte, entsteht durch Beweidung ein viel größeres Mosaik und auch ein größerer Gradient an Standorten als in Streuwiesen, was bereits auf der Ebene von wenigen Zentimetern nachweisbar war. Auf größerem Maßstab – etwa in halboffenen Weidelandschaften – ist die durch das

Weideverhalten der Tiere bedingte Heterogenität der Weiden mit intensiv genutzten Bereichen bis hin zu ungenutzten Flächen, z.B. mit Gehölzaufwuchs, von Bedeutung (Riecken et al. 1999, Krüger 1999, Bokdam & Gleichman 2000).

4 IST WEIDE EINE ALTERNATIVE ZU STREUMAHD? - EMPFEHLUNGEN FÜR DEN NATURSCHUTZ

Beweidung verändert die Artenzusammensetzung von Kleinseggenrieden und Kalk-Pfeifengraswiesen im Vergleich zur Streumahd, die Artenzahl wird reduziert und Zielarten des Naturschutzes kommen in geringerer Dichte und Häufigkeit vor. Andererseits waren vor der Einführung der Streunutzung im 19. Jahrhundert manche Arten sicherlich seltener als heute (Pfadenhauer 1989). Nur wenige Arten werden durch Beweidung so stark geschädigt, dass sie ausfallen. Die Beweidung als historische Nutzung sollte daher durchaus als Alternative zur Streumahd für die Erhaltung artenreicher Magerwiesen kalkreicher Niedermoore betrachtet werden; insbesondere, sofern von Seiten der Landwirtschaft Interesse an dieser kostengünstigen Nutzung besteht, während die Streumahd oftmals nur noch aufgrund staatlicher Fördermitteln durchgeführt wird und so die Entsorgung des Mahdguts teilweise zusätzlich Probleme bereitet (Radlmair et al. 1999). Bei der Beweidung kalkreicher Niedermoore sollten aber einige Punkte beachtet werden, um den negativen Einfluss der einzelnen Faktoren der Beweidung auf die Zielarten des Naturschutzes zu reduzieren.

Eine Gefahr der Euthrophierung der Niedermoorbereiche durch Dung besteht an den untersuchten Standorten bislang nicht. In der vorliegenden Arbeit konnten keine Veränderung der Vegetation hin zu mehr nährstoffliebenden Arten festgestellt werden, da sich die Kühe nur zeitweise auf den Niedermoorflächen aufhalten und ihre Lager- und Ruhezeiten auf den mineralischen Böden verbringen. Vereinzelt auftretende lokale Kotstellen erhöhen lediglich die Struktur- und Standortsvielfalt. Wichtig ist vielmehr, die angrenzenden Weideflächen auf Mineralböden nicht mit mineralischem Dünger zu düngen, da dadurch die Gefahr der Eutrophierung durch Auswaschung in die Niedermoorbereiche besteht und dann mit einer Artenverschiebung zu rechnen ist (Pauli et al. 2002, Bollens & Ramseier 2001). Eine ungedüngte Pufferzone von 5 bis 10 m Breite vor den Niedermoorbereichen muss eingehalten werden, vor allem bei hängigem Gelände mit den Niedermoorbereichen in der Senke.

Der Verbiss gefährdet die meisten Arten der kalkreichen Niedermoore kaum, da der Biomasseverlust in der Regel verkraftet werden kann und die Pflanze überlebt. Auf der Populationsebene muss gesehen werden, dass durch den geringen Weidedruck auf den Niedermoorbereichen die Flächen nicht komplett abgefressen werden und einzelne Individuen gar nicht oder erst zu einem späteren Zeitpunkt am Ende der Vegetationsperiode verbissen werden. Sehr starken Einfluss hat dagegen die Trittbelastung, die maßgeblich für die erhöhte Mortalität der Pflanzen verantwortlich ist. Die weichen Torfböden werden bei Trittbelastungen stark geschädigt, während Tritt in Weiden auf mineralischem Boden die Artenvielfalt sogar durch die Schaffung von Regenerationsnischen erhöht (Hillier 1990, Schläpfer et al. 1998). Starke Trittschäden auf den Niedermoorböden können durch eine ausreichende Menge an

Mineralböden (mindestens 50 % der Fläche) und einen entsprechenden Besatz (maximal eine Großvieheinheit pro Hektar, vgl. Barth et al. 2001) vermieden werden. Diese Zahlen orientieren sich an den Verhältnissen der bestehenden Allmendeflächen, auf denen durch Beweidung seit Jahrhunderten die Artenvielfalt erhalten werden konnte (Brudi n.p.). Dort werden die Niedermoorböden nur zwischen Ende Juni und Anfang August stärker vom Weidevieh besucht, wenn das Futter auf den mineralischen Böden abgefressen ist. In dieser Zeit sind die negativen Auswirkungen des Tritts durch einen meist niedrigeren Wasserstand (Quinger et al. 1995) weniger gravierend. In besonders nassen Jahren muss durch Auszäunung besonders gefährdeter Bereiche einer zu starken Verschlämmung der Böden durch die Trittbelastung entgegengewirkt werden. Allgemein müssen neue Kontrollen entwikkelt werden, um die Schäden durch Beweidung einzudämmen und andererseits den Erfolg bei der Erhaltung der Artenvielfalt zu gewährleisten. So sollte z.B. ein Anteil von 15 % offener Bodenstellen nicht überschritten werden. Auf der anderen Seite muss der Besatz so hoch sein, dass die Akkumulation einer Streuschicht und auch die Verbuschung verhindert wird. Als Kontrollwert sollte maximal eine Verbuschung von 30 % der Fläche zulässige sein. Durch die Beweidung kann so ein Nebeneinander unterschiedlich intensiv genutzten Bereichen, von Offenstellen bis hin zu bracheähnlichen Bereichen oder Gehölzbeständen entstehen. Der Struktur- und Artenreichtum der Vegetation solcher Flächen ist insbesondere für die Fauna von großer Bedeutung, für die sowohl die Mahd der kompletten Fläche im Herbst als auch das Brachfallen schädlich sein kann (Radlmair & Laußmann 1997, Dolek 2000). Eine kurze Bestoßdauer in Form einer Umtriebsweide kann ebenfalls die negativen Auswirkungen der Beweidung auf die Vegetation gering halten. Neben dem erhöhten Aufwand für den Landwirt und damit höheren Kosten werden jedoch auf Umtriebsweiden zusätzlich die positiven Effekte der Heterogenität im Vergleich zur Standweide reduziert.

Insbesondere auf bestehenden Niedermoorweiden ist die Beweidung zu erhalten, da diese Nutzungsform bisher selten ist und damit die Vielfalt der Nutzungsformen erhöht. Besteht die Gefahr, dass größere Streuwiesen brach fallen, so ist die Einführung der Beweidung auch auf bisher nicht beweideten Flächen sinnvoll. Durch Beweidung können einige Arten, die sich in Brachen stark ausbreiten (z.B. *Phragmites australis*) besser zurückgedrängt werden als durch eine Herbstmahd (Dolek 2000, Schopp-Guth 1993). Eine Reaktivierung der Artenvielfalt auf bereits länger brachliegenden Flächen durch die Beweidung wird ebenso wie bei einer Wiedereinführung der Mahd nur eingeschränkt möglich sein, da der Anteil zoochorer Pflanzenarten gering ist (Kap. 2), die meisten Arten nur eine kurz- bis mittelfristige Samenbank besitzen und sich dadurch in Trittstellen kaum neue Arten etablieren (Kap. 4). Ein vereinzelter Verlust von Arten in manchen Flächen kann in großen Niedermoorgebieten akzeptiert werden. Bei Vorkommen besonders schützenswerter Pflanzenarten, deren Reaktion auf Beweidung unbekannt ist, können die Bestände, zumindest während ihres Blüh- und Fruchtzeitraumes, ausgezäunt werden. In isolierten, kleinflächigen Niedermooren muss aufgrund der höheren Aussterbewahrscheinlichkeit von Arten die Einführung der Beweidung gut abgewägt werden. Sie ist nicht angemessen, solange seltene Arten, deren Reaktion auf Beweidung unbekannt ist, erhalten werden sollen und eine Mahd bzw. Pflegemahd möglich ist.

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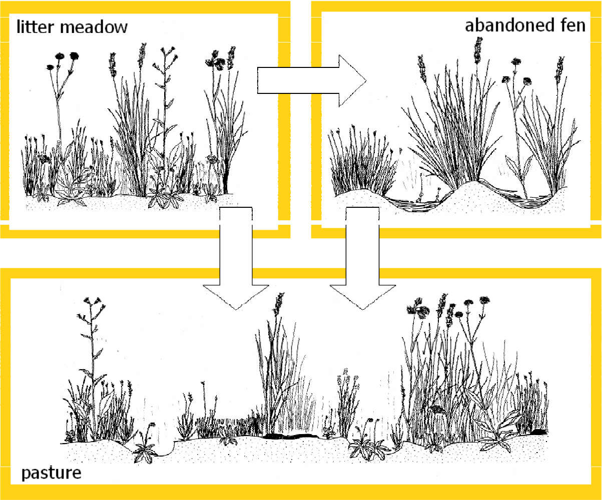
ZUSAMMENFASSUNG

SUMMARY



ZUSAMMENFASSUNG

Kalkreiche Niedermoore, im Alpenvorland traditionell als Streuwiese genutzt, sind durch eine artenreiche Vegetation (Caricion davallianae, Molinietum caeruleae) charakterisiert. Fehlender Streubedarf in der Landwirtschaft führt heute oft zum Brachfallen dieser Wiesen, was einen Rückgang typischer Streuwiesenarten durch die Streuakkumulation und die Dominanz weniger, konkurrenzkräftiger Pflanzenarten nach sich zieht. In dieser Arbeit wurde untersucht, ob Rinderbeweidung eine geeignete Alternative zur Streunutzung darstellt. Dabei wurde der Einfluss von Beweidung und Mahd auf die Vegetation kalkreicher Niedermoore im süddeutschen Alpenvorland verglichen, wobei neben einzelnen Pflanzenindividuen und der Alters-Entwicklungsklassen-Struktur von Populationen auch Pflanzengemeinschaften betrachtet wurden. Sechs Kennarten des Caricion davallianae oder Molinion caeruleae wurden aufgrund ihrer unterschiedlichen Wuchs- und Reproduktionseigenschaften für die nähere Untersuchung ausgewählt (*Parnassia palustris*, *Pinguicula vulgaris*, *Primula farinosa*, *Serratula tinctoria, Succisa pratensis*, *Tofieldia calyculata*). Deskriptiv wurde die Gesamtheit der Einflussfaktoren der Weide untersucht, in Experimenten wurde der Einfluss der einzelnen Faktoren (Verbiss, Tritt) ermittelt.

Der Vergleich der Artenzusammensetzung der Vegetation benachbarter Weiden und Streuwiesen (**Kapitel 2**) zeigte, dass Beweidung die Artenvielfalt zwar signifikant reduziert, der Anteil an Zielarten aber unverändert bleibt. Nur wenige Pflanzenarten zeigten deutliche Unterschiede hinsichtlich ihres Vorkommens auf Weide oder Streuwiese, allerdings war ein klarer Trend in der Artenzusammensetzung von den Weiden zu den Streuwiesen in einer DCA (de-trended correspondence analysis) zu erkennen. Auf Weiden war der Anteil an Gräsern und kleinen Kräutern höher, Arten mit Abwehrmechanismen gegen Beweidung wurden dagegen nur selten gefördert. Arteigenschaften, die die generative Reproduktion betreffen, wurden nicht durch den Nutzungstyp beeinflusst, während Arten mit der Fähigkeit zur schnellen vegetativen Vermehrung auf Weiden häufiger vorkamen.

In **Kapitel 3** wird der Einfluss von Weide und Mahd auf die Populationsdichte und die Altersklassen-Struktur von vier ausgewählten Arten dargestellt. *Succisa pratensis* zeigte weder in ihrer Dichte noch in der Frequenz oder der Altersklassen-Struktur eine Reaktion auf die Nutzung, da sie als spätblühende Art sowohl durch Mahd als auch durch Weide gestört werden kann. *Parnassia palustris*, *Primula farinosa* und *Tofiledia calyculata* kamen dagegen auf Weiden in deutlich geringerer Dichte und Frequenz vor. *Parnassia* und *Tofieldia* konnten die geringere Anzahl an Keimlingen durch eine erhöhte vegetative Vermehrung (*Tofieldia*) oder durch mehr blühende Individuen (*Parnassia*) teilweise ausgleichen. *Primula* hatte in beiden Nutzungsformen den gleichen Anteil an Keimlingen, jedoch war deren Etablierung auf den Weiden stark eingeschränkt. Der geringere Anteil blühender Individuen konnte für diese Art durch eine höhere Samenzahl pro Pflanze nahezu ausgeglichen werden.

Die Untersuchung der Wiederbesiedlung von Huftritten in Weiden und in Brachen zeigte (**Kapitel 4**), dass sie nur von geringer Bedeutung für die Etablierung neuer oder konkurrenzschwacher Arten ist. Die Huftritte waren auch nach zwei Jahren nur spärlich besiedelt. Die beiden klar getrennten Bereiche eines Huftritts (der steile, dränierte Rand und der dunkle, nasse Boden) bieten keine günstigen Wuchsbedingungen, die Wiederbesiedlung war aber im Randbereich höher. Weder in Weiden noch in Brachen konnten Unterschiede hinsichtlich des Vorkommens häufiger Arten und der Artenzahlen zwischen den Huftritten und der umgebenden Vegetation festgestellt werden. Trotz hoher Keimraten dominierten in beiden Huftritt-Zonen letztlich die vegetativen Wiederbesiedler, da die Mortalität der Keimlinge sehr hoch war. Nur wenige Arten wurden durch das Entstehen von Huftritten gefördert; einige niedrigwüchsige Arten wie z.B. *Linum catharticum* oder *Drosera rotundifolia* konnten am Rand besser keimen als in der umgebenden Vegetation.

Die Auswirkungen von Mahd, Weide und Brache auf die Keimung und Etablierung von sechs ausgewählten Arten wurde in zwei Aussaatexperimenten unter simulierter und echter Nutzung untersucht (**Kapitel 5)**. Unter Brachebedingungen wurde für alle Arten eine geringe Keimrate aufgrund der dichten Streu- und Moosschicht beobachtet. Die Keimungs- und Etablierungsraten auf der Weide und der gemähten Streuwiese waren deutlich höher, unterschieden sich aber kaum voneinander. Die künstliche Schaffung von Trittstellen führte nicht zur Erhöhung der Keimrate. Starke Trittbelastung wirkte sich negativ auf das Überleben der Keimlinge aller Arten aus. Die untersuchten Arten unterschieden sich sowohl hinsichtlich ihrer Keimfähigkeit als auch der Intensität ihrer Reaktion auf die Landnutzung. Die Samen von *Succisa pratensis* waren am schwersten und keimten gut. Keimung und Etablierung wurden durch die Nutzung kaum beeinflusst. Die Samen von *Parnassia palustris* zeigten geringe Keimraten und eine deutliche Abhängigkeit von Keimnischen. Die Keimung von *Serratula tinctoria* und *Primula farinosa* war in hohem Maße durch die Verfügbarkeit von Keimnischen eingeschränkt. *Tofieldia calyculata* und *Pinguicula vulgaris*, die beiden Arten mit den leichtesten Samen, keimten im Freiland kaum; die klonale Ausbreitung ist für diese Arten offenbar erfolgreicher.

Die Fähigkeit von Pflanzenindividuen Biomasseverluste zu kompensieren wurde in einem Beweidungssimulationexperiment (**Box)** überprüft. Lediglich die Segge *Carex davalliana* konnte einmaligen Biomasseverlust durch Nachwachsen kompensieren, wiederholte Verluste konnten dagegen nicht ausgeglichen werden. Die hochwüchsigen Kräuter *Succisa pratensis* und *Serratula tinctoria* produzierten nach simuliertem Verbiss nicht erneut Biomasse. *Primula farinosa* als niedrigwüchsige Rosettenpflanze verliert durch Verbiss nur Reproduktionsorgane, die im weiteren Verlauf der Vegetationsperiode allerdings nicht ersetzt wurden. Die Art konnte auch keinen Vorteil (höhere Biomasse) aus dem Biomasseverlust der umgebenden Vegetation ziehen.

In der Synthese (**Kapitel 6**) wird der Einfluss der Beweidung auf einzelne Altersklassen, auf die Population und auf die Pflanzengemeinschaft im Vergleich zur Streumahd und zur Brache diskutiert. Offenbar stellt die Trittbelastung den am stärksten limitierender Faktor für das Wachstum adulter

Pflanzen und insbesondere für die Etablierung der Keimlinge dar. Auf Weiden ist deswegen von einem höheren Mortalitätsrisiko der einzelnen Individuen auszugehen. Der Verbiss schädigt die Keimlinge dagegen nicht; adulte Pflanzen können Verbiss auf Weiden ertragen, in dem sie ihn durch ihre Wuchsform vermeiden oder durch die Fähigkeit zur Kompensation tolerieren. Die generative Reproduktion ist sowohl durch Verbiss als auch durch Tritt gefährdet. Das Risiko des Verlustes reproduktiver Organe ist dabei von der Blütezeit abhängig, kann aber auch durch vermehrte Samenbildung, höhere Keimlingszahlen oder einen höheren Anteil blühender Individuen ausgeglichen werden. Die Vegetationszusammensetzung auf Weiden verändert sich im Vergleich zu Streuwiesen hin zu Arten, die Beweidung besser vermeiden oder kompensieren können. Auf der anderen Seite ist sie aber auch durch zufällige Verluste von Arten aufgrund einer höheren Mortalität, unabhängig von den Arteigenschaften beeinflusst. Die Beweidung stellt also für den Naturschutz eine Alternative zur Streumahd auf kalkreichen Niedermooren dar, da die Veränderung der Vegetationszusammensetzung nicht stark sind. Das höhere Mortalitätsrisiko der Individuen durch die Trittbelastung muss aber eingeschränkt werden. Dazu werden neue Kontrollen nötig (z.B. maximal 15 % offener Boden). Hinsichtlich geeigneter Besatzdichten (etwa 1 GV/ha) und eines angemessenen Anteils an Niedermoorboden an der gesamten Weidefläche (maximal 50 %) können bestehende Allmendeweiden als Beispiel dienen, auf denen seit Jahrhunderten eine artenreiche Vegetation durch Beweidung erhalten wird. Gilt es aber speziell seltene Arten auf Niedermooren zu schützen, sollte die Beweidung aufgrund des höheren Aussterberisikos nicht eingeführt werden, solange das Verhalten der einzelnen Art nicht näher untersucht ist.

SUMMARY

Calcareous fens are traditionally mown in autumn, which maintains species rich vegetation types (Caricion davallianae, Molinion caeruleae). Nowadays, abandonment due to changes in agriculture causes a decline of many characteristic plant species of fen meadows due to litter accumulation and dominance of few competitive species. The aim of this study is to evaluate grazing as an alternative management tool to mowing. The impact of grazing and mowing on the vegetation of calcareous fens in the prealpine region of Southern Germany was compared, regarding different organisation levels (individual plants, populations, communities). Six characteristic species of Caricion davallianae or Molinion caeruleae differing in growth form and reproductive behaviour were selected for the study (*Parnassia palustris*, *Pinguicula vulgaris*, *Primula farinosa*, *Serratula tinctoria, Succisa pratensis*, *Tofieldia calyculata*). The effects of grazing in general on the vegetation were investigated in a descriptive way whereas experiments were used to study the effects of single factors of the pasture (foraging, trampling) on the vegetation and on selected age states (e.g. germination).

In **chapter 2** vegetation composition was compared between adjacent pairs of fen meadows and pastures. Species richness was significantly reduced by grazing, but the percentage of target species was not affected by land use type. Only a few species showed a clear trend in their occurrence on meadows or pastures, but a clear land use gradient concerning species composition was indicated by a detrended correspondence analysis and by the proportions of species with selected traits. Grazing favoured grasses and small forbs, whereas species with “defence mechanisms” against foraging were seldom favoured on pastures. Reproductive traits were not significantly affected by land use type, but clonal behaviour differed significantly: species with fast-spreading stem-derived clonal organs were favoured on pastures.

The effects of grazing and mowing on population density and age-state structure of four plant species were investigated in **chapter 3**. *Succisa pratensis* did not respond to land use type concerning population density, frequency or age-state structure because the late-flowering species was harmed by late mowing as well as by grazing. *Parnassia palustris*, *Primula farinosa* and *Tofieldia calyculata* showed a significantly lower population density and abundance on pastures. For *Parnassia* and *Tofieldia*, the lower proportion of seedlings was only partly compensated by clonal growth (*Tofieldia*) or balanced by a higher number of flowering individuals (*Parnassia*). For *Primula*, the number of seedlings was the same in both land use types, but seedling establishment was harmed more severely on pastures. The lower number of flowering individuals on pastures was partly compensated by a higher number of seeds per individual.

The analysis of revegetation of hoof prints in fen pastures and abandoned sites (**chapter 4**) showed that trampling induced gaps were of minor importance for maintenance of species richness in fens. After two years, hoof prints were not recolonized reasonably as both hoof print zones, the steep,

drained, but light edge and the dark, but wet bottom, did not offer suitable conditions for revegetation:. Recolonization on the edge, however, was more successful than on the bottom. Occurrence of frequent species and species numbers were similar in hoof prints and in the surrounding vegetation for both pastures and abandoned sites. In both zones, vegetative spreaders finally dominated in spite of high germination rates, because seedling mortality was high. Only few were able to take advantage by the creation of hoof prints compared to the surrounding vegetation. These were exclusively prostrate species (e.g. *Linum catharticum* and *Drosera rotundifolia*) germinating on the edges.

The effects of mowing, grazing or abandonment on germination and establishment of six fen species were investigated in two sowing experiments (simulating land use or real land use) in **chapter 5**. On abandoned plots, the lack of suitable microsites due to litter accumulation and high moss cover almost hindered germination. Grazing and mowing offered similar germination conditions which were better than those on abandoned sites. Gap creation by trampling did not increase germination rate. Trampling, in contrast, had a severe negative effect on seedling survival. Species differed in their germination ability and in their response to land use which could be related to seed size. *Succisa pratensis* with the heaviest seeds germinated well in all land use types. *Parnassia palustris* seeds were less germinable and germination depended on microsite availability. *Serratula tinctoria* and *Primula farinosa* were mostly microsite limited. *Tofieldia calyculata* and *Pinguicula vulgaris* did hardly germinate at all under natural conditions, in spite of high germination rates in the growth chamber. Obviously, clonal reproduction was more successful for these species.

The ability of individuals to compensate biomass loss by foraging was tested by a clipping experiment (**box**). Only the sedge *Carex davalliana* was able to compensate for single biomass loss by regrowth, whereas repeated clipping harmed the individuals. The upgrowing herbs *Succisa pratensis* and *Serratula tinctoria* could not compensate biomass loss at all. *Primula farinosa*, a procumbent rosette plant, lost only reproductive organs by simulated grazing and was not able to produce new flowers. *Primula* plants were not able to take advantage of the better light conditions by the reduced surrounding vegetation.

In the synthesis in **chapter 6** the impact of grazing in comparison to mowing is discussed on the level of individual plants, on the population level and on the level of the plant community. In general, trampling was the most harming factor on pastures especially for the establishment of seedlings, but also for adult plants. So, mortality risk was enhanced by grazing. Foraging did not affect seedlings, whereas only those adult plants which could avoid or tolerate the biomass loss due to their growth form (prostrate species, grasses/sedges) were favoured on pastures. Reproduction was endangered by both trampling and foraging. So, reproductive success of species depends on the flowering time. Some species, however, were also able to balance the loss of reproductive organs by a higher number of seeds, seedlings or flowering plants. For nature conservation grazing can be recommended as an alternative management tool to autumn mowing on calcareous fens, as the shift in vegetation composition is only small. The higher mortality risk of individuals due to trampling should be reduced by optimisation of grazing management. New control mechanisms for pastures are necessary to reduce trampling damage (e.g. a maximum of 15 % bare ground). Stocking rate on the fen soils should not be higher than 1 cattle per ha, and the proportion of fen soils on the total area of the pasture should not exceed 50 % according to data from species rich fen pastures existing since centuries. If very rare plant species were present on the fen, grazing might not be introduced due to the higher mortality risk as long as the response of the species to grazing is not investigated.